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1 Genetic population structure and variation at phenology-
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36 **Running Head:** Phenology-related loci in Arctic char
37

38 **Abstract**

39 The Arctic will be especially affected by climate change, resulting in altered seasonal timing.
40 Anadromous Arctic char (*Salvelinus alpinus*) is strongly influenced by sea surface temperature
41 (SST) delimiting time periods available for foraging in the sea. Recent studies of salmonid species
42 have shown variation at phenology-related loci associated with timing of migration and spawning.
43 We contrasted genetic population structure at 53 SNPs versus four phenology-related loci among 15
44 anadromous Arctic char populations from Western Greenland and three outgroup populations.
45 Among anadromous populations, the time period available for foraging at sea ($> 2^{\circ}\text{C}$) ranges from a
46 few weeks to several months, motivating two research questions: 1) Is population structure
47 compatible with possibilities for evolutionary rescue of anadromous populations during climate
48 change? 2) Does selection associated with latitude or SST regimes act on phenology-related loci? In
49 Western Greenland, strong isolation-by-distance at SNPs was observed and spatial autocorrelation
50 analysis showed genetic patch size up to 450 km, documenting contingency and gene flow among
51 populations. Outlier tests provided no evidence for selection at phenology-related loci. However, in
52 Western Greenland, mean allele length at *OtsClock1b* was positively associated with the time of
53 year when SST first exceeded 2°C and negatively associated with duration of the period where SST
54 exceeded 2°C . This is consistent with local adaptation for making full use of the time period
55 available for foraging in the sea. Current adaptation may become maladaptive under climate
56 change, but long-distance connectivity of anadromous populations could redistribute adaptive
57 variation across populations and lead to evolutionary rescue.

58
59 **Key Words:** Arctic char, climate change, clock gene, phenology, sea surface temperature, spatial
60 autocorrelation
61

63 **Introduction**

64 Ongoing anthropogenic climate change has the potential to profoundly affect the living conditions
65 of biota, involving e.g. physiological stress during warm periods, altered ecological interactions and
66 colonization of new species (Hoffmann and Sgro 2011; Parmesan 2006; Pörtner and Peck 2010;
67 Thackeray et al. 2016). A much debated issue concerns whether or not organisms are able to
68 respond to rapid climate change by genetically based microevolution or have to rely on phenotypic
69 plasticity (Hansen et al. 2012; Hoffmann and Sgro 2011; Merila and Hendry 2014). Crozier and
70 Hutchings (2014) found that very few studies of fishes had documented adaptive change that could
71 be ascribed to changing climate, with a few notable exceptions such as a study of altered migration
72 timing in pink salmon (*Oncorhynchus gorbuscha*) (Kovach et al. 2012). Nevertheless, several
73 studies have presented results consistent with adaptation to extant climate and temperature regimes
74 in fishes at phenotypic traits and/or candidate genes that supposedly reflect evolution over longer
75 time spans than those over which anthropogenic climate change occurs (Bernatchez 2016; Bradbury
76 et al. 2010; Harrison et al. 2017; Jensen et al. 2008; Koskinen et al. 2002; Narum et al. 2010;
77 Perrier et al. 2017). Adaptations to current climate conditions could become increasingly
78 maladaptive as the climate changes, but could also act as a source of genetic variation for future
79 evolutionary rescue, through the influx of genetic variation into populations *via* gene flow to allow
80 adaptation to altered environmental conditions (Gonzalez et al. 2013).

81
82 It has been argued that in temperate and Arctic regions, the most pronounced changes to living
83 conditions concern altered seasonal timing, including later arrival of winter and earlier arrival of
84 spring, rather than increased temperature *per se* (Bradshaw and Holzapfel 2006, 2008). This means
85 that phenological traits, such as timing of migration and reproduction, may be particularly important
86 for the future persistence of organisms. Many phenological traits are regulated by an internal clock
87 that is synchronized particularly by photoperiods and temperature. A core set of genes form and
88 regulate the circadian clock system across vertebrate taxa: *Clock*, *Bmal*, *Period* and *Cryptochrome*
89 (Idda et al. 2012; Lincoln et al. 2003; Lowrey and Takahashi 2004). *Clock*, in particular, has
90 received considerable attention. A critical domain in this gene is the carboxyl-terminal
91 polyglutamine repeat motif (polyQ), in which increases and decreases in the number of polyQ
92 repeats affect gene expression (Darlington et al. 1998; Hayasaka et al. 2002). Several studies of
93 birds have revealed positive associations between *clock* (polyQ) allele lengths and breeding latitude
94 (Bazzi et al. 2016; Johnsen et al. 2007), but also examples of no association in some species (Dor et
95 al. 2012).

96 The salmonid fish *clock* gene *OtsClock1b* has similarly been found to be associated with variation
97 in run time and/or latitudinal gradient in Chinook salmon (*Oncorhynchus tshawytscha*), Chum
98 salmon (*O. keta*), and Atlantic salmon (*Salmo salar*) (O'Malley and Banks 2008; O'Malley et al.
99 2014; O'Malley et al. 2010a; O'Malley et al. 2013). Furthermore, the gene localizes to a QTL
100 (quantitative trait locus) region for spawning time and developmental growth in Coho salmon (*O.*
101 *kisutch*) and Rainbow trout (*O. mykiss*) (Leder et al. 2006; O'Malley et al. 2010a). Nevertheless, in
102 Coho (*O. kisutch*) and Pink salmon (*O. gorbuscha*) along with the non-salmonid Threespine
103 stickleback (*Gasterosteus aculeatus*), no association between *clock* polyQ variation, latitudinal
104 gradients and spawning time has been observed (Kovach et al. 2012; O'Brien et al. 2013; O'Malley
105 et al. 2010a). In Coho and Pink salmon, however, this was in fact a predicted result as these species
106 show minimal geographical variation in age at spawning and time of spawning (O'Malley et al.
107 2010a). *clock* is therefore a potentially important candidate gene for migratory and reproductive
108 phenological traits in many, but not all fishes, and could be an important target for monitoring
109 adaptive responses to climate change (Hansen et al. 2012).

110
111 Arctic regions are particularly affected by climate change (Leduc et al. 2016). For instance, the
112 decade from 2001-2010 was the warmest period on record in Greenland from 1784 to the present
113 and by 2050 temperature is projected to have increased by 3°C in winter, 4°C in spring and 2°C in
114 summer and autumn (Cappelen and Vinther 2014). Arctic char (*Salvelinus alpinus*) is a cold water-
115 adapted salmonid widely distributed in the northern circumpolar Arctic region (Klemetsen et al.
116 2003), and in Greenland anadromous populations are found throughout coastal regions. They
117 exhibit a complex life-history involving repeat spawning interrupted by years of no spawning. It is
118 generally assumed that anadromous populations spawn around October (Klemetsen et al. 2003).
119 Due to logistic constraints, no systematic records of spawning time are available for Arctic char in
120 Greenland. However, ripe and spent spawners were observed in late September - early October in
121 Southern Greenland during the course of the present study, and it is assumed that spawning takes
122 place earlier in more northern regions.

123
124 Both spawning and non-spawning anadromous char overwinter in freshwater, the latter presumably
125 in order to avoid osmotic stress in the marine environment during cold Arctic winters (Klemetsen et
126 al. 2003; Moore et al. 2017). Experimental work by Finstad et al. (1989) demonstrated osmotic
127 stress and high mortality when Arctic char were exposed to high salinity and a temperature of 1°C

128 during winter, but not when they were exposed to the same conditions during summer. This
129 suggests that complex interactions exist between osmoregulatory capacity and seasonal change,
130 possibly regulated by photoperiod. In general, the total length of the season that anadromous Arctic
131 char are able to spend foraging at sea, as determined by the sea temperature, is assumed to be a
132 critical parameter determining growth and life history (Dutil 1986). Greenlandic anadromous char
133 populations are distributed at a range of more than 20 latitudinal degrees, implying that
134 considerable geographical variation in the length of the growth season must be expected, leading to
135 the possibility of local adaptation of associated phenological traits.

136

137 The goal of this study was to address two key research questions: 1) Is the genetic structure and
138 differentiation among anadromous populations compatible with possibilities for evolutionary rescue
139 during climate change? 2) Does selection associated with latitude or marine temperature regimes act
140 on the phenology-related markers? Toward this end, the genetic structure of anadromous char
141 populations in Western Greenland were analyzed along with "outgroup" populations from Eastern
142 Greenland, Iceland and Norway, the latter two represented by landlocked lake populations. Two
143 data sets of fifty-three presumably neutral SNPs (single nucleotide polymorphisms) and four
144 phenology-related loci (*OtsClock1b*, *Ots515NWFSC*, *Cryptochrome2b.2* and *Cryptochrome3*),
145 respectively, were analyzed in 18 populations. Moreover, remotely sensed data were extracted on
146 sea surface temperature close to the mouths of the sampled rivers and lakes to estimate the onset,
147 end, and duration of the periods of time that local populations could potentially spend at sea.

148 **Materials and Methods**

149

150 Samples

151 Adipose fin clips were collected from 2005-2016 by angling, net fishing and electrofishing. We
152 aimed for sample sizes of twenty, as higher sample sizes generally do not improve estimates of
153 standard population genetic statistics as compared to increasing number of loci (Takezaki and Nei
154 1996). Among the 18 populations included in the study, 15 were anadromous populations located
155 along the West coast of Greenland. Three additional populations represented anadromous char from
156 Eastern Greenland and two landlocked lake populations from Iceland and Norway (see Fig. 1 and
157 Table 1). Collection and handling of samples in Greenland took place according to survey licenses
158 G14-034 and G15-013 from the Government of Greenland.

159

160 Molecular analyses

161 DNA was extracted using the E.Z.N.A DNA Tissue Extraction Kit (Omega Bio-Tek, Norcross,
162 USA) according to the manufacturer's recommendations. Two sets of loci were analyzed: 1) 53
163 single nucleotide polymorphisms (SNPs) developed for Arctic char (Jacobsen et al. 2017) and
164 assumed to represent neutral markers as based on outlier tests conducted in Christensen et al.
165 (2018), and 2) four candidate loci assumed to be involved in phenology. SNPs were genotyped on a
166 96.96 Dynamic Array on the Fluidigm Biomark platform (Fluidigm Corporation, San Francisco,
167 USA). As explained in Jacobsen et al. (2017) the initial set consisted of 96 SNPs, of which 43 could
168 not be scored reliably due particularly to the presence of paralogs presumably resulting from ancient
169 tetraploidy in salmonid fishes (Allendorf et al. 2015). Genotypes were scored using the associated
170 Fluidigm® SNP Genotyping Analysis software.

171

172 The candidate loci consisted of the polyQ region of the *Clock* gene *OtsClock1b*, microsatellites
173 closely linked to the two duplicated copies *Cryptochrome2b.2* and *Cryptochrome3* of the circadian
174 rhythm gene *Cryptochrome*, and a microsatellite *Ots515NWFSC*, which is a QTL for spawning time
175 and body weight in rainbow trout (O'Malley et al. 2003). Primer sequences for the loci are
176 described in Naish and Park (2002), O'Malley et al. (2007) and O'Malley et al. (2010b). The
177 forward primers of *OtsClock1b*, *Ots515NWFSC*, *Cryptochrome2b.2* and *Cryptochrome3* were
178 labeled with the fluorescent dyes PET, NED, FAM and VIC, respectively. The loci were PCR
179 amplified at an annealing temperature of 55 C in 30 µl reactions containing 15 µl QIAGEN
180 Multiplex PCR Mastermix (QIAGEN, Hilden, Germany), 3 µl 100 µM primer mix; 10 µl
181 fluorescently labeled primer and 10 µl reverse primer, 11 µl H₂O and 1 µl sample DNA
182 (concentrations between ca. 80 and 400 ng/µl). Genotyping was outsourced to Macrogen Inc.
183 (Seoul, Korea), where fragments were resolved on an ABI 3730XL capillary sequencer using a 600
184 LIZ internal size standard (Applied Biosystems, Cheshire, UK). Scoring of genotypes was
185 conducted using the software Geneious 10.0.7 (Kearse et al. 2012).

186

187 Salmonid fishes are ancient tetraploids, and simple Mendelian inheritance cannot always be
188 assumed (Allendorf et al. 2015; Allendorf and Thorgaard 1984). Also, scoring of multiallelic loci
189 may in itself be complicated. In order to validate Mendelian inheritance and scoring of the
190 phenology-related loci, two full-sib family crosses were therefore established, based on two males

191 and two females sampled in October 2013 in the NUUK-2 population (see Table 1 and Fig. 1).
192 Fertilized eggs were incubated in Petri dishes at 5 C following Wedekind and Muller (2004). This
193 took place at the Greenland Institute of Natural Resources, Nuuk, where Petri dishes were inspected
194 daily, and upon hatching the larvae were euthanized and stored in 96% ethanol at -18 C. The
195 parents and 10 offspring from each family were genotyped.

196

197 Genetic population structure

198 For all analyses of population structure, SNPs and candidate loci were analyzed separately. Mean
199 heterozygosity was estimated using GENEPOP version 4.2 (Rousset 2008) and the same software
200 was used to test for Hardy-Weinberg equilibrium at all loci in all populations. Genetic
201 differentiation for the two datasets was analyzed by 1) an AMOVA (Analysis of Molecular
202 Variance) involving all populations and 2) a hierarchical AMOVA involving populations from
203 Western Greenland, as implemented in ARLEQUIN version 3.5.2.2 (Excoffier et al. 2005). For this
204 study, five regional groups of Western Greenland populations were defined by the geographical
205 location of populations: region 1 (UUMM-1, UUMM-2 and DISK-1), region 2 (KANG-1 and SISI-
206 1), region 3 (MANI-1 and MANI-2), region 4 (NUUK-1, NUUK-2, NUUK-3, NUUK-4 and
207 NUUK-5), region 5 (QAQO-1 and QAQO-2). The geographically remote QAAN-1 population
208 could not be meaningfully included in a regional group with other populations and was omitted
209 from this analysis. Finally, F_{ST} between all pairs of populations was estimated, also using
210 ARLEQUIN.

211

212 The genetic relationships among populations at the SNPs were further analyzed by DAPC
213 (Discriminant Analysis of Principal Components) (Jombart et al. 2010), implemented in the R
214 package adegenet (Jombart 2008). Briefly, the method defines clusters of individuals without prior
215 knowledge of their sample of origin and identifies discriminant functions that distinguish clusters
216 while at the same time minimizing variation within clusters. We first identified the most likely
217 number of clusters and the individuals belonging to them based on k-means clustering and Bayesian
218 Information Criterion, followed by choosing the optimal number of principal components (using
219 cross-validation) and discriminant axes, as detailed in the documentation for DAPC.

220

221 Isolation-by-distance (IBD) for the two classes of markers was tested using Mantel tests
222 implemented in the software Isolation-By-Distance, web service version 3.23 (Jensen et al. 2005).

223 Pairwise F_{ST} estimates were used as genetic distance, and geographical distance (shortest waterway
224 distance) was estimated using Google Earth. Moreover, IBD was visualized by genetic-
225 geographical distance scatter plots along with their regression lines and 95% confidence intervals.
226 The analyses focused exclusively on the 15 populations from Western Greenland (i.e. excluding the
227 geographically distant SCOR-1, ICEL-1 and NORW-1 populations).

228

229 Finally, we used spatial autocorrelation analysis (Sokal and Oden 1991) implemented in GenAlEx
230 6.5 (Peakall and Smouse 2006, 2012; Smouse and Peakall 1999) in order to assess the geographical
231 scale in Western Greenland over which individual genotypes show non-random association. This
232 was based on all pairwise individual genetic distances (Smouse and Peakall 1999) and a
233 corresponding geographical distance matrix based on waterway distances between sites, as
234 described for the isolation-by-distance analyses. We assumed a geographical distance of 0 for
235 individuals from the same rivers. In order to balance the number of individuals within geographical
236 distance classes we assumed classes with increments of 50 km from 0 to 500, and subsequently with
237 increments of 500 km. Both the 95% confidence interval of distance-class specific r values and the
238 95% confidence interval in case of no spatial structure of individuals were estimated by
239 bootstrapping over pairs of individuals 9999 times.

240

241 Sea surface temperature data

242 Remotely sensed sea surface temperature data (in the following denoted SST), encompassing a
243 resolution of 0.25 degree latitude x 0.25 degree longitude on a global grid and measured for each
244 day were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Website at
245 <http://www.esrl.noaa.gov/psd/>. Data from 1984, 1994, 2004 and 2014 were used, hence covering
246 temperatures for a time span of 40 years. Data for each day of the year from the position closest to
247 the sampled river/lake mouths inhabited by anadromous char (hence excluding the resident
248 populations ICEL-1 and NORW-1) were retrieved using the function `extractOISSTdaily` from the R
249 script `NOAA_OISST_ncdf4.R` (<http://lukemiller.org/index.php/2014/11/extracting-noaa-sea-surface-temperatures-with-ncdf4/>). Subsequently, the mean temperature per day over the total time
250 period was calculated. As anadromous char experience osmotic stress at 1°C (Finstad et al. 1989),
251 SST < 2°C was tentatively defined as unfavorable to char in the sea. For each locality the time
252 period (in the following denoted SST window) was estimated during which SST was $\geq 2^\circ\text{C}$. The
253

254 start and end-points of the SST-window, measured in numbers of days starting from 1 January, and
255 the duration of the SST-window were subsequently used for some of the selection tests (see below).

256

257 Selection tests

258 Outlier tests implemented in ARLEQUIN (Excoffier et al. 2009) were used for assessing possible
259 selection at the phenology-related loci, with the SNP data set included to provide a putatively
260 neutral baseline of differentiation (Christensen et al. 2018). The first, involving all populations was
261 the F_{ST} -based test by Beaumont and Nichols (1996). The second was an extension of this test by
262 Excoffier et al. (2009), which takes underlying hierarchical structure of populations into account.
263 The latter test was based on the same populations and regional groups in Western Greenland as
264 described for the hierarchical AMOVA (see above). The analyses were based on 10,000
265 simulations.

266

267 A third outlier test was conducted, i.e. BAYESCENV (de Villemereuil et al. 2015) which tests for
268 association between loci and environmental parameters. It is an extension of the outlier test
269 BAYESCAN (Foll and Gaggiotti 2008) and distinguishes between 1) neutrality, 2) a locus-specific
270 effect, possibly representing selection but not associated with the environmental parameter tested
271 and 3) an effect of the environmental parameter on a specific locus which could represent selection.
272 The total set of SNPs and phenology-related loci were included, and the environmental parameters
273 tested were the start dates, end dates and duration of SST windows, along with latitude of the
274 sample localities. The recommended default settings of the program were used (20 pilot runs each
275 consisting of 2,000 steps, burn-in of 50,000 steps followed by 50,000 steps and a thinning interval
276 size of 10).

277

278 Finally, we tested for an association between mean allele lengths (assumed to represent polyQ copy
279 number variation) in populations at *OtsClock1b* and 1) latitude, 2) start, 3) end dates and 4) duration
280 of SST windows, using linear models (as in e.g. O'Malley and Banks (2008)) implemented in R (R
281 Core Team 2018).

282

283 **Results**

284

285 Mendelian inheritance of phenology-related genes

286 The experimental crosses were informative for resolving inheritance except for *Cryptochrome2b.2*
287 (Supporting Information, Table S1). At *Ots515NWFSC* and *OtsClock1b* all genotypes of parents
288 and offspring were congruent, whereas only a single heterozygote at *Cryptochrome3* occurred in
289 one parent, although the offspring showed the expected genotypes. Although sample sizes were too
290 low for statistical testing, the results nevertheless lend support for correct scoring of genotypes and
291 simple Mendelian inheritance at three of the four loci.

292

293 Summary statistics and genetic population structure

294 Among 18603 genotypes in the SNP data set (351 individuals x 53 loci) only 57 could not be
295 resolved, leading to 0.3% missing data. Estimated mean heterozygosity across SNPs per population
296 varied from 0.06 (NORW-1) to 0.32 (SISI-1). There was a distinct pattern of lower heterozygosity
297 in the landlocked populations ICEL-1 and NORW-1 along with the Eastern Greenland population
298 SCOR-1 as compared to the anadromous populations from Western Greenland ($p < 0.001$ as
299 determined by a permutation test in FSTAT 2.9.3 (Goudet 1995); see also Table 1 and Supporting
300 Information, Table S2). The phenology-related loci encompassed 1404 genotypes (351 individuals
301 x 4 loci), of which only 13 (0.9%) could not be resolved. Estimated mean heterozygosity across
302 phenology-related loci ranged from 0.18 (QAAN-1) to 0.65 (MANI-2) (Table 1, Supporting
303 Information, Table S2). In contrast to SNPs these loci were all multiallelic with numbers of alleles
304 ranging from 4 to 24 per locus (Supporting Information, Table S2). Three out of a total of 741 tests
305 for Hardy-Weinberg equilibrium yielded significant outcomes ($p < 0.001$) after False Discovery Rate
306 (FDR) correction by the B-Y method (Narum 2006) (Supporting Information, Table S2). Hence,
307 the populations can be assumed to be in Hardy-Weinberg equilibrium.

308

309 Overall genetic differentiation (F_{ST}) across all populations and over all SNPs was 0.27 ($p < 0.001$).
310 The hierarchical AMOVA involving only Western Greenland populations showed that the largest
311 part of differentiation was distributed among geographic groups of populations ($F_{CT} = 0.11$, $p <$
312 0.001), whereas a relatively smaller part was distributed among populations within geographic
313 groups ($F_{SC} = 0.09$, $p < 0.001$). Genetic differentiation at phenology-related loci was similar, with
314 overall $F_{ST} = 0.23$ ($p < 0.001$) across all populations. For the hierarchical AMOVA F_{CT} was 0.10 (p
315 < 0.001) and F_{SC} was 0.06 ($p < 0.001$). F_{ST} between pairs of populations for the SNP dataset ranged
316 from 0.02 (NUUK-2 versus NUUK-3 and NUUK-2 versus NUUK-4) to 0.67 (QAAN-1 versus

317 NORW-1), whereas for the phenology-related loci F_{ST} ranged from 0.02 (several pairs of
318 populations) to 0.47 (QAAN-1 versus SCOR-1; Supporting Information, Table S3).

319

320 For the DAPC analysis of the SNP data, the most likely number of groups represented by the
321 individual multi-locus genotypes was 9, as determined by the Bayesian Information Criterion (see
322 Supporting Information, Fig. S1). Grouping of individuals (Fig. 2.a) showed that the northernmost
323 populations (QAAN-1, UUMM-1, UUMM-2, DISK-1) were composed of three clusters (Cluster 1,
324 7 and 9), and individuals from KANG-1 belonged exclusively to Cluster 2. Individuals from the
325 populations SISI-1, MANI-1, MANI-2, NUUK-1, NUUK-2, NUUK-3, NUUK-4 and NUUK-5
326 were distributed across Clusters 1, 2, 3, 4, 5, 6, 7, and 8. QAQO-1 individuals were exclusively
327 assigned to Cluster 8, whereas QAQO-2 individuals were assigned to Clusters 3 and 8. Finally, all
328 individuals from SCOR-1, ICEL-1 and NORW-1 were assigned to Cluster 3. The first 25 Principal
329 Components and 7 discriminant axes were retained for the DAPC scatterplot. Axes 1 and 2 (Fig.
330 2.b) demonstrated a strong geographic structure among the nine inferred clusters, with Clusters 9, 1
331 and 7 (northernmost populations in Western Greenland) representing one end of a continuum and
332 Cluster 3 (Southwestern and Eastern Greenland, Iceland and Norway) representing the other end.
333 Hence, the results of DAPC showed good correspondence with the geographical location of
334 populations, justifying the groupings of populations used for the hierarchical AMOVA.

335

336 The close relationships between geographical and genetic relationships were further illustrated for
337 both SNPs and candidate loci by analysis of isolation-by-distance involving only the anadromous
338 Western Greenland populations (Fig. 3.a and b). Hence, there was significant correlation between
339 genetic differentiation and geographical distance for SNPs ($R^2 = 0.92$, $p=0.0000$) and for
340 phenology-related loci ($R^2 = 0.55$, $p=0.0000$).

341

342 The spatial autocorrelation analysis (Fig. 4) showed a mean correlation among individuals from the
343 same freshwater localities of 0.330 and subsequently declined and reached its first intercept with the
344 x-axis at 450 km. This value is usually referred to as the genetic patch size (Smouse and Peakall
345 1999; Sokal and Wartenberg 1983). Using distance classes of 100 km instead of 50 km yielded a
346 similar genetic patch size (data not shown).

347

348 Sea surface temperature data

349 Sea surface temperature (SST) data were retrieved from all coastal regions close to the river mouths
350 of the sampled anadromous populations. In the case of NUUK-2, NUUK-3, NUUK-4, and NUUK-5
351 the geographical distances between river mouths were short. Therefore, these populations shared the
352 same pixel of the SST grid and thereby similar temperature regimes. The SST windows, defined by
353 the time periods during the year when SST exceeded 2°C, varied considerably across populations
354 (Fig. 5, Supporting Information, Table S4). Hence, SST exceeded 2°C for only a few weeks in the
355 northernmost populations QAAN-1, UUMM-1, UUMM-2 and in SCOR-1 from Eastern Greenland
356 (Fig. 5.a, b, c and m). In contrast, SST exceeded 2°C for several months in most of the other
357 populations, potentially leaving longer time periods for Arctic char to forage in the sea. The lower
358 temperatures in the south-western localities QAQO-1 and QAQO-2 (Fig. 5.k and l) as opposed to
359 the more northern localities DISK-1, SISI-1, KANG-1, MANI-1, MANI-2 and NUUK-1 to 5 (Fig.
360 5.d to j) reflects the influence of the West Greenland Current (Lloyd et al. 2007). Hence, variation
361 in SST windows did not merely reflect latitudinal variation.

362

363 Selection tests

364 The F_{ST} -based outlier test (Beaumont and Nichols 1996) involving all populations identified three
365 SNPs (*Contig7991*, *Contig11261* and *Contig10740_78*) to be high-divergence outliers, whereas
366 seven SNPs and one phenology-related locus *Ots515NWFSC* showed lower F_{ST} than expected
367 under neutrality (Supporting Information, Fig. S2.a). The hierarchical outlier test (Excoffier et al.
368 2009) involving only populations from Western Greenland identified only *Contig10740_78* as a
369 high divergence outlier, and also again identified *Ots515NWFSC* as a low divergence outlier along
370 with two SNPs (Supporting Information, Fig. S2.b). The results for *Ots515NWFSC* are likely to
371 reflect the higher allelic diversity (microsatellite; 24 alleles) relative to bi-allelic SNPs. Hence, its
372 outlier status is assumed to represent differences in mutation rate between microsatellites and SNPs
373 rather than evidence for balancing selection. The absence of clearly identifiable selection was also
374 evident from the landscape outlier test analyses using the method by de Villemereuil et al. (2015).
375 Hence, there were no significant associations between any of the loci and 1) latitude, 2) start of
376 SST-window, 3) end of SST-window and 4) duration of SST-window. Also, none of the loci were
377 outliers without association with environmental parameters (data not shown). In order to rule out
378 that there was an issue with including highly polymorphic loci and bi-allelic SNPs in the outlier
379 tests, they were repeated including only *Cryptochrome3* and *OtsClock1b* (each showing four

380 alleles) along with the SNPs. However, this did not lead to identification of more outliers (data not
381 shown).

382

383 The above outlier tests only consider allele frequencies, whereas functional variation at *OtsClock1b*
384 consists of the number of polyQ repeats, that is, the length of alleles. At the scale of all populations
385 (landlocked and anadromous) there was no significant association between mean allele length at
386 *OtsClock1b* and latitude (Table 2; Supporting Information Fig. S3.a), and this was also the case at
387 the scale of all anadromous populations from Greenland and at the scale of anadromous populations
388 from Western Greenland, i.e. omitting the population SCOR-1 from Eastern Greenland (see Table
389 2). Across all anadromous populations from Greenland, there was also no significant association
390 between mean allele length and both SST-window start date, end date, or duration (Table 2,
391 Supporting Information Fig. S3.b-d). At the scale of anadromous populations from Western
392 Greenland there was, however, a positive association between mean allele length and both SST-
393 window start date or duration (Table 2 and Supporting Information Fig. S3.e-f), though we note that
394 SST-window start date and duration were strongly correlated and hence cannot be considered
395 independent ($y = -0.567x + 229.738$, $R^2_{\text{adjusted}} = 0.762$, $p = 1.38 \times 10^{-5}$).

396

397 **Discussion**

398 Our results revealed a pattern of strong genetic differentiation among Arctic char populations
399 encompassing both anadromous and landlocked populations, and a distinct geographical structure
400 among Western Greenland anadromous populations. SST data suggested strong geographical
401 variation with respect to the time at which temperatures provided favourable conditions for
402 migration and foraging in the sea. Despite this variation providing different selection regimes acting
403 at phenological traits, evidence for selection acting on phenology-related loci was mixed. However,
404 in Western Greenland populations, a significant association was detected between mean allele
405 length at *OtsClock1b* and the start date or duration of the time window during which SST exceeded
406 2°C.

407

408 Genetic population structure

409 Although large-scale phylogeographical studies of Arctic char based on analysis of mitochondrial
410 DNA have been conducted previously (Brunner et al. 2001; Moore et al. 2015) and large scale
411 genetic differentiation among European landlocked char populations has been reported (Wilson et

412 al. 2004), the present study represents a first assessment of genetic variation and structure at nuclear
413 loci in anadromous Arctic char on a large geographical scale. Genetic variation at SNPs was clearly
414 lower in the two landlocked populations than in the majority of anadromous populations, reflecting
415 well-established patterns of variation observed across marine, anadromous and freshwater fish
416 species and populations (Martinez et al. 2018; Ward et al. 1994).

417

418 Focusing exclusively on SNP variation in anadromous populations in Western Greenland, the
419 hierarchical AMOVA showed stronger differentiation among regional groups of populations as
420 compared to differentiation among populations within groups. Along with the distinct clustering of
421 populations according to geography in the DAPC analysis, the highly significant isolation by
422 distance and the outcome of the spatial autocorrelation analysis this provides evidence for a system
423 connected by gene flow and with geographical distance as a major factor influencing genetic
424 divergence. This could in principle represent a true hierarchical structure with distinct groups of
425 local populations, or it could represent a continuous structure with isolation by distance, with the
426 seemingly hierarchical structure reflecting an artefact due to gaps in the geographical coverage of
427 sampling. The fact that strong isolation by distance was observed and points did not separate into
428 different clusters (Fig. 3.a), which could otherwise indicate genetic breaks, favours the latter option.
429 As a whole, the genetic structure of anadromous char populations along the Western Greenland
430 coast is congruent with previous studies focusing on smaller geographical regions (Bernatchez et al.
431 1998; Christensen et al. 2018; Harris et al. 2013; Harris et al. 2016; Moore et al. 2017; Moore et al.
432 2013).

433

434 Christensen et al. (2018) analyzed historical (DNA extracted from otoliths and scales from the
435 1950s) and contemporary samples from a subset of the anadromous populations included in this
436 study (NUUK-1, NUUK-2, NUUK-4 and QAQO-2), and they found that the genetic structure was
437 remarkably stable over time. Moreover, using a temporal method for estimating effective population
438 size (N_e) and migration rate (m) (Wang and Whitlock 2003), they found N_e point estimates to
439 exceed 500 in most populations and m to be at most 0.058. Based on the temporal stability, the
440 estimated N_e and m values and a model incorporating the relative importance of genetic drift, gene
441 flow and strength of selection (Yeaman and Otto 2011) it was suggested that anadromous Arctic
442 char populations have the potential to be locally adapted (Christensen et al. (2018); see also Moore
443 et al. (2013) and Santaquiteria et al. (2016)). This is certainly likely to be the case for populations

444 distributed across the > 1,500 km geographical span along the Western Greenland coast,
445 encompassing considerable climatic and other environmental variation. Climate change in the
446 Arctic is in general expected to lead to a northward shift of climate regimes, with southern
447 populations being adapted to climate conditions that more northern populations will experience in
448 the future, although the situation appears more complex for SST regimes and possible associated
449 adaptation (see below). Does this mean that possible adaptive genetic variation could move across
450 populations by gene flow, leading to future evolutionary rescue of populations maladapted to
451 altered climatic conditions (Gonzalez et al. 2013)? The pronounced isolation by distance suggests
452 that populations across the range are indeed connected. This is further supported by the genetic
453 patch size of 450 km estimated by spatial autocorrelation analysis; although it is difficult to
454 interpret this value directly in terms of gene flow, it does suggest connectivity among populations
455 over long geographical distances. Hence, evolutionary rescue is possible, although the results do not
456 inform about the rate at which beneficial variation for evolutionary rescue could disperse into
457 increasingly maladapted populations affected by climate change.

458

459 Variation at phenology-related loci

460 The Arctic char populations of this study represented habitats showing strong variation in latitude
461 and thereby photoperiod and sea-surface temperature, the latter visualized by SST-windows in Fig.
462 5. Although it is often argued that Arctic char have only a short annual period available for foraging
463 in the sea in some parts of their distribution range (Moore et al. 2017), in Greenland the time
464 periods where sea-surface temperature exceeded 2°C in fact varied from a few weeks to several
465 months, leaving ample opportunity for local adaptation to this crucial environmental factor. Yet, the
466 evidence for selection acting on the phenology-related loci was mixed.

467

468 The outlier tests applied (Beaumont and Nichols 1996; de Villemereuil et al. 2015; Excoffier et al.
469 2009) suggested only one of the SNPs (Contig10740_78) to be a consistent high differentiation
470 outlier, and none of the phenology-related candidate loci were indicated to be under divergent
471 selection. It is possible that the choice of bi-allelic SNPs as supposedly neutral baseline loci was
472 suboptimal, as two of the phenology-related loci showed twenty-four (*Ots515NWFSC*) and seven
473 (*Cryptochrome2b.2*) alleles, respectively. On the other hand, *Cryptochrome3* and *OtsClock1b* each
474 showed only four alleles and overall low heterozygosity within populations. Hence, using
475 multiallelic microsatellite loci as a neutral background would not have been appropriate in such

476 cases. Therefore, it cannot be ruled out entirely that some of the loci are in reality under selection,
477 but that the outlier tests failed to detect this.

478

479 The tests incorporating allele lengths at *OtsClock1b*, thereby reflecting functional polyQ repeat
480 variation, showed no significant association between mean allele length and latitude, as otherwise
481 reported in Chinook and Chum salmon (O'Malley et al. 2010a; O'Malley et al. 2013). However, we
482 did observe significant association between *OtsClock1b* mean allele length and start date of SST-
483 window or total duration of the SST-window, whereas no association was revealed for SST-window
484 end date. It is puzzling that the associations became non-significant when the geographically remote
485 population SCOR-1 from Eastern Greenland was included. One possibility may be due to
486 phylogeographic complexity; mitochondrial DNA representing the two distinct Arctic and Atlantic
487 phylogeographic lineages have previously been documented in Western Greenland, presumably
488 reflecting postglacial secondary contact (Brunner et al. 2001; Moore et al. 2015). Preliminary
489 results based on mitogenome sequencing suggest that SCOR-1 belongs exclusively to the Atlantic
490 lineage and hence allele lengths at *OtsClock1b* might not be functionally equivalent to alleles from
491 Western Greenland (where both the Arctic and Atlantic phylogeographic lineages are found). A
492 second possibility is that the sea surface temperature regime in SCOR-1 is distinctly different and
493 not comparable to those of Western Greenland populations, as the start date of the SST-window is
494 considerably later than in other populations (Fig. 5, Supporting Information, Table S4).

495

496 Under the assumption that the association between *OtsClock1b* mean allele length and start date of
497 SST-windows represents a genuine biological signal, then this would suggest adaptation to emigrate
498 from freshwater to the sea at the time that marine temperature regimes become favourable. Such
499 adaptations would be highly important for making full use of the potential for foraging in the sea, a
500 crucial factor in growth and survival (Jensen et al. 2018). Whereas there was also a significant
501 association between mean allele length SST-window duration, the strong correlation between start
502 date and SST-window duration raises questions about the specific parameter involved. The duration
503 of SST-window is defined by the start and end date of the window, and as there was no significant
504 association between mean allele length and end date, then this would suggest that it is really the
505 start date that is the parameter of biological significance.

506

507 It is somewhat surprising that no association was found with end date of SST-window, as studies of
508 other salmonids have documented association between *OtsClock1b* and run and/or spawning time
509 variation (O'Malley et al. 2014; O'Malley et al. 2010a; O'Malley et al. 2013). However, most SST-
510 window end dates occurred later than the assumed time of spawning; in some cases (QAQO-1 and
511 QAQO-2) as late as mid-November, whereas spawning is expected to take place no later than early
512 October. The optimal time of spawning must be assumed to be primarily determined by
513 temperature, waterflow and other factors in the freshwater environments although conditions in the
514 sea might also play a role, such as temperature affecting maturation. Hence, specific data on
515 spawning time would be required for directly testing its association with *OtsClock1b* variation.
516

517 In total, the results did not show association between *OtsClock1b* allele length and latitude, but
518 rather an association with SST-regimes. Due to the influence of the West Greenland Current (Lloyd
519 et al. 2007) SST-regimes do not simply reflect latitude, but are generally highest in a broad region
520 ranging from NUUK-1-5 to DISK-1 (see Fig. 1). It is possible that for other traits and genes
521 associated with selection in the freshwater environments, more clear-cut association with latitudinal
522 variation would be found.
523

524 **Conclusions**

525 The study documented strong genetic differentiation among Arctic char, including the most
526 intensively sampled region along the Greenland West Coast. A significant pattern of isolation-by-
527 distance was observed among Western Greenland anadromous populations, indicating connectivity
528 and an absence of clear genetic breaks. At most phenology-related loci, no evidence for selection
529 was observed, but in Western Greenland anadromous populations association was observed
530 between mean allele length at *OtsClock1b* and the start date of the time window during which sea
531 surface temperature exceeded 2°C, along with the duration of this time window. This suggests
532 potentially important adaptations to geographical variation in sea surface temperatures and the
533 optimal time of year for migrating to sea. At the same time, ongoing climate change is expected to
534 affect sea surface temperature regimes, possibly causing current adaptations to become maladaptive
535 in the future. The occurrence of gene flow among anadromous populations would facilitate
536 redistribution of functionally important alleles at *OtsClock1b* across populations, e.g. from the
537 populations DISK-1, KANG-1 and SISI-1 experiencing early onset of the SST-window, towards
538 northern populations like UUMM-1, UUMM-2 and QAAN that currently are subject to late onset of
539 the SST-window but may experience future earlier onset as a result of climate change. Hence, this

540 could provide possibilities for evolutionary rescue in a rapidly changing environment, at least for
541 phenological traits.

542

543 **Conflict of Interest Statement**

544

545 The authors declare no conflict of interest.

546

547 **Data Availability Statement**

548 Raw genotype data in Genepop format have been deposited in DRYAD doi:10.5061/dryad.sc30mr1
549 (Madsen et al. 2019).

550

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793

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795

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801

802 **Authors' Contribution Statement**

803

804 Conceived and designed the investigation: MMH, RPAM, MWJ, LB, DJF, RN, KGO.
805 Performed field and/or laboratory work: RPAM, MWJ, MMH, LB, DJF, KP, RN, BJ,
806 JMP. Analyzed the data: RPAM, MMH, MWJ. Contributed materials, reagents, and/or
807 analysis tools: MMH. Wrote the paper: RPAM, MMH, MWJ with contributions from
808 LB, DJF, KP, KGO, RN, BJ, JMP.

809

810 **Figure legends**

811

812 Fig. 1. Map showing the approximate location of the sampled localities. See Table 1
813 for geographical coordinates.

814

815 Fig. 2. Results of DAPC analysis (Jombart et al. 2010) based on SNPs for analyzing
816 genetic relationships between the sampled Arctic char. a) Number of individuals from
817 each sample assigned to the nine inferred groups. b) Scatterplot of individuals along
818 the two first discriminant functions and with a minimum spanning tree superimposed.
819 The inserted barplot shows the eigenvalues of the analysis.

820

821 Fig. 3. Analysis of isolation-by-distance involving the Western Greenland anadromous
822 populations. Shaded areas denote 95% confidence intervals of the fitted lines. a)
823 Isolation-by-distance based on SNPs ($R^2 = 0.92$, $p < 0.0001$). b) Isolation-by-distance
824 based on phenology-related loci ($R^2 = 0.55$, $p < 0.0001$).

825

826 Fig. 4. Results of spatial autocorrelation analysis based on individual-based genetic
827 distance and geographical distance, implemented in GenAlEx 6.5 (Peakall and Smouse
828 2006, 2012; Smouse and Peakall 1999). The results show the geographical scale in
829 Western Greenland over which individual genotypes show non-random association, as
830 determined by the first intercept with the x-axis. The shaded areas around the line
831 denotes the 95% confidence interval of r values, and the shaded area along the x-axis
832 denotes the 95% confidence interval in case of no spatial structure of individuals, both
833 determined by bootstrapping over individuals.

834

835 Fig. 5. SST (sea surface temperature) windows close to the river mouths of the
836 sampled populations, defined as the time periods during the year when SST exceeded
837 2°C based on mean SST of the years 1984, 1994, 2004 and 2014. The beginning of the
838 SST window is defined as the first date of the year when SST exceeds 2°C (marked by
839 the red dashed line) and the end of the SST window is defined as the date of the year
840 when SST again drops below 2°C . Figs. 5.a-m shows SST windows for all the sampled
841 anadromous populations. The mouths of the rivers inhabited by populations NUUK-2,

842 NUUK-3, NUUK-4 and NUUK-5 are geographically close, and these populations
843 therefore share the same SST window (Fig. 4.j).

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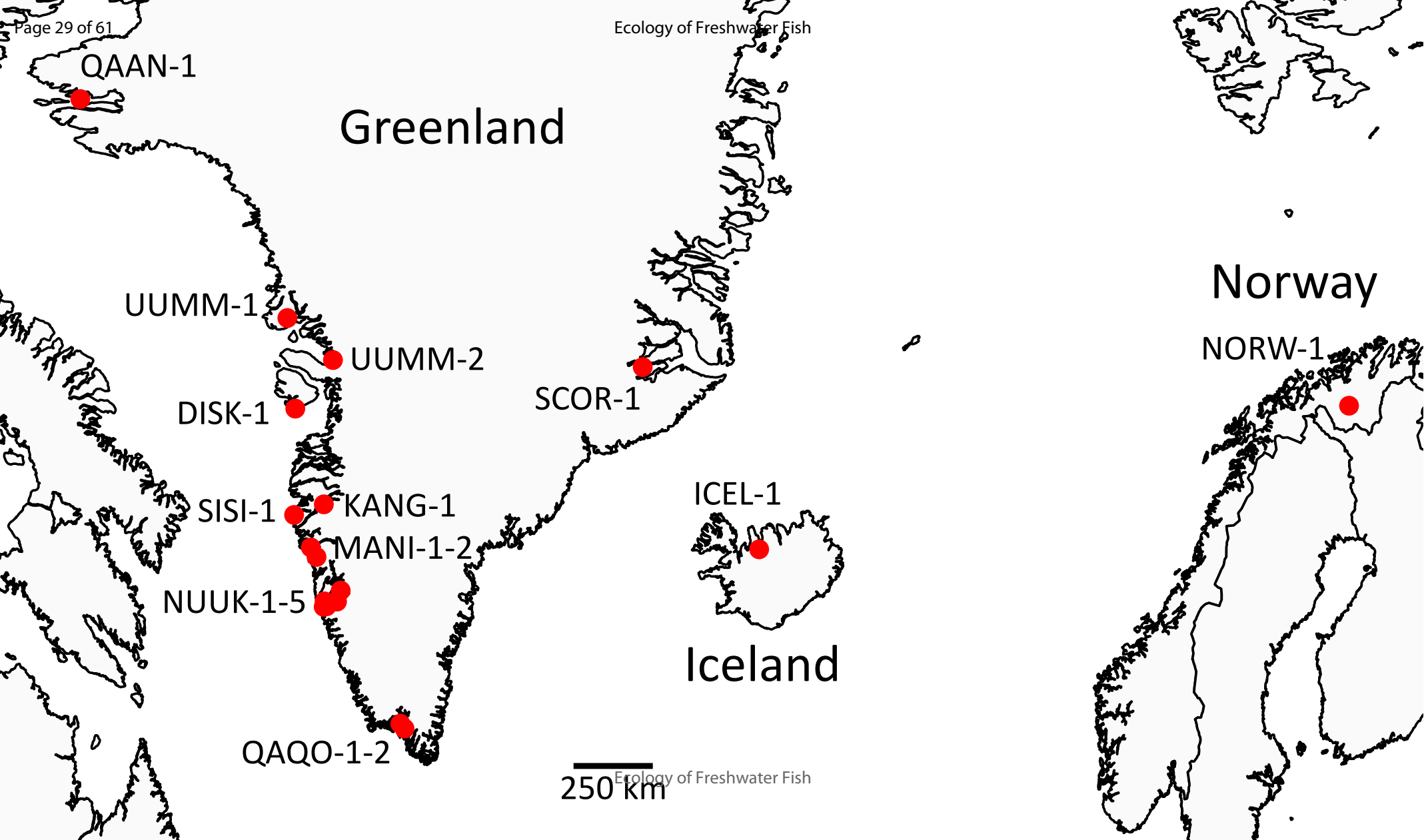
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Table 1. Overview of samples and localities showing sample codes, localities, geographical coordinates, major geographic regions, year of sampling, life history of populations, sample size (N) and mean expected heterozygosity (H_e) for SNPs and phenology-related markers, respectively.

| Sample code | Locality | Latitude | Longitude | Major geographic region | Year of sampling | Life history form | N | H_e (SNPs) | H_e (phenology-related) |
|-------------|-----------------|----------|-----------|-------------------------|------------------|-------------------|----|--------------|---------------------------|
| QAAN-1 | Qaanaaq | 77.46° N | -69.23 W | Western Greenland | 2012 | Anadromous | 18 | 0.11 | 0.18 |
| UUMM-1 | Umivik | 71.66° N | -54.10 W | Western Greenland | 2015 | Anadromous | 20 | 0.29 | 0.35 |
| UUMM-2 | Sermeerlat | 70.54° N | -50.77 W | Western Greenland | 2015 | Anadromous | 20 | 0.26 | 0.27 |
| DISK-1 | Disko Island | 69.25° N | -53.51 W | Western Greenland | 2014 | Anadromous | 20 | 0.28 | 0.40 |
| KANG-1 | Robinson River | 66.71° N | -51.43 W | Western Greenland | 2014 | Anadromous | 20 | 0.22 | 0.59 |
| SISI-1 | Sisimiut | 66.43° N | -53.61 W | Western Greenland | 2014 | Anadromous | 20 | 0.32 | 0.51 |
| MANI-1 | Kangerdluarssuk | 65.57° N | -52.38 W | Western Greenland | 2014 | Anadromous | 20 | 0.30 | 0.58 |
| MANI-2 | Kangia | 65.31° N | -51.97 W | Western Greenland | 2015 | Anadromous | 20 | 0.26 | 0.65 |
| NUUK-1 | Kapisilit | 64.42° N | -50.20 W | Western Greenland | 2012 | Anadromous | 18 | 0.22 | 0.47 |
| NUUK-2 | Kobbefjord | 64.14° N | -51.38 W | Western Greenland | 2013 | Anadromous | 19 | 0.27 | 0.55 |
| NUUK-3 | Præstefjord | 64.00° N | -51.24 W | Western Greenland | 2013 | Anadromous | 20 | 0.28 | 0.50 |
| NUUK-4 | Qarajat | 63.99° N | -51.45 W | Western Greenland | 2012 | Anadromous | 20 | 0.25 | 0.51 |
| NUUK-5 | Eqaluit | 64.13° N | -50.47 W | Western Greenland | 2012 | Anadromous | 20 | 0.30 | 0.63 |
| QAQO-1 | Lakseelv | 60.89° N | -45.84 W | Western Greenland | 2014 | Anadromous | 20 | 0.16 | 0.34 |
| QAQO-2 | Eqaluit | 60.76° N | -45.54 W | Western Greenland | 2014 | Anadromous | 20 | 0.15 | 0.41 |
| SCOR-1 | Scoresbysund | 70.35° N | -28.14 W | Eastern Greenland | 2012 | Anadromous | 20 | 0.08 | 0.26 |
| ICEL-1 | Vatnshlidarvatn | 65.52° N | -19.64 W | Iceland | 2016 | Landlocked | 20 | 0.07 | 0.59 |
| NORW-1 | Biggijavri | 69.33° N | 23.45 W | Norway | 2005 | Landlocked | 16 | 0.06 | 0.34 |

Table 2. Tests for association between mean allele length at *OtsClock1b* and latitude or sea surface temperature parameters at different geographical scales. Significant results are highlighted in bold.

| Parameter tested | Geographical scale | Result |
|-----------------------|---|--|
| Latitude | All populations | $y = 1.44x + 308.02$, $R^2_{\text{adjusted}} = 0.08$, $p = 0.129$ |
| Latitude | Anadromous populations, Eastern and Western Greenland | $y = 1.38x + 311.32$, $R^2_{\text{adjusted}} = 0.06$, $p = 0.175$ |
| Latitude | Anadromous populations, Western Greenland | $y = 1.62x + 296.84$, $R^2_{\text{adjusted}} = 0.11$, $p = 0.128$ |
| SST-window start date | Anadromous populations, Eastern and Western Greenland | $y = 0.29x + 359.18$, $R^2_{\text{adjusted}} = 0.17$, $p = 0.062$ |
| SST-window start date | Anadromous populations, Western Greenland | $y = 0.46x + 334.82$, $R^2_{\text{adjusted}} = 0.39$, $p = 0.007$ |
| SST-window end date | Anadromous populations, Eastern and Western Greenland | $y = -0.20x + 459.81$, $R^2_{\text{adjusted}} = -0.01$, $p = 0.365$ |
| SST-window end date | Anadromous populations, Western Greenland | $y = -0.27x + 483.70$, $R^2_{\text{adjusted}} = 0.04$, $p = 0.238$ |
| SST-window duration | Anadromous populations, Eastern and Western Greenland | $y = -0.17x + 425.95$, $R^2_{\text{adjusted}} = 0.12$, $p = 0.100$ |
| SST-window duration | Anadromous populations, Western Greenland | $y = -0.267x + 441.42$, $R^2_{\text{adjusted}} = 0.308$, $p = 0.019$ |



QAAN-1

Greenland

UUMM-1

UUMM-2

DISK-1

SCOR-1

SISI-1

KANG-1

MANI-1-2

NUUK-1-5

QAQO-1-2

ICEL-1

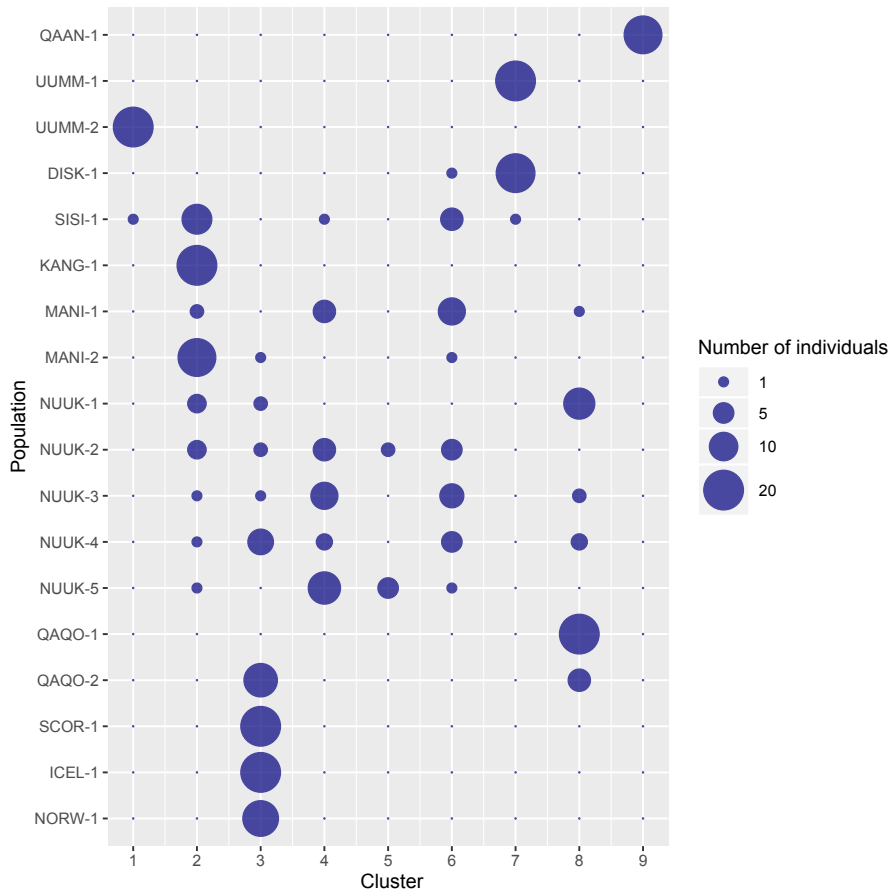
Iceland

Norway

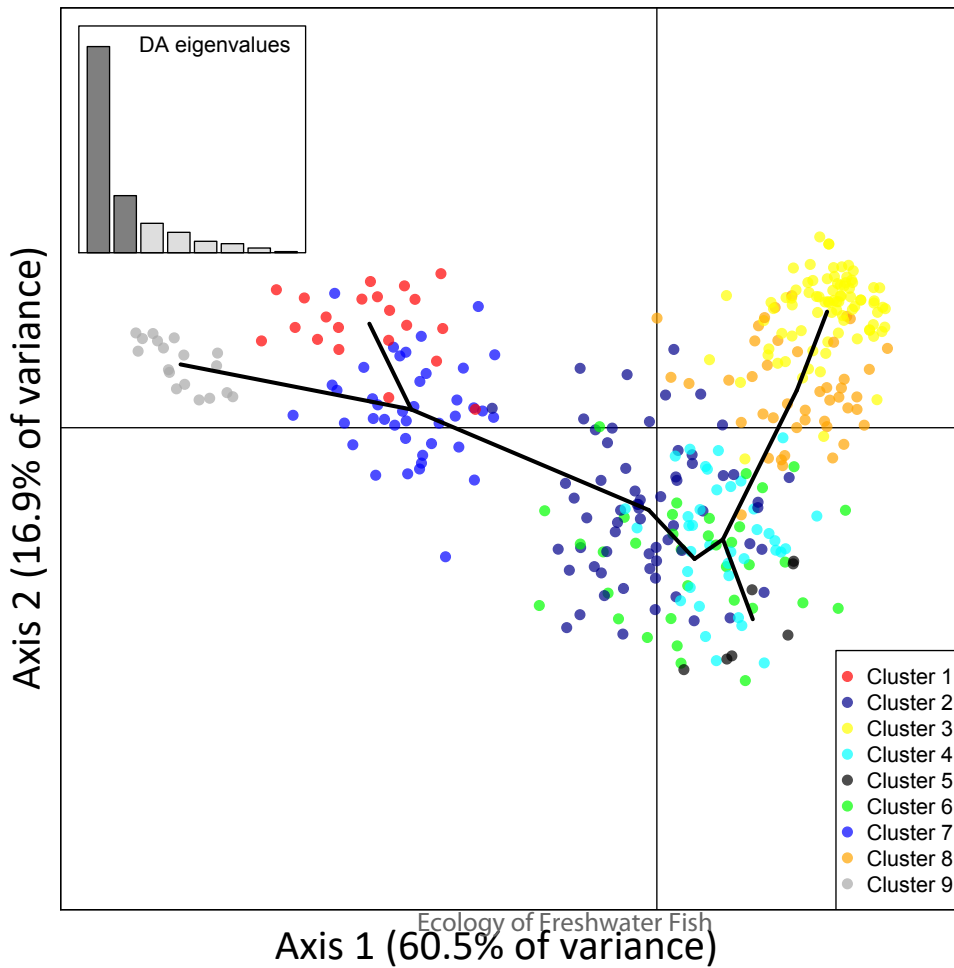
NORW-1

250 km

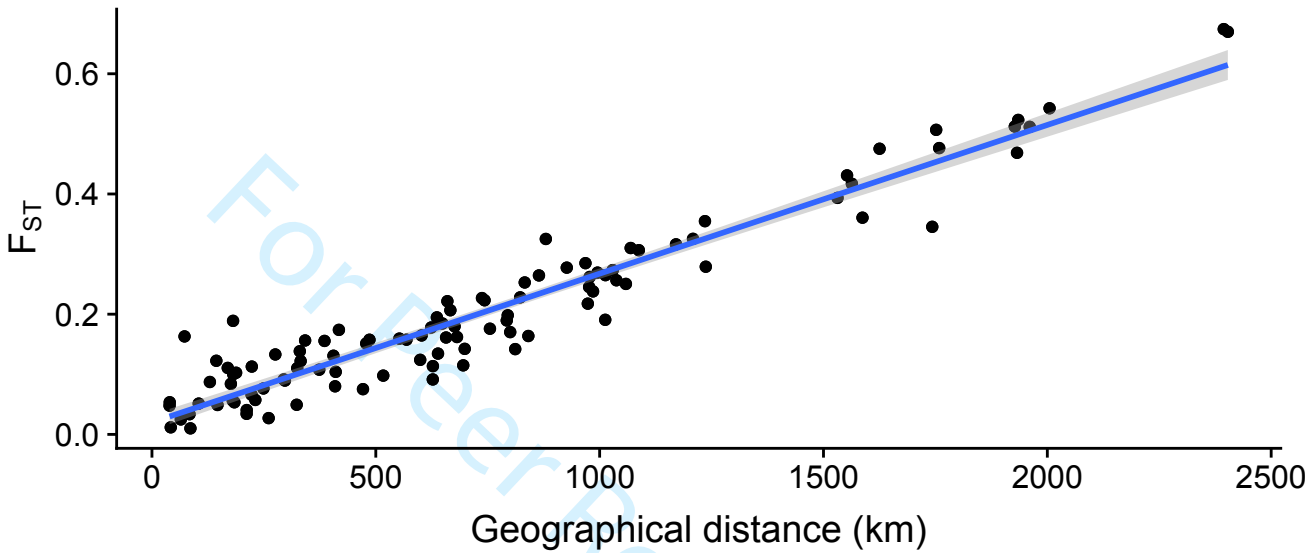
a)



b)

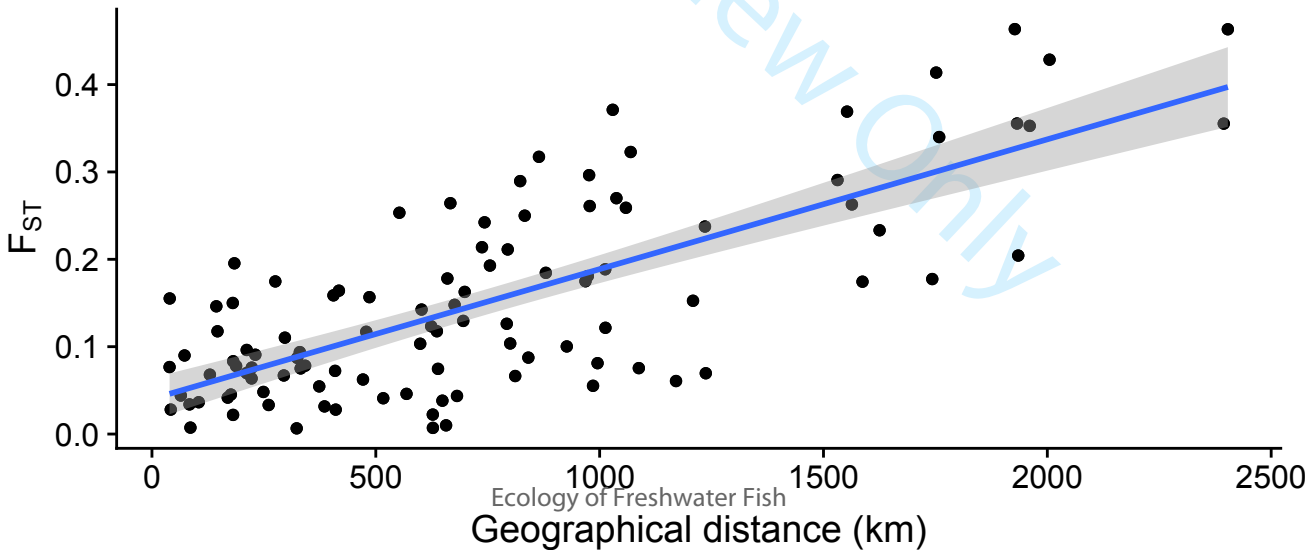


Ecology of Freshwater Fish
Isolation by distance, SNPs

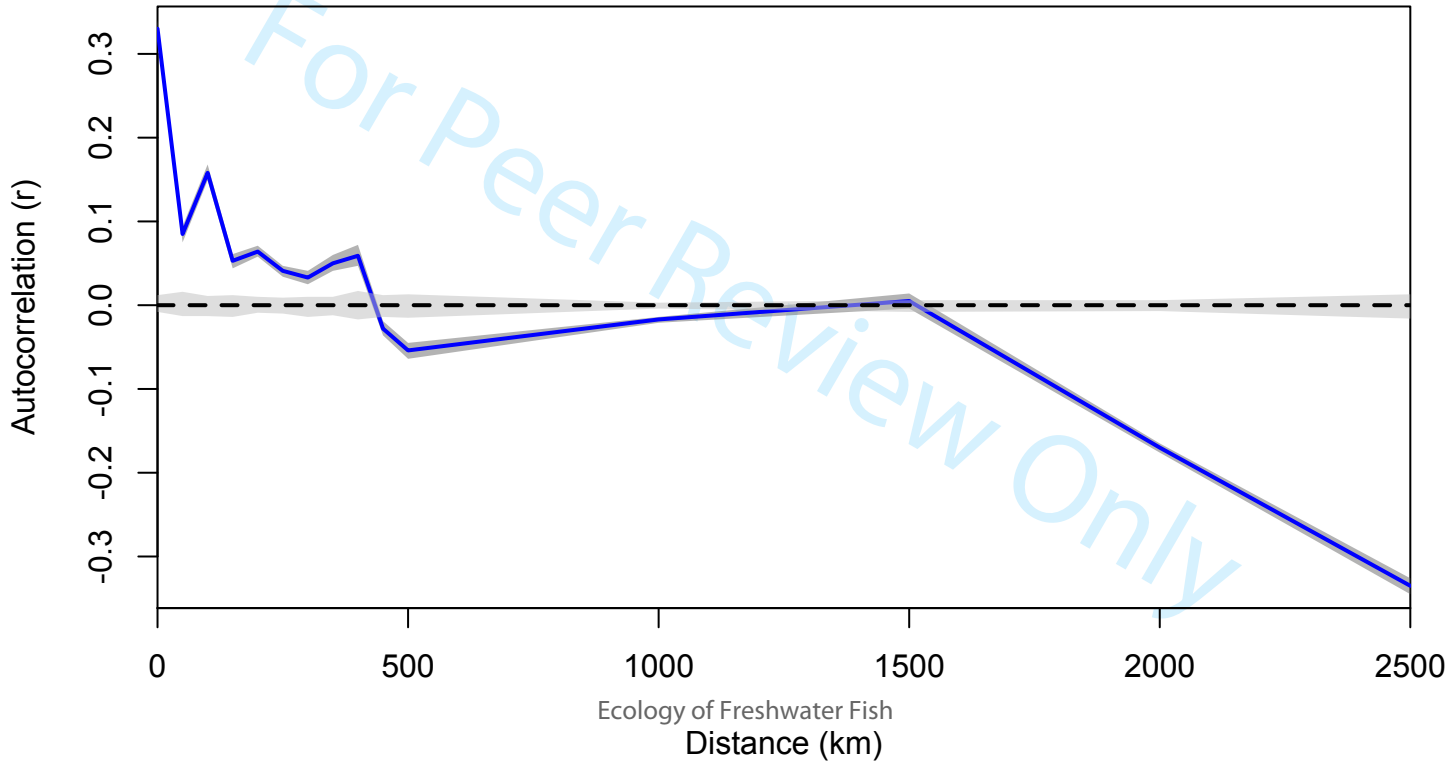


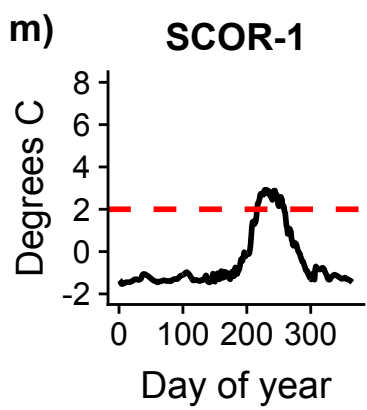
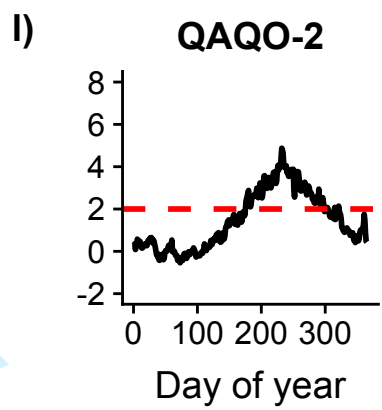
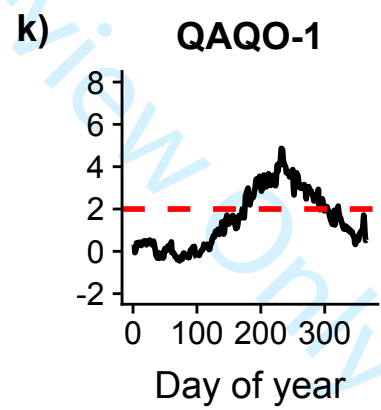
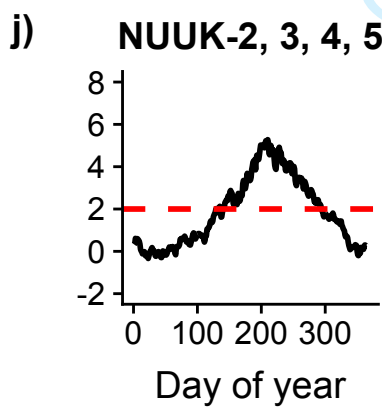
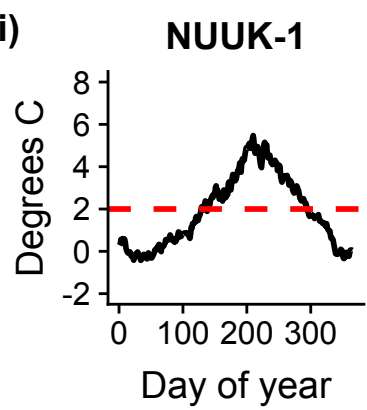
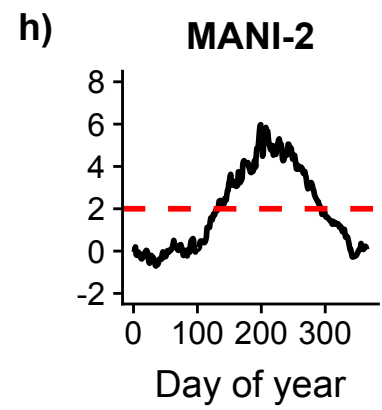
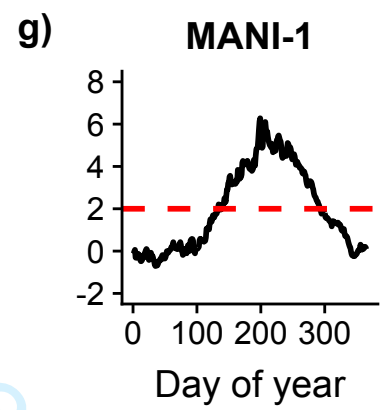
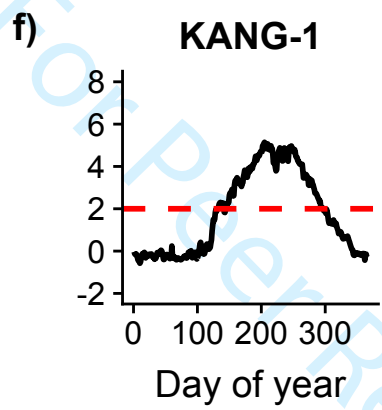
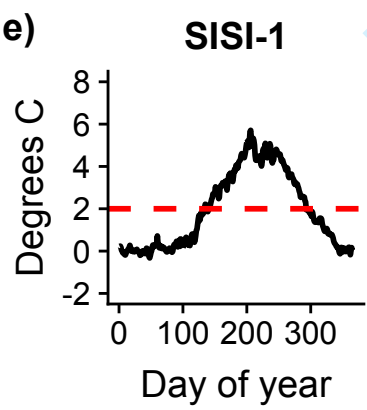
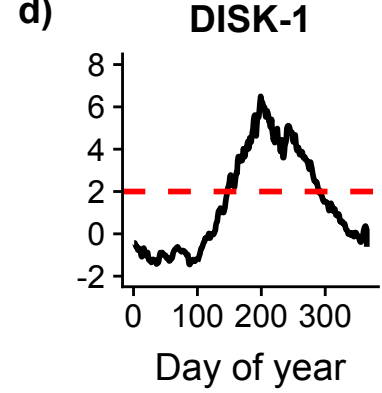
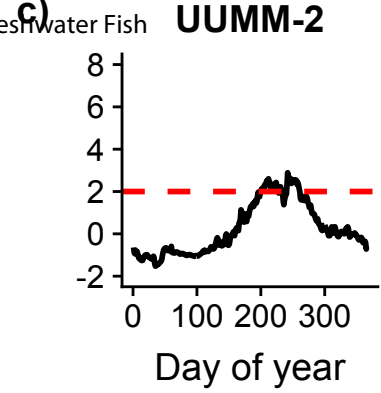
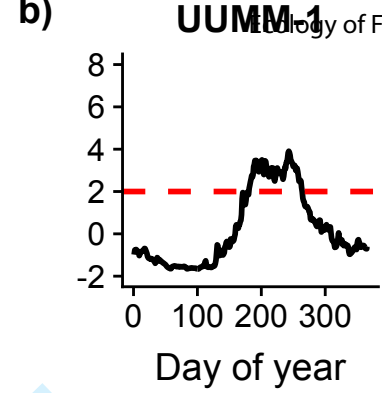
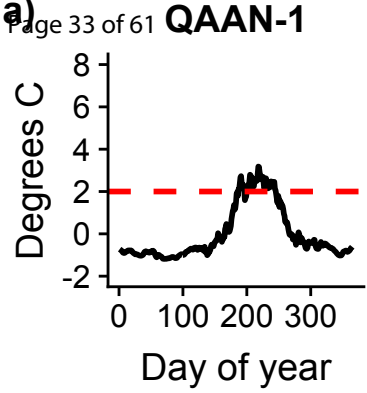
b)

Ecology of Freshwater Fish
Isolation by distance, phenology-related loci



Ecology of Freshwater Fish
Spatial Autocorrelation





Supporting Information for

Genetic population structure and variation at phenology-related loci in anadromous Arctic char (*Salvelinus alpinus*)

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Table S1. Genotypes at the three phenology-related loci Cryptochrome2.b.2, Cryptochrome3, Ots515NWFSC and OtsClock1b of parents and offspring in experimental crosses of Arctic char.

| Locus | Family 1 | | | Family 2 | | |
|-------------------|----------|---------|--|----------|---------|--|
| | Male | Female | Offspring | Male | Female | Offspring |
| Cryptochrome2.b.2 | 258/258 | 258/258 | 258/258 (10) | 258/258 | 258/258 | 258/258 (10) |
| Cryptochrome3 | 357/357 | 357/357 | 357/357 (10) | 357/359 | 357/357 | 357/357 (5) 357/359 (5) |
| Ots515NWFSC | 258/268 | 272/293 | 268/293 (2) 258/272 (3) 258/293 (3) 268/272 (2) | 272/303 | 262/272 | 262/303 (4) 262/272 (2) 272/303 (1) 272/272 (3) |
| OtsClock1b | 426/426 | 426/426 | 426/426 (10) | 391/426 | 337/426 | 337/391 (3) 337/426 (3) 391/426 (2) 426/426 (2) |

Table S3. F_{ST} between all pairs of samples. Above diagonal: F_{ST} at phenology-related loci. Below diagonal: F_{ST} at SNPs. Non-significant values are denoted by green.

| | QAAN-1 | UUMM-1 | UUMM-2 | DISK-1 | SISI-1 | KANG-1 | MANI-1 | MANI-2 | NUUK-1 | NUUK-2 | NUUK-3 | NUUK-4 | NUUK-5 | QAQO-1 | QAQO-2 | SCOR-1 | ICEL-1 | NORW-1 |
|--------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| QAAN-1 | 0.00 | 0.05* | 0.04 | 0.05* | 0.10*** | 0.14*** | 0.20*** | 0.27*** | 0.29*** | 0.23*** | 0.22*** | 0.13*** | 0.31*** | 0.31*** | 0.22*** | 0.47*** | 0.37*** | 0.33*** |
| UUMM-1 | 0.19*** | 0.00 | 0.02 | 0.02 | 0.05* | 0.08*** | 0.13*** | 0.19*** | 0.18*** | 0.12*** | 0.12*** | 0.04* | 0.19*** | 0.19*** | 0.10*** | 0.33*** | 0.26*** | 0.23*** |
| UUMM-2 | 0.20*** | 0.11*** | 0.00 | 0.03 | 0.06 | 0.11*** | 0.15*** | 0.21*** | 0.21*** | 0.17*** | 0.16*** | 0.08** | 0.24*** | 0.24*** | 0.16*** | 0.38*** | 0.30*** | 0.25*** |
| DISK-1 | 0.17*** | 0.04*** | 0.10*** | 0.00 | 0.03* | 0.06** | 0.09*** | 0.16*** | 0.13*** | 0.09*** | 0.10*** | 0.03* | 0.16*** | 0.15*** | 0.09*** | 0.28*** | 0.22*** | 0.20*** |
| SISI-1 | 0.21*** | 0.09*** | 0.10*** | 0.06*** | 0.00 | 0.03* | 0.03* | 0.07* | 0.08*** | 0.05* | 0.04* | 0.02 | 0.10*** | 0.11*** | 0.05* | 0.19*** | 0.19*** | 0.15*** |
| KANG-1 | 0.32*** | 0.12*** | 0.14*** | 0.09*** | 0.05*** | 0.00 | 0.04 | 0.05** | 0.10*** | 0.06** | 0.04* | 0.05*** | 0.05** | 0.11*** | 0.07** | 0.22*** | 0.13*** | 0.18*** |
| MANI-1 | 0.32*** | 0.12*** | 0.16*** | 0.10*** | 0.05*** | 0.07*** | 0.00 | 0.03* | 0.04*** | 0.04** | 0.03 | 0.06*** | 0.05** | 0.07*** | 0.06*** | 0.14*** | 0.14*** | 0.17*** |
| MANI-2 | 0.35*** | 0.14*** | 0.17*** | 0.10*** | 0.06*** | 0.07*** | 0.04*** | 0.00 | 0.11*** | 0.09*** | 0.06*** | 0.12*** | 0.05*** | 0.15*** | 0.12*** | 0.22*** | 0.18*** | 0.23*** |
| NUUK-1 | 0.38*** | 0.16*** | 0.20*** | 0.14*** | 0.09*** | 0.11*** | 0.06*** | 0.09*** | 0.00 | 0.05** | 0.05*** | 0.08*** | 0.09*** | 0.04 | 0.09*** | 0.11*** | 0.21*** | 0.21*** |
| NUUK-2 | 0.36*** | 0.13*** | 0.16*** | 0.11*** | 0.05*** | 0.07*** | 0.03*** | 0.04*** | 0.06*** | 0.00 | 0.02 | 0.03 | 0.05*** | 0.04* | 0.02 | 0.14*** | 0.18*** | 0.17*** |
| NUUK-3 | 0.32*** | 0.12*** | 0.16*** | 0.09*** | 0.05*** | 0.07*** | 0.03** | 0.04*** | 0.07*** | 0.02 | 0.00 | 0.03* | 0.03* | 0.05** | 0.02 | 0.18*** | 0.19*** | 0.18*** |
| NUUK-4 | 0.36*** | 0.14*** | 0.16*** | 0.11*** | 0.06*** | 0.08*** | 0.03** | 0.04*** | 0.04*** | 0.02 | 0.03** | 0.00 | 0.09*** | 0.07*** | 0.02 | 0.21*** | 0.20*** | 0.17*** |
| NUUK-5 | 0.36*** | 0.15*** | 0.17*** | 0.13*** | 0.08*** | 0.10*** | 0.05*** | 0.07*** | 0.08*** | 0.04*** | 0.03*** | 0.04*** | 0.00 | 0.09*** | 0.08*** | 0.20*** | 0.16*** | 0.23*** |
| QAQO-1 | 0.51*** | 0.25*** | 0.29*** | 0.23*** | 0.17*** | 0.21*** | 0.12*** | 0.14*** | 0.10*** | 0.10*** | 0.09*** | 0.08*** | 0.10*** | 0.00 | 0.06 | 0.15*** | 0.22*** | 0.22*** |
| QAQO-2 | 0.52*** | 0.23*** | 0.27*** | 0.21*** | 0.16*** | 0.17*** | 0.10*** | 0.11*** | 0.07*** | 0.07*** | 0.10*** | 0.06*** | 0.11*** | 0.10*** | 0.00 | 0.20*** | 0.23*** | 0.18*** |
| SCOR-1 | 0.63*** | 0.31*** | 0.33*** | 0.27*** | 0.22*** | 0.21*** | 0.15*** | 0.15*** | 0.15*** | 0.12*** | 0.14*** | 0.09*** | 0.17*** | 0.18*** | 0.12*** | 0.00 | 0.23*** | 0.26*** |
| ICEL-1 | 0.66*** | 0.34*** | 0.36*** | 0.32*** | 0.26*** | 0.29*** | 0.19*** | 0.21*** | 0.18*** | 0.16*** | 0.18*** | 0.12*** | 0.20*** | 0.17*** | 0.15*** | 0.15*** | 0.00 | 0.23*** |
| NORW-1 | 0.67*** | 0.31*** | 0.36*** | 0.29*** | 0.24*** | 0.23*** | 0.16*** | 0.17*** | 0.16*** | 0.13*** | 0.16*** | 0.11*** | 0.17*** | 0.21*** | 0.10*** | 0.09*** | 0.26*** | 0.00 |

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ after False Discovery Rate correction (B-Y method, Narum (2006))

Narum, S.R. 2006. Beyond Bonferroni: Less conservative analyses for conservation genetics. *Conservation Genetics* 7: 783-787.

Table S4. Mean allele length at *OtsClock1b* along with latitude, start and end day of SST window.

| Population | Mean allele length at <i>OtsClock1b</i> | Allele length s.d. | Latitude | Start of SST window (day of year) | End of SST window (day of year) |
|------------|---|--------------------|----------|-----------------------------------|---------------------------------|
| QAAN-1 | 426.00 | 0.00 | 77.47 | 187 | 245 |
| UUMM-1 | 424.16 | 7.92 | 71.66 | 180 | 263 |
| UUMM-2 | 416.45 | 25.92 | 70.54 | 201 | 260 |
| DISK-1 | 418.88 | 16.75 | 69.25 | 147 | 293 |
| KANG-1 | 398.25 | 39.91 | 66.43 | 131 | 297 |
| SISI-1 | 398.80 | 35.13 | 66.71 | 134 | 295 |
| MANI-1 | 387.93 | 36.86 | 65.57 | 133 | 292 |
| MANI-2 | 363.88 | 39.79 | 65.31 | 132 | 293 |
| NUUK-1 | 388.19 | 33.57 | 64.42 | 133 | 294 |
| NUUK-2 | 406.24 | 31.48 | 64.14 | 134 | 294 |
| NUUK-3 | 400.60 | 37.90 | 64.29 | 134 | 294 |
| NUUK-4 | 418.88 | 37.90 | 64 | 134 | 294 |
| NUUK-5 | 389.39 | 42.89 | 63.99 | 134 | 294 |
| QAQO-1 | 408.83 | 26.15 | 60.89 | 171 | 321 |
| QAQO-2 | 417.63 | 22.11 | 60.76 | 176 | 321 |
| SCOR-1 | 393.26 | 14.55 | 70.35 | 208 | 261 |
| ICEL-1 | 405.00 | 17.36 | 65.52 | NA | NA |
| NORW-1 | 415.06 | 16.48 | 69.33 | NA | NA |

Fig. S1. Bayesian Information Criterion values assuming k from 1 to 40 clusters based on individuals in the SNP data set. The lowest BIC value was obtained for $k = 9$.

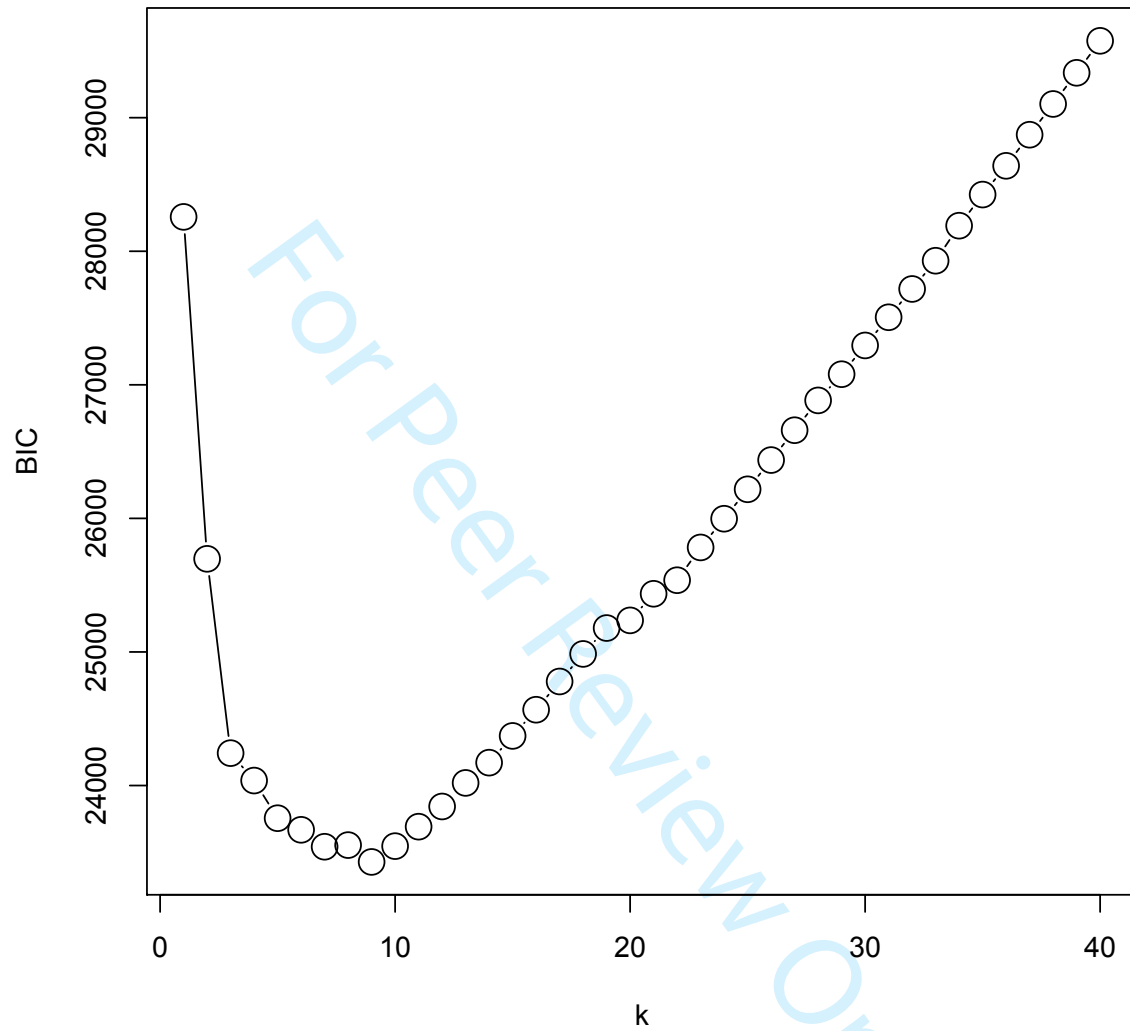
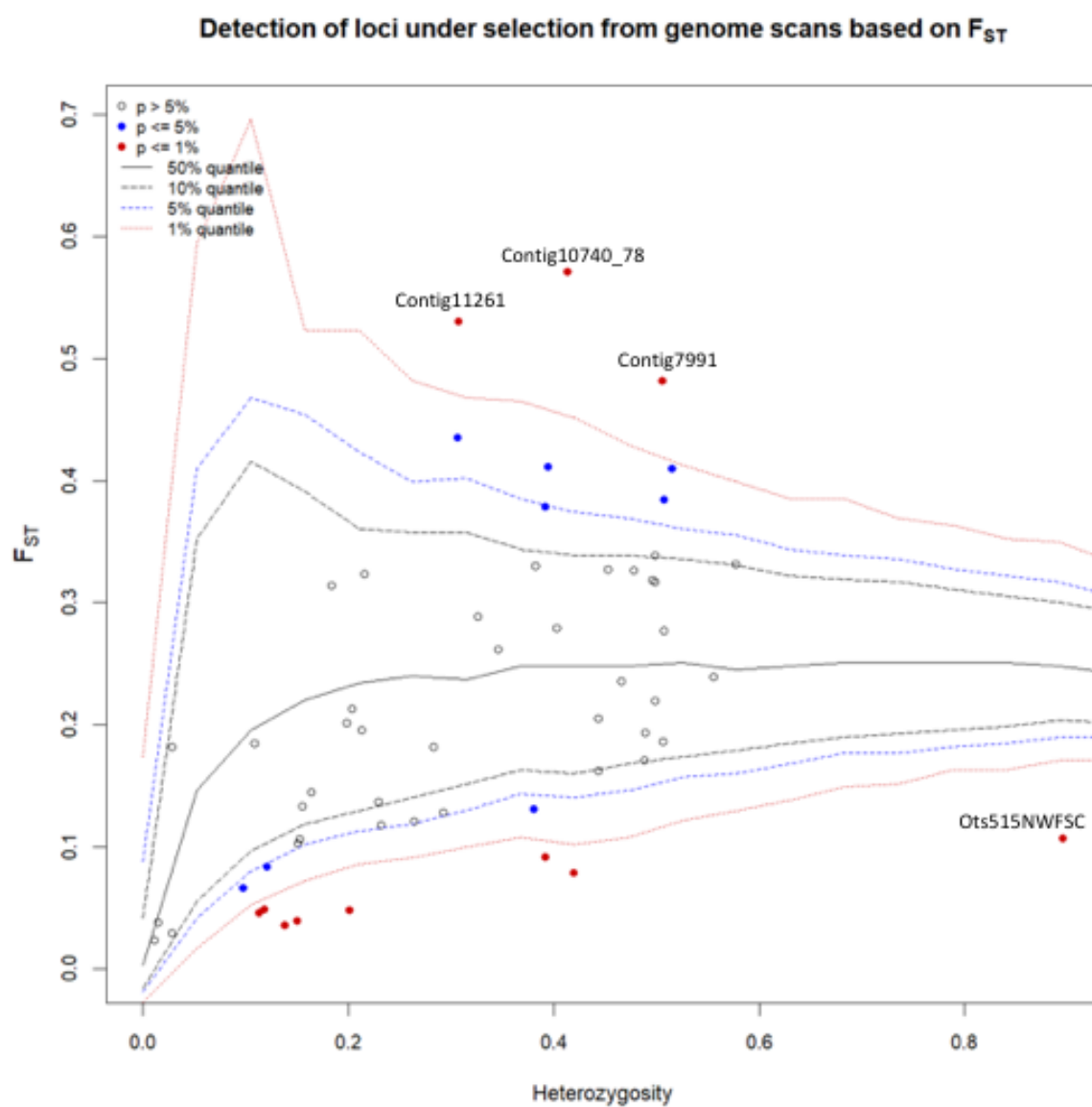


Fig. S2a. Results of F_{ST} -based outlier test (Beaumont & Nichols, 1996) involving all populations.



K

Fig. S2b. Results of hierarchical outlier test (Excoffier et al. 2009) involving Western Greenland populations (excluding QAAN-1).

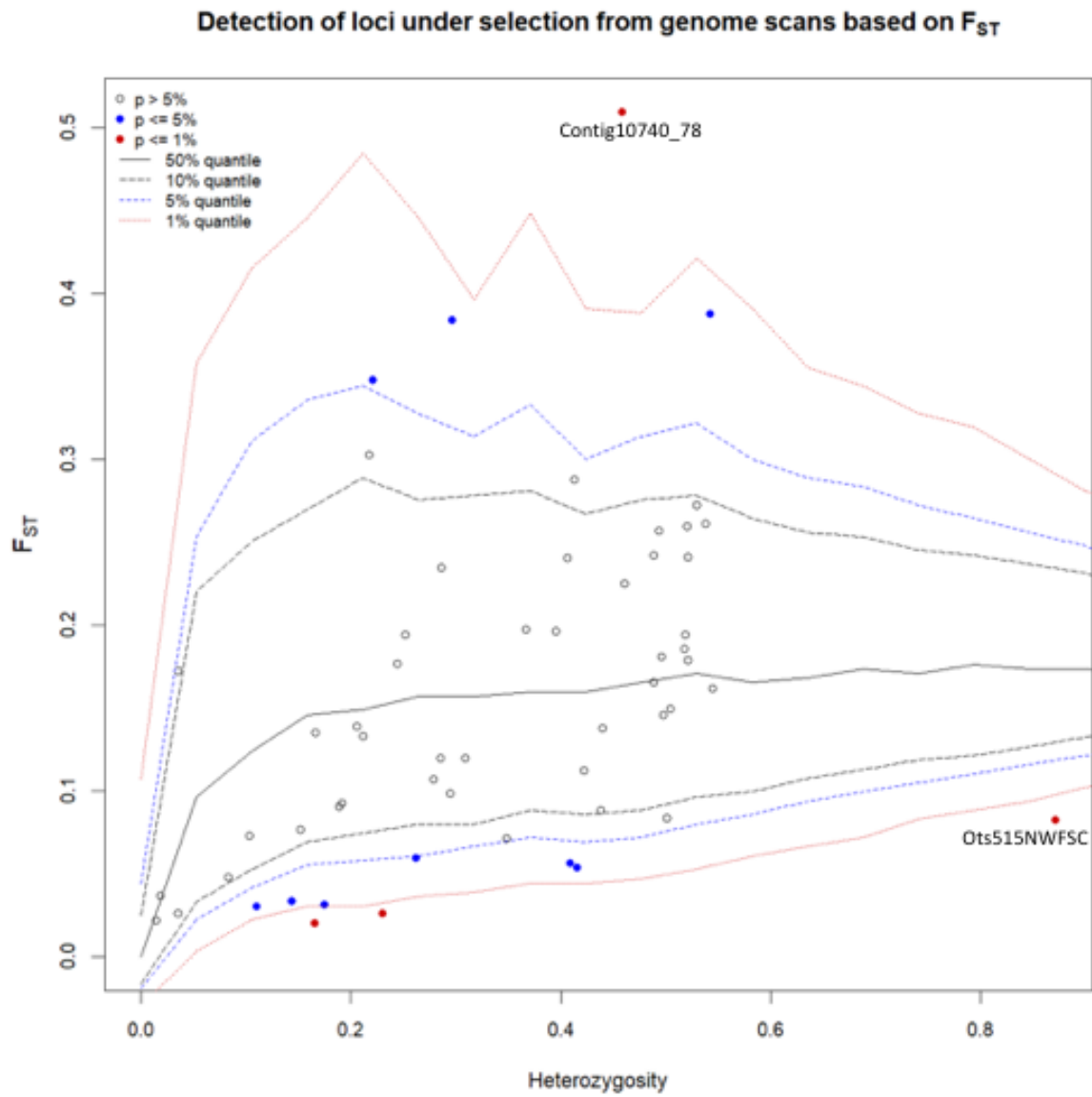


Fig. S3. Plots of association between mean allele length at *OtsClock1b* and geographical and environmental parameters for the sampled populations. Shaded areas denote 95% confidence intervals of the fitted lines. a) Mean allele length and latitude, encompassing all populations ($y = 1.44x + 308.02$, $R^2_{\text{adjusted}} = 0.08$, $p = 0.129$). b) Mean allele length and start day of SST (sea surface temperature) window, encompassing all anadromous populations ($y = 0.29x + 359.18$, $R^2_{\text{adjusted}} = 0.173$, $p = 0.0615$). c) Mean allele length and end day of SST window, encompassing all anadromous populations ($y = -0.20x + 459.81$, $R^2_{\text{adjusted}} = -0.01$, $p = 0.365$). d) Mean allele length and duration of SST window, encompassing all anadromous populations ($y = -0.167x + 425.95$, $R^2_{\text{adjusted}} = 0.12$, $p = 0.10$). e) Mean allele length and start day of SST window, encompassing all anadromous populations from Western Greenland ($y = 0.46x + 334.82$, $R^2_{\text{adjusted}} = 0.39$, $p = 0.007$). f) Mean allele length and duration of SST window, encompassing all anadromous populations from Western Greenland ($y = -0.267x + 441.42$, $R^2_{\text{adjusted}} = 0.308$, $p = 0.019$).

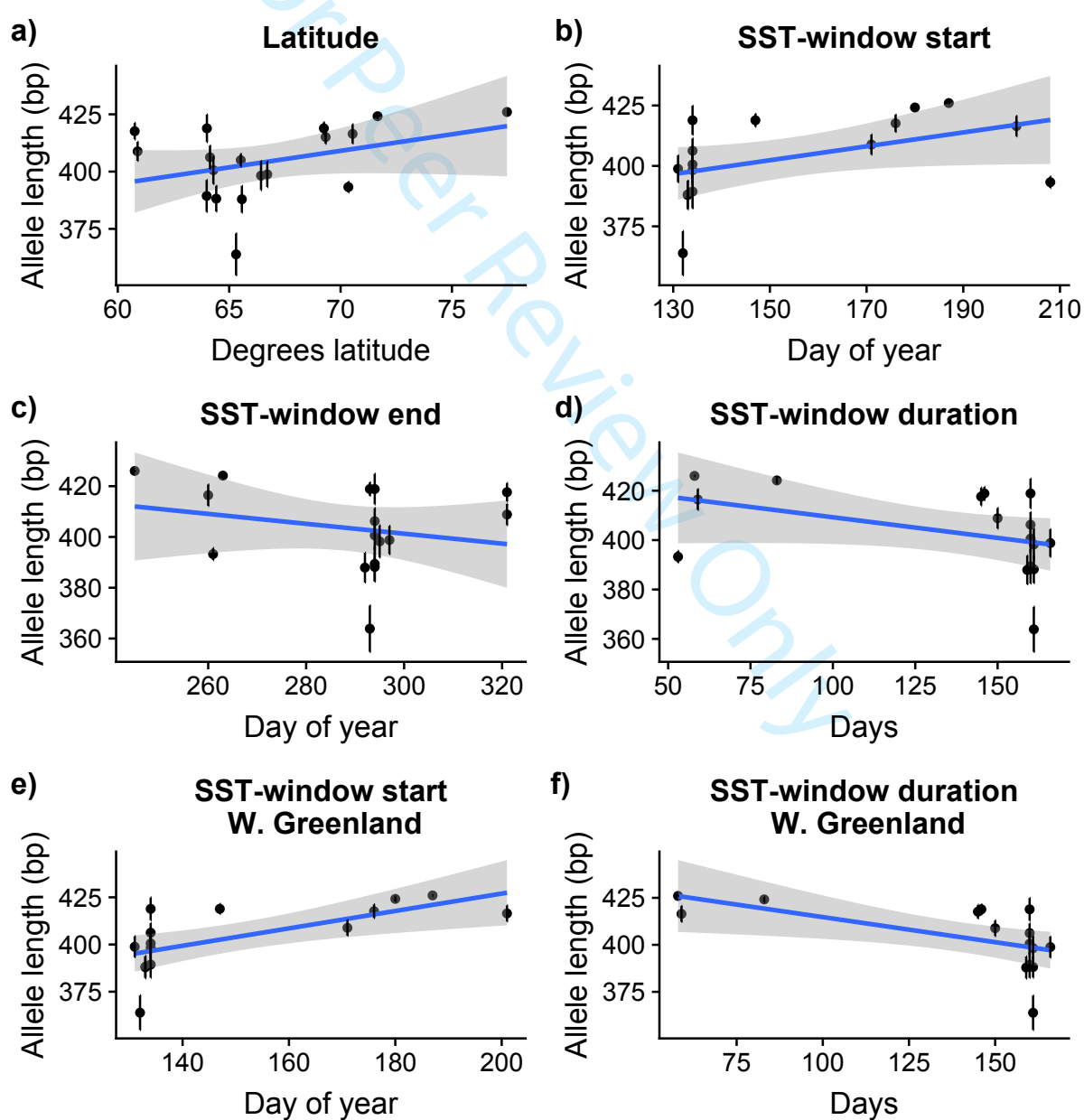


Table S2 Summary statistics

Summary of analyzed loci along with the total number of alleles observed

* Significance level $p < 0.001$ when adjusted for False Discovery Rate

| Locus | Reference | Type |
|------------------|-------------------------------|-------------------------|
| Cryptochrome2b.2 | O'Malley <i>et al</i> (2010b) | Phenology-related locus |
| Cryptochrome3 | O'Malley <i>et al</i> (2010b) | Phenology-related locus |
| Ots515NWFSC | Naish & Park 2002 | Phenology-related locus |
| OtsClock1b | O'Malley <i>et al</i> (2007) | Phenology-related locus |
| Cath2_KC590659 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11261 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig214_63 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2980_70 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig6336_73 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig7751_81 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig92_84 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11263_71 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig12050 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1776_87 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2194_67 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig9220 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11431_72 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1821_63 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2997 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig4510_74 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig6593 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig8674_69 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig9346_76 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11566 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig12176_62 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig3057_86 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig5808_61 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig7991 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig8752 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig3343 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig12281 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11742_67 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig9421 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig8976_82 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig711_65 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig481 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig3493_74 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2680_72 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1973 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1373 | Jacobsen <i>et al</i> (2017) | SNP |

| | | |
|----------------|------------------------------|-----|
| Contig10740_78 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig959_76 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig8978_60 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig7133_66 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig5917_74 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig4954 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig3498 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2705 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1525_59 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig11854_70 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig10812 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig9609 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig609_67 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig3603_79 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig2925 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig1570 | Jacobsen <i>et al</i> (2017) | SNP |
| Contig850 | Jacobsen <i>et al</i> (2017) | SNP |

Pre-proof
Peer Review Only

ved across all populations. For each population observed (H_o) and expected hete

QAAN-1

N = 18

| Total number of alleles | H_o | H_e | P |
|-------------------------|-------|-------|--------|
| 7 | - | - | - |
| 4 | - | - | - |
| 24 | 0.72 | 0.72 | 0.2297 |
| 4 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.33 | 0.51 | 0.1447 |
| 2 | - | - | - |
| 2 | 0.22 | 0.20 | 1.000 |
| 2 | 0.17 | 0.16 | 1.000 |
| 2 | 0.33 | 0.29 | 1.000 |
| 2 | - | - | - |
| 2 | 0.28 | 0.25 | 1.0000 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.89 | 0.51 | 0.000* |
| 2 | - | - | - |
| 2 | 0.17 | 0.25 | 0.2903 |
| 2 | - | - | - |
| 2 | 0.33 | 0.41 | 0.5464 |
| 2 | 0.50 | 0.44 | 1 |
| 2 | 0.06 | 0.06 | 1 |
| 2 | 0.11 | 0.11 | 1 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.0 | 0.11 | 0.0225 |
| 2 | 0.6 | 0.51 | 1 |
| 2 | - | - | - |
| 2 | 0.33 | 0.51 | 0.1525 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.39 | 0.32 | 1.0000 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.06 | 0.06 | 1.0000 |
| 2 | - | - | - |

| | | | |
|---|------|------|--------|
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.22 | 0.20 | 1.0000 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.33 | 0.49 | 0.3460 |
| 2 | 0.06 | 0.06 | 1.0000 |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | - | - | - |
| 2 | 0.44 | 0.46 | 1.0000 |
| 2 | - | - | - |
| 2 | - | - | - |

For Peer Review Only

heterozygosity (H_e) is listed along with P-values of tests for conformance to Hardy-Weinberg

UUMM-1

N = 20

| H_o | H_e | P |
|----------------------|----------------------|----------|
| 0.50 | 0.38 | 0.282 |
| 0.20 | 0.18 | 1.000 |
| 0.60 | 0.74 | 0.056 |
| 0.11 | 0.10 | 1.000 |
| 0.60 | 0.51 | 0.663 |
| 0.40 | 0.47 | 0.655 |
| 0.61 | 0.47 | 0.285 |
| 0.10 | 0.10 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| 0.58 | 0.49 | 0.632 |
| 0.55 | 0.48 | 0.648 |
| 0.45 | 0.45 | 1.000 |
| 0.55 | 0.41 | 0.245 |
| 0.35 | 0.41 | 0.594 |
| 0.40 | 0.38 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| - | - | - |
| 0.25 | 0.22 | 1.000 |
| 0.40 | 0.38 | 1.000 |
| 0.15 | 0.14 | 1.000 |
| 0.35 | 0.50 | 0.178 |
| 0.45 | 0.36 | 0.505 |
| 0.45 | 0.41 | 1.000 |
| 0.30 | 0.33 | 1.000 |
| 0.42 | 0.40 | 1.000 |
| 0.47 | 0.51 | 1.000 |
| - | - | - |
| 0.20 | 0.18 | 1.000 |
| 0.40 | 0.43 | 1.000 |
| 0.15 | 0.14 | 1.000 |
| 0.50 | 0.38 | 0.319 |
| 0.42 | 0.51 | 0.665 |
| 0.58 | 0.51 | 0.679 |
| - | - | - |
| 0.37 | 0.37 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| 0.35 | 0.30 | 1.000 |
| 0.30 | 0.26 | 1.000 |
| 0.35 | 0.30 | 1.000 |

UUMM-2

N = 20

| H_o | H_e | P |
|----------------------|----------------------|----------|
| 0.20 | 0.19 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| 0.50 | 0.73 | 0.000 |
| 0.26 | 0.25 | 1.000 |
| 0.40 | 0.43 | 1.000 |
| 0.25 | 0.30 | 0.469 |
| 0.10 | 0.18 | 0.116 |
| 0.05 | 0.05 | 1.000 |
| 0.45 | 0.41 | 1.000 |
| 0.40 | 0.38 | 1.000 |
| 0.45 | 0.48 | 1.000 |
| 0.35 | 0.48 | 0.337 |
| 0.35 | 0.45 | 0.344 |
| 0.50 | 0.43 | 0.602 |
| 0.45 | 0.51 | 0.674 |
| 0.50 | 0.47 | 1.000 |
| - | - | - |
| 0.35 | 0.30 | 1.000 |
| 0.90 | 0.51 | 0.002 |
| 0.20 | 0.18 | 1.000 |
| 0.30 | 0.33 | 1.000 |
| 0.15 | 0.22 | 0.235 |
| 0.60 | 0.47 | 0.321 |
| 0.60 | 0.51 | 0.661 |
| 0.60 | 0.51 | 0.651 |
| 0.55 | 0.50 | 1.000 |
| - | - | - |
| 0.15 | 0.22 | 0.247 |
| 0.35 | 0.36 | 1.000 |
| 0.40 | 0.43 | 1.000 |
| 0.30 | 0.26 | 1.000 |
| 0.20 | 0.26 | 0.342 |
| 0.00 | 0.10 | 0.025 |
| 0.05 | 0.05 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| - | - | - |
| - | - | - |
| 0.45 | 0.41 | 1.000 |
| 0.25 | 0.50 | 0.018 |

| | | | | | |
|------|------|-------|------|------|-------|
| 0.05 | 0.14 | 0.071 | 0.25 | 0.30 | 0.465 |
| 0.15 | 0.14 | 1.000 | - | - | - |
| 0.42 | 0.40 | 1.000 | 0.05 | 0.05 | 1.000 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.20 | 0.18 | 1.000 | 0.05 | 0.14 | 0.062 |
| 0.35 | 0.45 | 0.332 | 0.53 | 0.40 | 0.234 |
| 0.45 | 0.41 | 1.000 | 0.60 | 0.51 | 0.645 |
| 0.65 | 0.50 | 0.384 | 0.05 | 0.05 | 1.000 |
| 0.20 | 0.18 | 1.000 | - | - | - |
| - | - | - | 0.15 | 0.14 | 1.000 |
| 0.42 | 0.40 | 1.000 | 0.25 | 0.22 | 1.000 |
| - | - | - | - | - | - |
| 0.40 | 0.33 | 0.538 | 0.45 | 0.41 | 1.000 |
| 0.25 | 0.22 | 1.000 | 0.35 | 0.36 | 1.000 |
| 0.15 | 0.14 | 1.000 | 0.55 | 0.45 | 0.577 |

Veinberg Equilibrium. "-" denotes that the locus was monomorphic within the speci

DISK-1

N = 20

| Ho | He | P |
|------|------|--------|
| 0.45 | 0.36 | 0.536 |
| 0.15 | 0.22 | 0.234 |
| 0.75 | 0.84 | 0.000* |
| 0.25 | 0.30 | 0.601 |
| 0.15 | 0.14 | 1.000 |
| 0.45 | 0.48 | 1.000 |
| 0.65 | 0.50 | 0.361 |
| 0.05 | 0.05 | 1.000 |
| 0.15 | 0.14 | 1.000 |
| 0.65 | 0.50 | 0.331 |
| 0.20 | 0.26 | 0.345 |
| 0.40 | 0.49 | 0.637 |
| 0.45 | 0.45 | 1.000 |
| 0.20 | 0.33 | 0.137 |
| 0.30 | 0.47 | 0.138 |
| 0.25 | 0.22 | 1.000 |
| - | - | - |
| 0.40 | 0.38 | 1.000 |
| 0.75 | 0.48 | 0.010 |
| 0.10 | 0.10 | 1.000 |
| 0.25 | 0.50 | 0.031 |
| 0.30 | 0.51 | 0.081 |
| 0.20 | 0.26 | 0.398 |
| 0.35 | 0.30 | 1.000 |
| 0.25 | 0.41 | 0.099 |
| 0.45 | 0.50 | 0.684 |
| - | - | - |
| 0.40 | 0.43 | 1.000 |
| 0.40 | 0.51 | 0.369 |
| - | - | - |
| - | - | - |
| 0.60 | 0.51 | 0.660 |
| 0.40 | 0.51 | 0.398 |
| - | - | - |
| 0.40 | 0.38 | 1.000 |
| 0.05 | 0.14 | 0.096 |
| 0.25 | 0.22 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| 0.40 | 0.47 | 0.618 |
| 0.55 | 0.45 | 0.613 |

KANG-1

N = 20

| Ho | He | P |
|------|------|-------|
| 0.45 | 0.53 | 0.563 |
| 0.45 | 0.53 | 0.612 |
| 0.85 | 0.83 | 0.472 |
| 0.60 | 0.52 | 0.113 |
| - | - | - |
| 0.06 | 0.16 | 0.066 |
| 0.30 | 0.43 | 0.271 |
| 0.05 | 0.05 | 1.000 |
| 0.40 | 0.43 | 1.000 |
| 0.20 | 0.43 | 0.034 |
| 0.35 | 0.45 | 0.339 |
| 0.60 | 0.47 | 0.355 |
| 0.45 | 0.45 | 1.000 |
| - | - | - |
| 0.40 | 0.51 | 0.363 |
| 0.55 | 0.50 | 1.000 |
| - | - | - |
| - | - | - |
| 0.40 | 0.51 | 0.432 |
| 0.45 | 0.41 | 1.000 |
| 0.40 | 0.51 | 0.464 |
| 0.20 | 0.18 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| 0.15 | 0.14 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| 0.30 | 0.26 | 1.000 |
| 0.50 | 0.51 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| 0.05 | 0.05 | 1.000 |
| - | - | - |
| 0.65 | 0.48 | 0.168 |
| 0.10 | 0.10 | 1.000 |
| 0.10 | 0.10 | 1.000 |
| - | - | - |
| 0.15 | 0.22 | 0.231 |
| 0.15 | 0.14 | 1.000 |
| 0.55 | 0.45 | 0.633 |
| 0.10 | 0.10 | 1.000 |

| | | | | | |
|------|------|-------|------|------|-------|
| 0.55 | 0.50 | 1.000 | 0.55 | 0.51 | 1.000 |
| 0.20 | 0.18 | 1.000 | 0.10 | 0.10 | 1.000 |
| 0.35 | 0.30 | 1.000 | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.15 | 0.14 | 1.000 | 0.15 | 0.14 | 1.000 |
| 0.50 | 0.38 | 0.321 | 0.40 | 0.49 | 0.634 |
| 0.55 | 0.51 | 1.000 | 0.25 | 0.30 | 0.434 |
| 0.35 | 0.36 | 1.000 | 0.40 | 0.49 | 0.674 |
| 0.30 | 0.26 | 1.000 | - | - | - |
| 0.10 | 0.10 | 1.000 | 0.50 | 0.43 | 0.627 |
| 0.30 | 0.38 | 0.545 | 0.55 | 0.50 | 1.000 |
| 0.10 | 0.10 | 1.000 | - | - | - |
| 0.50 | 0.43 | 0.622 | 0.35 | 0.51 | 0.232 |
| 0.20 | 0.26 | 0.374 | - | - | - |
| 0.20 | 0.18 | 1.000 | 0.15 | 0.30 | 0.064 |

fic population.

| SISI-1 N = 20 | | | MANI-1 N = 20 | | | MANI-2 N = 20 |
|------------------|------|--------|------------------|------|-------|------------------|
| Ho | He | P | Ho | He | P | Ho |
| 0.50 | 0.52 | 0.653 | 0.60 | 0.51 | 0.647 | 0.70 |
| 0.25 | 0.22 | 1.000 | 0.33 | 0.48 | 0.158 | 0.60 |
| 0.75 | 0.87 | 0.000* | 0.75 | 0.77 | 0.074 | 0.65 |
| 0.53 | 0.61 | 0.266 | 0.65 | 0.68 | 0.346 | 0.65 |
| 0.35 | 0.36 | 1.000 | 0.30 | 0.43 | 0.304 | 0.70 |
| 0.21 | 0.27 | 0.344 | 0.10 | 0.26 | 0.033 | 0.05 |
| 0.25 | 0.36 | 0.217 | 0.35 | 0.30 | 1.000 | 0.05 |
| 0.15 | 0.30 | 0.061 | - | - | - | 0.05 |
| 0.50 | 0.47 | 1.000 | 0.50 | 0.47 | 1.000 | 0.40 |
| 0.40 | 0.38 | 1.000 | 0.50 | 0.51 | 1.000 | 0.45 |
| 0.45 | 0.36 | 0.531 | 0.10 | 0.10 | 1.000 | 0.20 |
| 0.55 | 0.45 | 0.622 | 0.35 | 0.36 | 1.000 | 0.40 |
| 0.50 | 0.47 | 1.000 | 0.45 | 0.51 | 0.658 | 0.40 |
| 0.37 | 0.31 | 1.000 | - | - | - | - |
| 0.25 | 0.22 | 1.000 | 0.40 | 0.43 | 1.000 | 0.30 |
| 0.35 | 0.48 | 0.327 | 0.40 | 0.43 | 1.000 | 0.50 |
| - | - | - | 0.10 | 0.10 | 1.000 | - |
| - | - | - | 0.15 | 0.14 | 1.000 | 0.10 |
| 0.30 | 0.38 | 0.594 | 0.15 | 0.36 | 0.023 | 0.40 |
| 0.55 | 0.45 | 0.600 | 0.60 | 0.51 | 0.661 | 0.50 |
| 0.55 | 0.45 | 0.633 | 0.30 | 0.43 | 0.269 | 0.45 |
| 0.26 | 0.31 | 0.513 | 0.20 | 0.26 | 0.358 | 0.45 |
| 0.15 | 0.14 | 1.000 | - | - | - | 0.10 |
| 0.25 | 0.36 | 0.196 | 0.35 | 0.30 | 1.000 | 0.30 |
| 0.47 | 0.42 | 1.000 | 0.20 | 0.26 | 0.374 | 0.15 |
| 0.26 | 0.42 | 0.095 | 0.25 | 0.30 | 0.469 | 0.35 |
| 0.26 | 0.23 | 1.000 | 0.30 | 0.38 | 0.553 | - |
| 0.63 | 0.48 | 0.303 | 0.58 | 0.42 | 0.240 | 0.60 |
| 0.32 | 0.27 | 1.000 | 0.65 | 0.51 | 0.326 | 0.55 |
| 0.26 | 0.49 | 0.088 | 0.40 | 0.43 | 1.000 | 0.20 |
| 0.26 | 0.23 | 1.000 | 0.35 | 0.30 | 1.000 | 0.05 |
| 0.21 | 0.19 | 1.000 | 0.05 | 0.05 | 1.000 | 0.10 |
| 0.53 | 0.51 | 1.000 | 0.45 | 0.51 | 0.652 | 0.55 |
| 0.47 | 0.37 | 0.517 | 0.40 | 0.38 | 1.000 | 0.55 |
| 0.47 | 0.37 | 0.508 | 0.50 | 0.49 | 1.000 | 0.20 |
| 0.11 | 0.10 | 1.000 | - | - | - | 0.10 |
| 0.11 | 0.10 | 1.000 | 0.30 | 0.26 | 1.000 | 0.35 |
| 0.21 | 0.19 | 1.000 | 0.10 | 0.10 | 1.000 | 0.20 |
| 0.42 | 0.40 | 1.000 | 0.55 | 0.41 | 0.269 | 0.50 |
| 0.32 | 0.27 | 1.000 | 0.20 | 0.18 | 1.000 | 0.25 |

| | | | | | | |
|------|------|-------|------|------|-------|------|
| 0.50 | 0.47 | 1.000 | 0.10 | 0.18 | 0.162 | 0.10 |
| 0.32 | 0.27 | 1.000 | 0.50 | 0.47 | 1.000 | 0.25 |
| 0.45 | 0.48 | 1.000 | 0.45 | 0.41 | 1.000 | 0.50 |
| - | - | - | 0.05 | 0.05 | 1.000 | - |
| - | - | - | - | - | - | - |
| 0.05 | 0.05 | 1.000 | 0.40 | 0.33 | 0.565 | - |
| 0.15 | 0.14 | 1.000 | 0.40 | 0.33 | 0.541 | 0.25 |
| 0.60 | 0.49 | 0.370 | 0.35 | 0.48 | 0.367 | 0.35 |
| 0.47 | 0.51 | 1.000 | 0.55 | 0.45 | 0.606 | 0.05 |
| 0.50 | 0.49 | 1.000 | 0.45 | 0.50 | 0.713 | 0.40 |
| 0.30 | 0.26 | 1.000 | 0.25 | 0.30 | 0.484 | - |
| 0.55 | 0.48 | 0.623 | 0.55 | 0.41 | 0.256 | 0.30 |
| 0.70 | 0.49 | 0.087 | 0.50 | 0.49 | 1.000 | 0.30 |
| - | - | - | - | - | - | - |
| 0.35 | 0.41 | 0.573 | 0.45 | 0.48 | 1.000 | - |
| 0.20 | 0.18 | 1.000 | 0.10 | 0.10 | 1.000 | 0.50 |
| 0.05 | 0.05 | 1.000 | 0.45 | 0.36 | 0.534 | 0.25 |

| NUUK-1 N = 20 | | NUUK-2 N = 20 | | | |
|------------------|-------|------------------|------|-------|------|
| He | P | Ho | He | P | Ho |
| 0.51 | 0.165 | 0.50 | 0.39 | 0.487 | 0.47 |
| 0.59 | 0.570 | 0.06 | 0.06 | 1.000 | 0.21 |
| 0.71 | 0.157 | 0.67 | 0.75 | 0.196 | 1.00 |
| 0.54 | 0.660 | 0.67 | 0.67 | 0.890 | 0.53 |
| 0.51 | 0.190 | 0.44 | 0.51 | 0.657 | 0.16 |
| 0.14 | 0.070 | 0.22 | 0.29 | 0.394 | 0.05 |
| 0.14 | 0.070 | 0.28 | 0.32 | 0.489 | - |
| 0.05 | 1.000 | - | - | - | 0.21 |
| 0.51 | 0.396 | 0.28 | 0.39 | 0.264 | 0.58 |
| 0.50 | 0.658 | 0.39 | 0.47 | 0.626 | 0.47 |
| 0.33 | 0.139 | 0.22 | 0.29 | 0.447 | 0.16 |
| 0.38 | 1.000 | 0.67 | 0.49 | 0.140 | 0.50 |
| 0.38 | 1.000 | 0.33 | 0.41 | 0.537 | 0.37 |
| - | - | - | - | - | 0.05 |
| 0.33 | 1.000 | 0.44 | 0.46 | 1.000 | 0.47 |
| 0.38 | 0.242 | 0.50 | 0.50 | 1.000 | 0.47 |
| - | - | - | - | - | 0.11 |
| 0.10 | 1.000 | - | - | - | 0.11 |
| 0.38 | 1.000 | 0.39 | 0.39 | 1.000 | 0.42 |
| 0.38 | 0.277 | 0.56 | 0.51 | 1.000 | 0.42 |
| 0.48 | 1.000 | 0.33 | 0.29 | 1.000 | 0.37 |
| 0.50 | 0.706 | 0.06 | 0.06 | 1.000 | 0.37 |
| 0.10 | 1.000 | - | - | - | 0.11 |
| 0.26 | 1.000 | 0.11 | 0.11 | 1.000 | 0.16 |
| 0.22 | 0.242 | 0.44 | 0.49 | 1.000 | 0.47 |
| 0.51 | 0.207 | 0.28 | 0.39 | 0.239 | 0.16 |
| - | - | 0.39 | 0.44 | 1.000 | 0.21 |
| 0.51 | 0.658 | 0.22 | 0.20 | 1.000 | 0.63 |
| 0.50 | 1.000 | 0.50 | 0.39 | 0.540 | 0.58 |
| 0.18 | 1.000 | - | - | - | 0.16 |
| 0.05 | 1.000 | 0.28 | 0.25 | 1.000 | 0.32 |
| 0.10 | 1.000 | - | - | - | 0.11 |
| 0.51 | 1.000 | 0.44 | 0.49 | 1.000 | 0.58 |
| 0.48 | 0.625 | 0.06 | 0.06 | 1.000 | 0.42 |
| 0.26 | 0.392 | 0.39 | 0.47 | 0.585 | 0.21 |
| 0.10 | 1.000 | 0.11 | 0.11 | 1.000 | 0.21 |
| 0.48 | 0.355 | 0.11 | 0.11 | 1.000 | 0.16 |
| 0.18 | 1.000 | 0.17 | 0.16 | 1.000 | 0.21 |
| 0.51 | 1.000 | 0.44 | 0.36 | 0.546 | 0.47 |
| 0.30 | 0.444 | 0.44 | 0.46 | 1.000 | 0.16 |

| | | | | | |
|------|-------|------|------|-------|------|
| 0.10 | 1.000 | - | - | - | 0.21 |
| 0.30 | 0.422 | - | - | - | 0.16 |
| 0.49 | 1.000 | 0.11 | 0.11 | 1.000 | 0.58 |
| - | - | - | - | - | - |
| - | - | - | - | - | 0.11 |
| - | - | 0.11 | 0.11 | 1.000 | 0.05 |
| 0.30 | 0.456 | 0.11 | 0.11 | 1.000 | 0.16 |
| 0.30 | 1.000 | 0.11 | 0.11 | 1.000 | 0.37 |
| 0.05 | 1.000 | 0.50 | 0.44 | 1.000 | 0.32 |
| 0.49 | 0.644 | 0.28 | 0.32 | 0.478 | 0.26 |
| - | - | - | - | - | 0.16 |
| 0.47 | 0.127 | 0.06 | 0.16 | 0.087 | 0.42 |
| 0.47 | 0.131 | 0.17 | 0.39 | 0.014 | 0.53 |
| - | - | - | - | - | 0.05 |
| - | - | 0.28 | 0.32 | 0.513 | 0.26 |
| 0.43 | 0.618 | 0.28 | 0.32 | 0.515 | 0.11 |
| 0.22 | 1.000 | 0.17 | 0.16 | 1.000 | 0.11 |

For Peer Review Only

| NUUK-5 N = 20 | | | NUUK-3 N = 20 | | | |
|------------------|-------|------|------------------|-------|------|------|
| He | P | Ho | He | P | Ho | He |
| 0.37 | 0.521 | 0.41 | 0.62 | 0.015 | 0.65 | 0.51 |
| 0.20 | 1.000 | 0.26 | 0.28 | 0.291 | 0.20 | 0.19 |
| 0.93 | 1.000 | 0.80 | 0.79 | 0.338 | 0.90 | 0.88 |
| 0.53 | 0.879 | 0.60 | 0.53 | 0.091 | 0.30 | 0.30 |
| 0.46 | 0.002 | 0.45 | 0.48 | 1.000 | 0.50 | 0.51 |
| 0.05 | 1.000 | - | - | - | - | - |
| - | - | 0.30 | 0.26 | 1.000 | - | - |
| 0.19 | 1.000 | 0.25 | 0.22 | 1.000 | - | - |
| 0.46 | 0.356 | 0.55 | 0.51 | 1.000 | 0.60 | 0.52 |
| 0.51 | 1.000 | 0.45 | 0.48 | 1.000 | 0.58 | 0.51 |
| 0.23 | 0.263 | 0.10 | 0.10 | 1.000 | 0.25 | 0.22 |
| 0.39 | 0.523 | 0.30 | 0.33 | 1.000 | 0.20 | 0.38 |
| 0.37 | 1.000 | 0.25 | 0.41 | 0.089 | 0.30 | 0.47 |
| 0.05 | 1.000 | 0.05 | 0.05 | 1.000 | 0.10 | 0.10 |
| 0.51 | 1.000 | 0.35 | 0.41 | 0.564 | 0.25 | 0.48 |
| 0.49 | 1.000 | 0.25 | 0.36 | 0.233 | 0.30 | 0.51 |
| 0.10 | 1.000 | - | - | - | - | - |
| 0.10 | 1.000 | 0.20 | 0.18 | 1.000 | 0.10 | 0.18 |
| 0.40 | 1.000 | 0.25 | 0.41 | 0.103 | 0.37 | 0.42 |
| 0.40 | 1.000 | 0.50 | 0.51 | 1.000 | 0.40 | 0.43 |
| 0.49 | 0.362 | 0.40 | 0.47 | 0.652 | 0.50 | 0.47 |
| 0.42 | 0.572 | 0.40 | 0.49 | 0.655 | 0.30 | 0.47 |
| 0.10 | 1.000 | 0.10 | 0.10 | 1.000 | 0.20 | 0.18 |
| 0.23 | 0.292 | 0.35 | 0.41 | 0.595 | 0.32 | 0.40 |
| 0.42 | 1.000 | 0.50 | 0.43 | 0.630 | 0.50 | 0.49 |
| 0.15 | 1.000 | 0.15 | 0.14 | 1.000 | 0.30 | 0.33 |
| 0.27 | 0.368 | 0.40 | 0.38 | 1.000 | 0.25 | 0.22 |
| 0.50 | 0.346 | 0.50 | 0.51 | 1.000 | 0.35 | 0.30 |
| 0.51 | 0.645 | 0.45 | 0.51 | 0.690 | 0.45 | 0.48 |
| 0.15 | 1.000 | 0.30 | 0.26 | 1.000 | 0.30 | 0.26 |
| 0.40 | 0.555 | 0.15 | 0.14 | 1.000 | 0.20 | 0.26 |
| 0.10 | 1.000 | 0.20 | 0.18 | 1.000 | 0.10 | 0.10 |
| 0.51 | 0.617 | 0.25 | 0.45 | 0.114 | 0.55 | 0.48 |
| 0.40 | 1.000 | 0.25 | 0.22 | 1.000 | 0.20 | 0.18 |
| 0.34 | 0.127 | 0.40 | 0.47 | 0.597 | 0.45 | 0.50 |
| 0.27 | 0.353 | 0.15 | 0.22 | 0.219 | 0.25 | 0.22 |
| 0.15 | 1.000 | 0.05 | 0.14 | 0.083 | 0.10 | 0.10 |
| 0.19 | 1.000 | 0.15 | 0.14 | 1.000 | 0.20 | 0.18 |
| 0.51 | 1.000 | 0.40 | 0.51 | 0.392 | 0.40 | 0.47 |
| 0.15 | 1.000 | 0.40 | 0.43 | 1.000 | 0.20 | 0.18 |

| | | | | | | |
|------|-------|------|------|-------|------|------|
| 0.19 | 1.000 | 0.30 | 0.33 | 1.000 | 0.10 | 0.10 |
| 0.15 | 1.000 | 0.10 | 0.18 | 0.201 | 0.15 | 0.30 |
| 0.46 | 0.386 | 0.40 | 0.38 | 1.000 | 0.25 | 0.36 |
| - | - | - | - | - | - | - |
| 0.10 | 1.000 | - | - | - | - | - |
| 0.15 | 0.096 | 0.15 | 0.14 | 1.000 | 0.10 | 0.10 |
| 0.15 | 1.000 | 0.25 | 0.22 | 1.000 | 0.15 | 0.14 |
| 0.51 | 0.351 | 0.35 | 0.48 | 0.351 | 0.35 | 0.41 |
| 0.27 | 1.000 | 0.25 | 0.22 | 1.000 | 0.15 | 0.14 |
| 0.23 | 1.000 | 0.60 | 0.43 | 0.120 | 0.45 | 0.36 |
| 0.23 | 0.248 | 0.25 | 0.22 | 1.000 | 0.20 | 0.18 |
| 0.34 | 0.531 | 0.40 | 0.33 | 0.524 | 0.25 | 0.22 |
| 0.50 | 1.000 | 0.65 | 0.48 | 0.168 | 0.40 | 0.47 |
| 0.05 | 1.000 | 0.10 | 0.10 | 1.000 | - | - |
| 0.31 | 0.516 | 0.30 | 0.26 | 1.000 | 0.25 | 0.22 |
| 0.19 | 0.170 | 0.15 | 0.22 | 0.262 | 0.20 | 0.26 |
| 0.10 | 1.000 | 0.20 | 0.18 | 1.000 | 0.30 | 0.26 |

For Peer Review Only

NUUK-4

N = 20

QAQO-1

N = 20

| P | Ho | He | P | Ho | He | P |
|----------|-----------|-----------|----------|-----------|-----------|----------|
| 0.35 | 0.26 | 1.00 | 0.000* | 0.10 | 0.18 | 0.159 |
| 1.00 | 0.75 | 0.52 | 0.023 | 0.15 | 0.14 | 1.000 |
| 0.78 | 0.90 | 0.75 | 0.603 | 0.65 | 0.72 | 0.223 |
| 0.19 | 0.58 | 0.57 | 0.408 | 0.45 | 0.53 | 0.335 |
| 1.00 | 0.45 | 0.45 | 1.000 | 0.30 | 0.33 | 1.000 |
| - | 0.15 | 0.14 | 1.000 | - | - | - |
| - | 0.10 | 0.10 | 1.000 | - | - | - |
| - | 0.10 | 0.10 | 1.000 | - | - | - |
| 0.67 | 0.45 | 0.48 | 1.000 | 0.20 | 0.18 | 1.000 |
| 0.66 | 0.35 | 0.30 | 1.000 | 0.45 | 0.48 | 1.000 |
| 1.00 | 0.20 | 0.18 | 1.000 | - | - | - |
| 0.08 | 0.40 | 0.33 | 0.538 | 0.50 | 0.51 | 1.000 |
| 0.17 | 0.35 | 0.36 | 1.000 | 0.20 | 0.38 | 0.083 |
| 1.00 | 0.25 | 0.22 | 1.000 | - | - | - |
| 0.07 | 0.35 | 0.45 | 0.377 | 0.35 | 0.30 | 1.000 |
| 0.08 | 0.45 | 0.45 | 1.000 | 0.30 | 0.33 | 1.000 |
| - | - | - | - | - | - | - |
| 0.17 | 0.30 | 0.33 | 1.000 | - | - | - |
| 0.61 | 0.30 | 0.43 | 0.281 | 0.05 | 0.05 | 1.000 |
| 1.00 | 0.40 | 0.38 | 1.000 | 0.30 | 0.38 | 0.519 |
| 1.00 | 0.25 | 0.22 | 1.000 | 0.05 | 0.05 | 1.000 |
| 0.15 | 0.75 | 0.51 | 0.070 | 0.45 | 0.48 | 1.000 |
| 1.00 | 0.10 | 0.18 | 0.142 | - | - | - |
| 0.54 | 0.45 | 0.45 | 1.000 | - | - | - |
| 1.00 | 0.30 | 0.43 | 0.307 | 0.40 | 0.51 | 0.413 |
| 1.00 | 0.30 | 0.33 | 1.000 | - | - | - |
| 1.00 | 0.15 | 0.14 | 1.000 | 0.55 | 0.50 | 1.000 |
| 1.00 | 0.45 | 0.48 | 1.000 | 0.15 | 0.14 | 1.000 |
| 1.00 | 0.60 | 0.51 | 0.653 | 0.25 | 0.22 | 1.000 |
| 1.00 | 0.10 | 0.10 | 1.000 | - | - | - |
| 0.36 | 0.25 | 0.50 | 0.043 | - | - | - |
| 1.00 | 0.10 | 0.10 | 1.000 | - | - | - |
| 0.62 | 0.65 | 0.50 | 0.346 | 0.10 | 0.10 | 1.000 |
| 1.00 | 0.20 | 0.18 | 1.000 | 0.05 | 0.05 | 1.000 |
| 0.66 | 0.55 | 0.48 | 0.631 | 0.35 | 0.51 | 0.210 |
| 1.00 | - | - | - | 0.25 | 0.22 | 1.000 |
| 1.00 | 0.05 | 0.05 | 1.000 | 0.15 | 0.14 | 1.000 |
| 1.00 | 0.15 | 0.14 | 1.000 | 0.30 | 0.38 | 0.533 |
| 0.63 | 0.35 | 0.36 | 1.000 | 0.21 | 0.19 | 1.000 |
| 1.00 | 0.25 | 0.22 | 1.000 | 0.35 | 0.36 | 1.000 |

| | | | | | | |
|------|------|------|-------|------|------|-------|
| 1.00 | 0.25 | 0.30 | 0.460 | - | - | - |
| 0.07 | 0.35 | 0.30 | 1.000 | - | - | - |
| 0.23 | 0.40 | 0.33 | 0.565 | 0.55 | 0.48 | 0.691 |
| - | 0.35 | 0.36 | 1.000 | - | - | - |
| - | 0.15 | 0.14 | 1.000 | - | - | - |
| 1.00 | 0.40 | 0.33 | 0.536 | 0.05 | 0.14 | 0.062 |
| 1.00 | 0.25 | 0.36 | 0.250 | - | - | - |
| 0.59 | 0.45 | 0.48 | 1.000 | 0.55 | 0.51 | 1.000 |
| 1.00 | 0.15 | 0.22 | 0.246 | 0.15 | 0.14 | 1.000 |
| 0.53 | 0.45 | 0.41 | 1.000 | 0.30 | 0.38 | 0.527 |
| 1.00 | 0.20 | 0.18 | 1.000 | - | - | - |
| 1.00 | 0.50 | 0.38 | 0.318 | - | - | - |
| 0.62 | 0.40 | 0.51 | 0.395 | 0.05 | 0.05 | 1.000 |
| - | 0.20 | 0.18 | 1.000 | - | - | - |
| 1.00 | 0.25 | 0.30 | 0.467 | - | - | - |
| 0.34 | 0.20 | 0.26 | 0.373 | 0.15 | 0.22 | 0.281 |
| 1.00 | 0.20 | 0.26 | 0.331 | 0.50 | 0.49 | 1.000 |

QAQO-2

N = 20

SCOR-1

N = 20

| Ho | He | P | Ho | He | P |
|-----------|-----------|----------|-----------|-----------|----------|
| 0.50 | 0.44 | 1.000 | 0.20 | 0.27 | 0.370 |
| 0.05 | 0.05 | 1.000 | - | - | - |
| 0.84 | 0.88 | 0.443 | 0.70 | 0.86 | 0.141 |
| 0.26 | 0.28 | 0.217 | 0.16 | 0.24 | 0.319 |
| 0.35 | 0.30 | 1.000 | 0.40 | 0.43 | 1.000 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.40 | 0.33 | 0.529 | - | - | - |
| 0.45 | 0.48 | 1.000 | 0.60 | 0.51 | 0.653 |
| - | - | - | - | - | - |
| 0.45 | 0.50 | 0.678 | 0.10 | 0.10 | 1.000 |
| 0.40 | 0.47 | 0.656 | 0.05 | 0.05 | 1.000 |
| 0.10 | 0.10 | 1.000 | - | - | - |
| 0.10 | 0.10 | 1.000 | - | - | - |
| 0.25 | 0.30 | 0.455 | 0.35 | 0.48 | 0.346 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.15 | 0.30 | 0.065 | 0.20 | 0.26 | 0.342 |
| 0.25 | 0.22 | 1.000 | 0.05 | 0.05 | 1.000 |
| - | - | - | - | - | - |
| 0.60 | 0.51 | 0.629 | 0.55 | 0.50 | 1.000 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.55 | 0.51 | 1.000 | 0.10 | 0.10 | 1.000 |
| 0.25 | 0.22 | 1.000 | - | - | - |
| 0.10 | 0.18 | 0.105 | - | - | - |
| - | - | - | - | - | - |
| 0.10 | 0.18 | 0.157 | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.25 | 0.30 | 0.513 | 0.60 | 0.51 | 0.690 |
| - | - | - | - | - | - |
| 0.35 | 0.45 | 0.345 | - | - | - |
| - | - | - | 0.15 | 0.14 | 1.000 |
| 0.30 | 0.38 | 0.575 | - | - | - |
| 0.10 | 0.10 | 1.000 | 0.10 | 0.10 | 1.000 |
| 0.30 | 0.38 | 0.546 | 0.25 | 0.51 | 0.021 |
| 0.25 | 0.22 | 1.000 | - | - | - |

| | | | | | |
|------|------|-------|------|------|-------|
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.30 | 0.26 | 1.000 | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | 0.25 | 0.22 | 1.000 |
| - | - | - | - | - | - |
| 0.20 | 0.18 | 1.000 | - | - | - |
| 0.15 | 0.14 | 1.000 | - | - | - |
| 0.10 | 0.10 | 1.000 | 0.45 | 0.48 | 1.000 |
| 0.10 | 0.10 | 1.000 | - | - | - |
| 0.05 | 0.05 | 1.000 | - | - | - |
| 0.30 | 0.49 | 0.152 | - | - | - |
| 0.05 | 0.05 | 1.000 | - | - | - |
| 0.05 | 0.14 | 0.078 | - | - | - |
| 0.10 | 0.10 | 1.000 | - | - | - |
| 0.30 | 0.26 | 1.000 | 0.25 | 0.22 | 1.000 |

Preprint
Peer Review Only

ICEL-1
N = 20**NORW-1**
N = 16

| Ho | He | P | Ho | He | P |
|-----------|-----------|----------|-----------|-----------|----------|
| 0.65 | 0.67 | 0.683 | 0.27 | 0.42 | 0.300 |
| 0.30 | 0.26 | 1.000 | 0.06 | 0.06 | 1.000 |
| 0.90 | 0.81 | 0.151 | 0.80 | 0.80 | 0.798 |
| 0.50 | 0.49 | 1.000 | 0.25 | 0.44 | 0.088 |
| 0.25 | 0.36 | 0.211 | 0.13 | 0.39 | 0.014 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.20 | 0.18 | 1.000 | - | - | - |
| - | - | - | - | - | - |
| 0.35 | 0.30 | 1.000 | 0.56 | 0.42 | 0.257 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.75 | 0.50 | 0.063 | 0.38 | 0.44 | 0.588 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | 0.00 | 0.23 | 0.002 |
| 0.10 | 0.10 | 1.000 | - | - | - |
| - | - | - | - | - | - |
| 0.50 | 0.43 | 0.589 | 0.31 | 0.42 | 0.530 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.40 | 0.51 | 0.457 | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.20 | 0.26 | 0.390 | 0.25 | 0.23 | 1.000 |
| - | - | - | - | - | - |
| 0.20 | 0.18 | 1.000 | 0.06 | 0.18 | 0.067 |
| - | - | - | 0.31 | 0.35 | 1.000 |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.65 | 0.51 | 0.395 | 0.38 | 0.51 | 0.354 |
| - | - | - | - | - | - |

| | | | | | |
|------|------|-------|------|------|-------|
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| 0.05 | 0.05 | 1.000 | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | 0.38 | 0.31 | 1.000 |
| - | - | - | - | - | - |
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| - | - | - | - | - | - |
| - | - | - | - | - | - |
| - | - | - | 0.38 | 0.31 | 1.000 |
| 0.30 | 0.43 | 0.280 | - | - | - |

For Peer Review Only