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

Rikke P.A. Madsen[1], Magnus W. Jacobsen[1$], Kathleen G. O'Malley[2], Rasmus Nygaard[3], Kim Præbel[4], Bjarni Jónsson[5], Jose M. Pujolar[1€], Dylan J. Fraser[6], Louis Bernatchez[7], Michael M. Hansen[1§]

[1]Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark
[2]Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97356 U.S.A.
[3]Greenland Institute of Natural Resources, Kivioq 2, P.O. Box 570, 3900 Nuuk, Greenland
[4]Norwegian College of Fishery Science, UiT the Arctic University of Norway, N-9032 Tromsø, Norway
[5]North West Iceland Nature Center, Adalgata 2, 550 Sudárkrókur, Iceland

[6]Department of Biology, Concordia University, Montreal, Québec, Canada
[7]IBIS (Institut de Biologie Intégrative et des Systèmes), Université Laval, Québec, Canada

[$]Present address: National Institute of Aquatic Resources, Technical University of Denmark, Vejlsøvej 39, DK-8600 Silkeborg, Denmark
[€]Present address: University of Copenhagen, National History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen, Denmark

[§]Corresponding author, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark, e-mail mmh@bios.au.dk

Running Head: Phenology-related loci in Arctic char

Abstract

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

Key Words: Arctic char, climate change, clock gene, phenology, sea surface temperature, spatial autocorrelation

Introduction

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

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

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

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

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

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

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

Materials and Methods

Samples

Adipose fin clips were collected from 2005-2016 by angling, net fishing and electrofishing. We aimed for sample sizes of twenty, as higher sample sizes generally do not improve estimates of standard population genetic statistics as compared to increasing number of loci (Takezaki and Nei 1996). Among the 18 populations included in the study, 15 were anadromous populations located along the West coast of Greenland. Three additional populations represented anadromous char from Eastern Greenland and two landlocked lake populations from Iceland and Norway (see Fig. 1 and Table 1). Collection and handling of samples in Greenland took place according to survey licenses 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, Crytochrome2b.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 H_2O 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

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

Genetic population structure

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

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

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

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

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

Sea surface temperature data

Remotely sensed sea surface temperature data (in the following denoted SST), encompassing a resolution of 0.25 degree latitude x 0.25 degree longitude on a global grid and measured for each day were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Website at http://www.esrl.noaa.gov/psd/. Data from 1984, 1994, 2004 and 2014 were used, hence covering temperatures for a time span of 40 years. Data for each day of the year from the position closest to the sampled river/lake mouths inhabited by anadromous char (hence excluding the resident populations ICEL-1 and NORW-1) were retrieved using the function extractOISSTdaily from the R 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 period was calculated. As anadromous char experience osmotic stress at 1°C (Finstad et al. 1989), SST < 2°C was tentatively defined as unfavorable to char in the sea. For each locality the time period (in the following denoted SST window) was estimated during which SST was ≥ 2°C. The

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

Selection tests

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

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

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

Results

Mendelian inheritance of phenology-related genes

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

Summary statistics and genetic population structure

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

Overall genetic differentiation (F_{ST}) across all populations and over all SNPs was 0.27 ($p < 0.001$). The hierarchical AMOVA involving only Western Greenland populations showed that the largest part of differentiation was distributed among geographic groups of populations ($F_{CT} = 0.11$, $p < 0.001$), whereas a relatively smaller part was distributed among populations within geographic groups ($F_{SC} = 0.09$, $p < 0.001$). Genetic differentiation at phenology-related loci was similar, with overall $F_{ST} = 0.23$ ($p < 0.001$) across all populations. For the hierarchical AMOVA F_{CT} was 0.10 ($p < 0.001$) and F_{SC} was 0.06 ($p < 0.001$). F_{ST} between pairs of populations for the SNP dataset ranged 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

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

Selection tests

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

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

The above outlier tests only consider allele frequencies, whereas functional variation at *OtsClock1b* consists of the number of polyQ repeats, that is, the length of alleles. At the scale of all populations (landlocked and anadromous) there was no significant association between mean allele length at *OtsClock1b* and latitude (Table 2; Supporting Information Fig. S3.a), and this was also the case at the scale of all anadromous populations from Greenland and at the scale of anadromous populations from Western Greenland, i.e. omitting the population SCOR-1 from Eastern Greenland (see Table 2). Across all anadromous populations from Greenland, there was also no significant association between mean allele length and both SST-window start date, end date, or duration (Table 2, Supporting Information Fig. S3.b-d). At the scale of anadromous populations from Western Greenland there was, however, a positive association between mean allele length and both SST-window start date or duration (Table 2 and Supporting Information Fig. S3.e-f), though we note that SST-window start date and duration were strongly correlated and hence cannot be considered independent ($y = -0.567x + 229.738$, $R^2_{adjusted} = 0.762$, $p = 1.38x10^{-5}$).

Discussion

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

Genetic population structure

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

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

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

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

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

Variation at phenology-related loci

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

The outlier tests applied (Beaumont and Nichols 1996; de Villemereuil et al. 2015; Excoffier et al. 2009) suggested only one of the SNPs (Contig10740_78) to be a consistent high differentiation outlier, and none of the phenology-related candidate loci were indicated to be under divergent selection. It is possible that the choice of bi-allelic SNPs as supposedly neutral baseline loci was suboptimal, as two of the phenology-related loci showed twenty-four (*Ots515NWFSC*) and seven (*Cryptochrome2b.2*) alleles, respectively. On the other hand, *Cryptochrome3* and *OtsClock1b* each showed only four alleles and overall low heterozygosity within populations. Hence, using 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

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

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

Conclusions

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

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

Conflict of Interest Statement

The authors declare no conflict of interest.

Data Availability Statement

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

References

Allendorf, F.W., Bassham, S., Cresko, W.A., Limborg, M.T., Seeb, L.W. & Seeb, J.E. 2015. Effects of crossovers between homeologs on inheritance and population genomics in polyploid-derived salmonid fishes. *Journal of Heredity* 106: 217-227.

Allendorf, F.W. & Thorgaard, G.H. 1984. Tetraploidy and the evolution of salmonid fishes. In: Turner, B.J., ed. *Evolutionary Genetics of Fishes*. New York: Plenum Press, pp. 55-93.

Bazzi, G., Cecere, J.G., Caprioli, M., Gatti, E., Gianfranceschi, L., Podofillini, S., Possenti, C.D., Ambrosini, R., Saino, N., Spina, F. & Rubolini, D. 2016. Clock gene polymorphism, migratory behaviour and geographic distribution: a comparative study of trans-Saharan migratory birds. *Molecular Ecology* 25: 6077-6091.

Beaumont, M.A. & Nichols, R.A. 1996. Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 263: 1619-1626.

Bernatchez, L. 2016. On the maintenance of genetic variation and adaptation to environmental change: considerations from population genomics in fishes. *Journal of Fish Biology* 89: 2519-2556.

Bernatchez, L., Dempson, J.B. & Martin, S. 1998. Microsatellite gene diversity analysis in anadromous arctic char, *Salvelinus alpinus*, from Labrador, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1264-1272.

Bradbury, I.R., Hubert, S., Higgins, B., Borza, T., Bowman, S., Paterson, I.G., Snelgrove, P.V.R., Morris, C.J. & Gregory, R.S. 2010. Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 277: 3725-3734.

576 Bradshaw, W.E. & Holzapfel, C.M. 2006. Climate change - Evolutionary response to
577 rapid climate change. *Science* 312: 1477-1478.

578 Bradshaw, W.E. & Holzapfel, C.M. 2008. Genetic response to rapid climate change:
579 it's seasonal timing that matters. *Molecular Ecology* 17: 157-166.

580 Brunner, P.C., Douglas, M.R., Osinov, A., Wilson, C.C. & Bernatchez, L. 2001.
581 Holarctic phylogeography of Arctic charr (*Salvelinus alpinus* L.) inferred from
582 mitochondrial DNA sequences. *Evolution* 55: 573-586.

583 Cappelen, J. & Vinther, B.M. 2014. SW Greenland temperature data 1784-2013.
584 *Technical Report from the Danish Meteorological Institute 14-06* No. 06. Copenhagen,
585 Denmark. Retrieved from http://www.dmi.dk/fileadmin/Rapporter/TR/tr14-06.pdf.

586 Christensen, C., Jacobsen, M.W., Nygaard, R. & Hansen, M.M. 2018. Spatiotemporal
587 genetic structure of anadromous Arctic char (*Salvelinus alpinus*) populations in a
588 region experiencing pronounced climate change. *Conservation Genetics* 19: 687-700.

589 Crozier, L.G. & Hutchings, J.A. 2014. Plastic and evolutionary responses to climate
590 change in fish. *Evolutionary Applications* 7: 68-87.

591 Darlington, T.K., Wager-Smith, K., Ceriani, M.F., Staknis, D., Gekakis, N., Steeves,
592 T.D.L., Weitz, C.J., Takahashi, J.S. & Kay, S.A. 1998. Closing the circadian loop:
593 CLOCK-induced transcription of its own inhibitors per and tim. *Science* 280: 1599-
594 1603.

595 de Villemereuil, P., Gaggiotti, O.E. & O'Hara, R.B. 2015. A new FST-based method to
596 uncover local adaptation using environmental variables. *Methods in Ecology and*
597 *Evolution* 6: 1248-1258.

598 Dor, R., Cooper, C.B., Lovette, I.J., Massoni, V., Bulit, F., Liljesthrom, M. &
599 Winkler, D.W. 2012. Clock gene variation in *Tachycineta* swallows. *Ecology and*
600 *Evolution* 2: 95-105.

601 Dutil, J.D. 1986. Energetic constraints and spawning interval in the anadromous
602 Arctic Charr (*Salvelinus alpinus*). *Copeia*: 945-955.

603 Excoffier, L., Guillaume, L. & Schneider, S. 2005. Arlequin (version 3.0): An
604 integrated software package for population genetics data analysis. *Evolutionary*
605 *Bioinformatics Online*: 47-50.

606 Excoffier, L., Hofer, T. & Foll, M. 2009. Detecting loci under selection in a
607 hierarchically structured population. *Heredity* 103: 285-298.

608 Finstad, B., Nilssen, K.J. & Arnesen, A.M. 1989. Seasonal changes in sea water
609 tolerance of Arctic charr (*Salvelinus alpinus*). *Journal of Comparative Physiology B-*
610 *Biochemical Systemic and Environmental Physiology* 159: 371-378.

Foll, M. & Gaggiotti, O. 2008. A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* 180: 977-993.

Gonzalez, A., Ronce, O., Ferriere, R. & Hochberg, M.E. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368: 20120404.

Goudet, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. *Journal of Heredity* 86: 485-486.

Hansen, M.M., Waller, D.M., Olivieri, I., Nielsen, E.E. & The Genetic Monitoring Group. 2012. Monitoring adaptive genetic responses to environmental change. *Molecular Ecology* 21: 1311-1329.

Harris, L.N., Moore, J.-S., Galpern, P., Tallman, R.F. & Taylor, E.B. 2013. Geographic influences on fine-scale, hierarchical population structure in northern Canadian populations of anadromous Arctic Char (Salvelinus alpinus). *Environmental Biology of Fishes* 97: 1233-1252.

Harris, L.N., Moore, J.S., Bajno, R. & Tallman, R.F. 2016. Genetic stock structure of anadromous Arctic char in Canada's Central Arctic: Potential implications for the management of Canada's largest Arctic char commercial fishery. *North American Journal of Fisheries Management* 36: 1473-1488.

Harrisson, K.A., Amish, S.J., Pavlova, A., Narum, S.R., Telonis-Scott, M., Rourke, M.L., Lyon, J., Tonkin, Z., Gilligan, D.M., Ingram, B.A., Lintermans, M., Gan, H.M., Austin, C.M., Luikart, G. & Sunnucks, P. 2017. Signatures of polygenic adaptation associated with climate across the range of a threatened fish species with high genetic connectivity. *Molecular Ecology* 26: 6253-6269.

Hayasaka, N., LaRue, S.I. & Green, C.B. 2002. In vivo disruption of Xenopus CLOCK in the retinal photoreceptor cells abolishes circadian melatonin rhythmicity without affecting its production levels. *Journal of Neuroscience* 22: 1600-1607.

Hoffmann, A.A. & Sgro, C.M. 2011. Climate change and evolutionary adaptation. *Nature* 470: 479-485.

Idda, M.L., Bertolucci, C., Vallone, D., Gothilf, Y., Sanchez-Vazquez, F.J. & Foulkes, N.S. 2012. Circadian clocks: Lessons from fish. *Neurobiology of Circadian Timing* 199: 41-57.

Jacobsen, M.W., Christensen, C., Madsen, R., Nygaard, R., Jonsson, B., Praebel, K. & Hansen, M.M. 2017. Single nucleotide polymorphism markers for analysis of historical and contemporary samples of Arctic char (*Salvelinus alpinus*). *Conservation Genetics Resources* 9: 587-589.

Jensen, A.J., Finstad, B., Fiske, P., Forseth, T., Rikardsen, A.H. & Ugedal, O. 2018. Relationship between marine growth and sea survival of two anadromous salmonid fish species. *Canadian Journal of Fisheries and Aquatic Sciences* 75: 621-628.

650 Jensen, J.L., Bohonak, A.J. & Kelley, S.T. 2005. Isolation by distance, web service.
651 *Bmc Genetics* 6: 13.

652 Jensen, L.F., Hansen, M.M., Pertoldi, C., Holdensgaard, G., Mensberg, K.-L.D. &
653 Loeschcke, V. 2008. Local adaptation in brown trout early life-history traits:
654 implications for climate change adaptability. *Proceedings of the Royal Society B:*
655 *Biological Sciences* 275: 2859.

656 Johnsen, A., Fidler, A., Kuhn, S., Carter, K., Hoffmann, A., Barr, I., Biard, C.,
657 Charmantier, A., Eens, M. & Korsten, P. 2007. Avian Clock gene polymorphism:
658 evidence for a latitudinal cline in allele frequencies. *Molecular Ecology* 16: 4867-
659 4880.

660 Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic
661 markers. *Bioinformatics* 24: 1403-1405.

662 Jombart, T., Devillard, S. & Balloux, F. 2010. Discriminant analysis of principal
663 components: a new method for the analysis of genetically structured populations. *Bmc*
664 *Genetics* 11: 94.

665 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton,
666 S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. &
667 Drummond, A. 2012. Geneious Basic: An integrated and extendable desktop software
668 platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647-
669 1649.

670 Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell,
671 M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta*
672 L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories.
673 *Ecology of Freshwater Fish* 12: 1-59.

674 Koskinen, M.T., Haugen, T.O. & Primmer, C.R. 2002. Contemporary fisherian life-
675 history evolution in small salmonid populations. *Nature* 419: 826-830.

676 Kovach, R.P., Gharrett, A.J. & Tallmon, D.A. 2012. Genetic change for earlier
677 migration timing in a pink salmon population. *Proceedings of the Royal Society B-*
678 *Biological Sciences* 279: 3870-3878.

679 Leder, E., Danzmann, R. & Ferguson, M. 2006. The candidate gene, Clock, localizes
680 to a strong spawning time quantitative trait locus region in rainbow trout. *Journal of*
681 *Heredity* 97: 74-80.

682 Leduc, M., Matthews, H.D. & de Elia, R. 2016. Regional estimates of the transient
683 climate response to cumulative CO2 emissions. *Nature Climate Change* 6: 474-+.

684 Lincoln, G.A., Andersson, H. & Loudon, A. 2003. Clock genes in calendar cells as the
685 basis of annual timekeeping in mammals – a unifying hypothesis. *Journal of*
686 *Endocrinology* 179: 1-13.

687 Lloyd, J.M., Kuijpers, A., Long, A., Moros, M. & Park, L.A. 2007. Foraminiferal
688 reconstruction of mid- to late-Holocene ocean circulation and climate variability in
689 Disko Bugt, West Greenland. *Holocene* 17: 1079-1091.

690 Lowrey, P.L. & Takahashi, J.S. 2004. Mammalian circadian biology: Elucidating
691 genome-wide levels of temporal organization. *Annual Review of Genomics and Human*
692 *Genetics* 5: 407-441.

693 Madsen, R.A.P., Jacobsen, M.W., O'Malley, K.G., Nygaard, R., Præbel, K., Jónsson,
694 B., Pujolar, J.M., Fraser, D.J., Bernatchez, L. & Hansen, M.M. 2019. Data from:
695 Genetic population structure and variation at phenology-related loci in anadromous
696 Arctic char (*Salvelinus alpinus*). doi:10.5061/dryad.sc30mr1.

697 Martinez, A.S., Willoughby, J.R. & Christie, M.R. 2018. Genetic diversity in fishes is
698 influenced by habitat type and life-history variation. *Ecology and Evolution* 8: in
699 press.

700 Merila, J. & Hendry, A.P. 2014. Climate change, adaptation, and phenotypic
701 plasticity: the problem and the evidence. *Evolutionary Applications* 7: 1-14.

702 Moore, J.S., Bajno, R., Reist, J.D. & Taylor, E.B. 2015. Post-glacial recolonization of
703 the North American Arctic by Arctic char (*Salvelinus alpinus*): genetic evidence
704 ofmultiple northern refugia and hybridization between glacial lineages. *Journal of*
705 *Biogeography* 42: 2089-2100.

706 Moore, J.S., Harris, L.N., Le Luyer, J., Sutherland, B.J.G., Rougemont, Q., Tallman,
707 R.F., Fisk, A.T. & Bernatchez, L. 2017. Genomics and telemetry suggest a role for
708 migration harshness in determining overwintering habitat choice, but not gene flow, in
709 anadromous Arctic Char. *Molecular Ecology* 26: 6784-6800.

710 Moore, J.S., Harris, L.N., Tallman, R.F. & Taylor, E.B. 2013. The interplay between
711 dispersal and gene flow in anadromous Arctic char (*Salvelinus alpinus*): implications
712 for potential for local adaptation. *Canadian Journal of Fisheries and Aquatic Sciences*
713 70: 1327-1338.

714 Naish, K.A. & Park, L.K. 2002. Linkage relationship for 35 new microsatellite loci in
715 chinook salmon *Oncorhynchus tshawytscha*. *Animal Genetics* 33: 312-327.

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

718 Narum, S.R., Campbell, N.R., Kozfkay, C.C. & Meyer, K.A. 2010. Adaptation of
719 redband trout in desert and montane environments. *Molecular Ecology* 19: 4622-4637.

720 O'Brien, C., Unruh, L., Zimmerman, C., Bradshaw, W.E., Holzapfel, C.M. & Cresko,
721 W.A. 2013. Geography of the circadian gene clock and photoperiodic response in
722 western North American populations of the three-spined stickleback *Gasterosteus*
723 *aculeatus*. *Journal of Fish Biology* 82: 827-839.

O'Malley, K.G. & Banks, M.A. 2008. A latitudinal cline in the Chinook salmon (Oncorhynchus tshawytscha) Clock gene: evidence for selection on PolyQ length variants. *Proceedings of the Royal Society B-Biological Sciences* 275: 2813-2821.

O'Malley, K.G., Camara, M.D. & Banks, M.A. 2007. Candidate loci reveal genetic differentiation between temporally divergent migratory runs of Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology* 16: 4930-4941.

O'Malley, K.G., Cross, T.F., Bailie, D., Carlsson, J., Coughlan, J.P., Dillane, E., Prodohl, P.A. & McGinnity, P. 2014. Circadian clock gene (OtsClock1b) variation and time of ocean return in Atlantic salmon *Salmo salar*. *Fisheries Management and Ecology* 21: 82-87.

O'Malley, K.G., Ford, M.J. & Hard, J.J. 2010a. Clock polymorphism in Pacific salmon: evidence for variable selection along a latitudinal gradient. *Proceedings of the Royal Society B-Biological Sciences* 277: 3703-3714.

O'Malley, K.G., Jacobson, D.P., Kurth, R., Dill, A.J. & Banks, M.A. 2013. Adaptive genetic markers discriminate migratory runs of Chinook salmon (*Oncorhynchus tshawytscha*) amid continued gene flow. *Evolutionary Applications* 6: 1184-1194.

O'Malley, K.G., McClelland, E.K. & Naish, K.A. 2010b. Clock genes localize to quantitative trait loci for stage-specific growth in juvenile coho salmon, *Oncorhynchus kisutch*. *Journal of Heredity* 101: 628-632.

O'Malley, K.G., Sakamoto, T., Danzmann, R.G. & Ferguson, M.M. 2003. Quantitative trait loci for spawning date and body weight in rainbow trout: Testing for conserved effects across ancestrally duplicated chromosomes. *Journal of Heredity* 94: 273-284.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637-669.

Peakall, R. & Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288-295.

Peakall, R. & Smouse, P.E. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* 28: 2537-2539.

Perrier, C., Ferchaud, A.L., Sirois, P., Thibault, I. & Bernatchez, L. 2017. Do genetic drift and accumulation of deleterious mutations preclude adaptation? Empirical investigation using RADseq in a northern lacustrine fish. *Molecular Ecology* 26: 6317-6335.

Pörtner, H.O. & Peck, M.A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* 77: 1745-1779.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rousset, F. 2008. GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources* 8: 103-106.

Santaquiteria, A., Svenning, M.A. & Praebel, K. 2016. Contrasting levels of strays and contemporary gene flow among anadromous populations of Arctic charr, Salvelinus alpinus (L.), in northern Norway. *Hydrobiologia* 783: 269-281.

Smouse, P.E. & Peakall, R. 1999. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity* 82: 561-573.

Sokal, R.R. & Oden, N.L. 1991. Spatial Autocorrelation Analysis as an Inferential Tool in Population-Genetics. *American Naturalist* 138: 518-521.

Sokal, R.R. & Wartenberg, D.E. 1983. A test of spatial autocorrelation analysis using an isolation-by-distance model. *Genetics* 105: 219-237.

Takezaki, N. & Nei, M. 1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics* 144: 389-399.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Hoye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J. & Wanless, S. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535: 241-245.

Wang, J.L. & Whitlock, M.C. 2003. Estimating effective population size and migration rates from genetic samples over space and time. *Genetics* 163: 429-446.

Ward, R.D., Woodwark, M. & Skibinski, D.O.F. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology* 44: 213-232.

Wedekind, C. & Muller, R. 2004. The experimental rearing of large salmonid eggs in Petri dishes. *Functional Ecology* 18: 138-140.

Wilson, A.J., Gislason, D., Skulason, S., Snorrason, S.S., Adams, C.E., Alexander, G., Danzmann, R.G. & Ferguson, M.M. 2004. Population genetic structure of Arctic Charr, *Salvelinus alpinus* from northwest Europe on large and small spatial scales. *Molecular Ecology* 13: 1129-1142.

Yeaman, S. & Otto, S.P. 2011. Establishment and maintenance of adaptive genetic divergence under migration, selection, and drift. *Evolution* 65: 2123-2129.

Acknowledgements

The authors thank Shenglin Liu, Rasmus Hedeholm, Lars Heilman, Anne-Laure Ferchaud and Nynne Hjort Nielsen for assistance with collecting samples, two

ananymous reviewers for comments and suggestions and The Danish Council for Independent Research, Natural Science for funding (grant no. 1323-00158A to Michael M. Hansen).

Authors' Contribution Statement

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

Figure legends

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

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

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

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

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

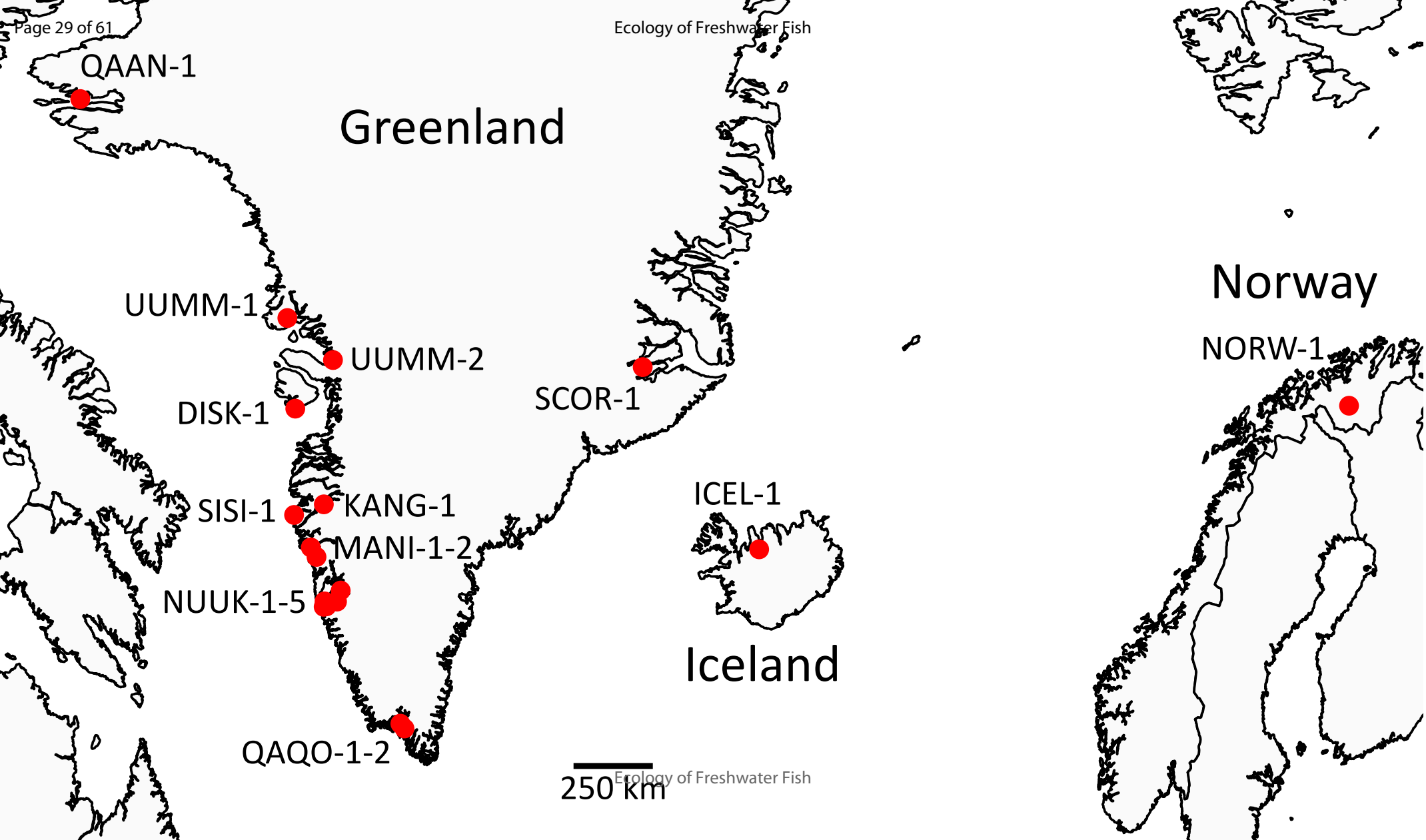
842 NUUK-3, NUUK-4 and NUUK-5 are geographically close, and these populations
843 therefore share the same SST window (Fig. 4.j).
844
845
846
847

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.

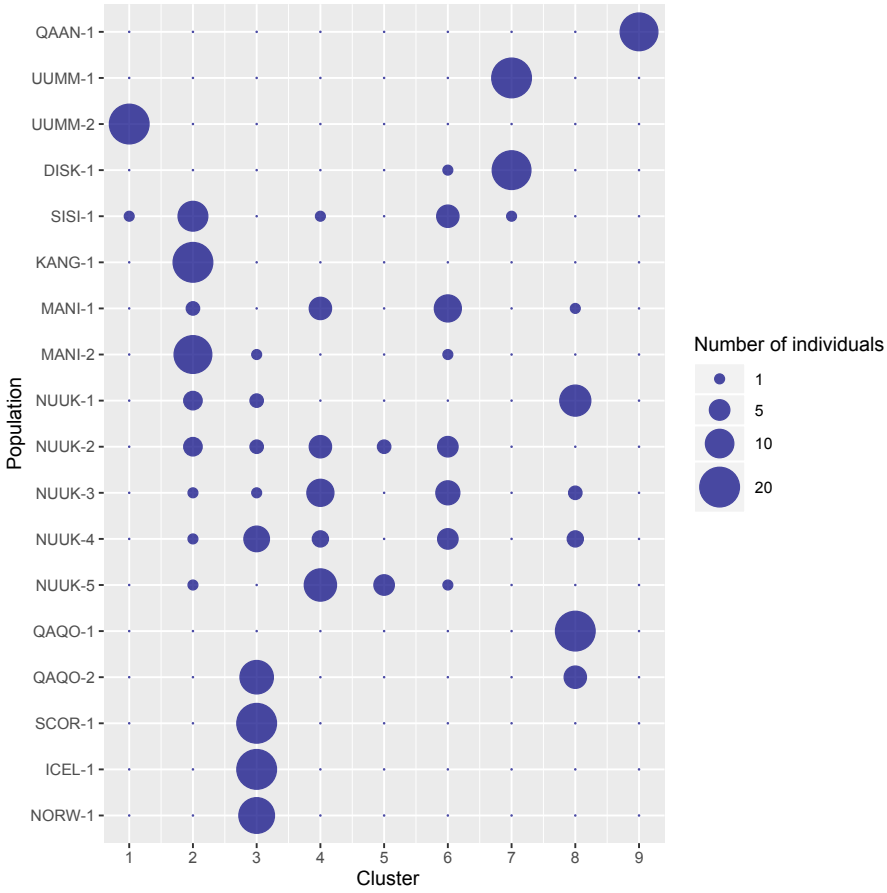
Sample code	Locality	Latitude	Longitude	Major geographic region	Year of sampling	Life history form	N	H_e (SNPs)	H_e (phenology-related)
QAAN-1	Qaanaaq	77.46° N	-69.23 W	Western Greenland	2012	Anadromous	18	0.11	0.18
UUMM-1	Umivik	71.66° N	-54.10 W	Western Greenland	2015	Anadromous	20	0.29	0.35
UUMM-2	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.

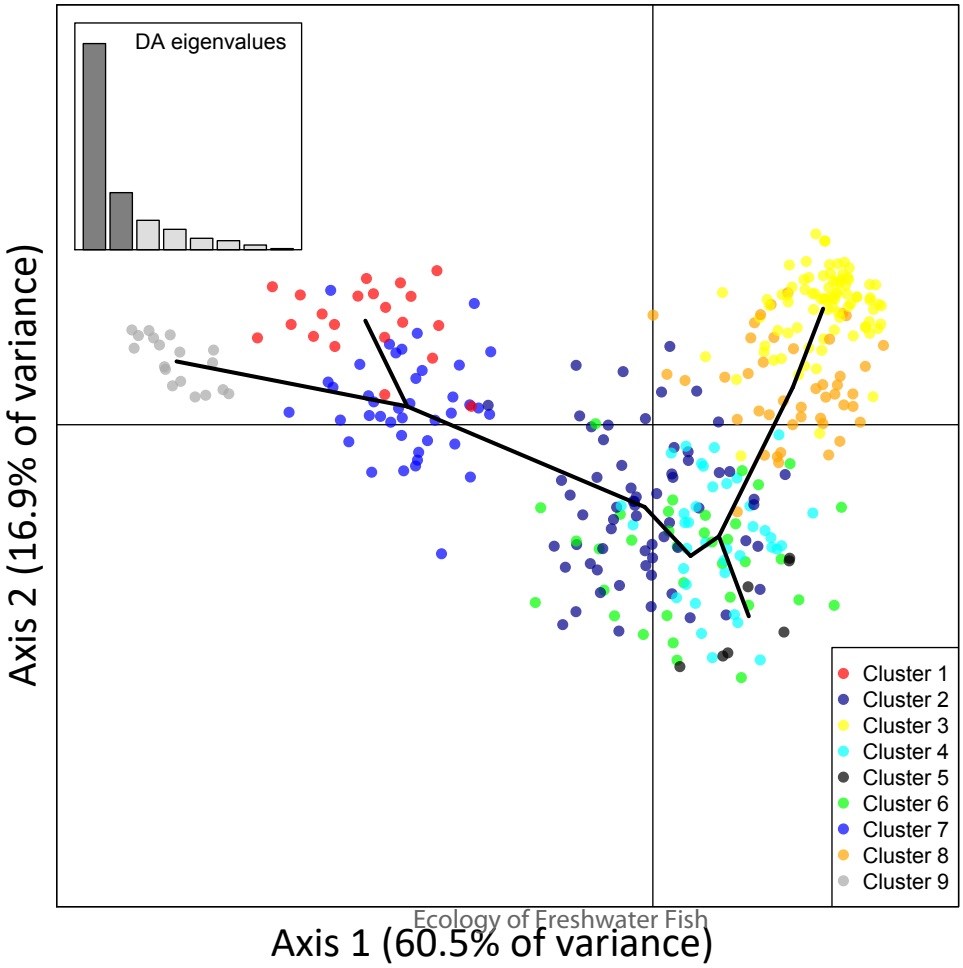
Parameter tested	Geographical scale	Result
Latitude	All populations	$y = 1.44x + 308.02$, $R^2_{adjusted} = 0.08$, $p = 0.129$
Latitude	Anadromous populations, Eastern and Western Greenland	$y = 1.38x + 311.32$, $R^2_{adjusted} = 0.06$, $p = 0.175$
Latitude	Anadromous populations, Western Greenland	$y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

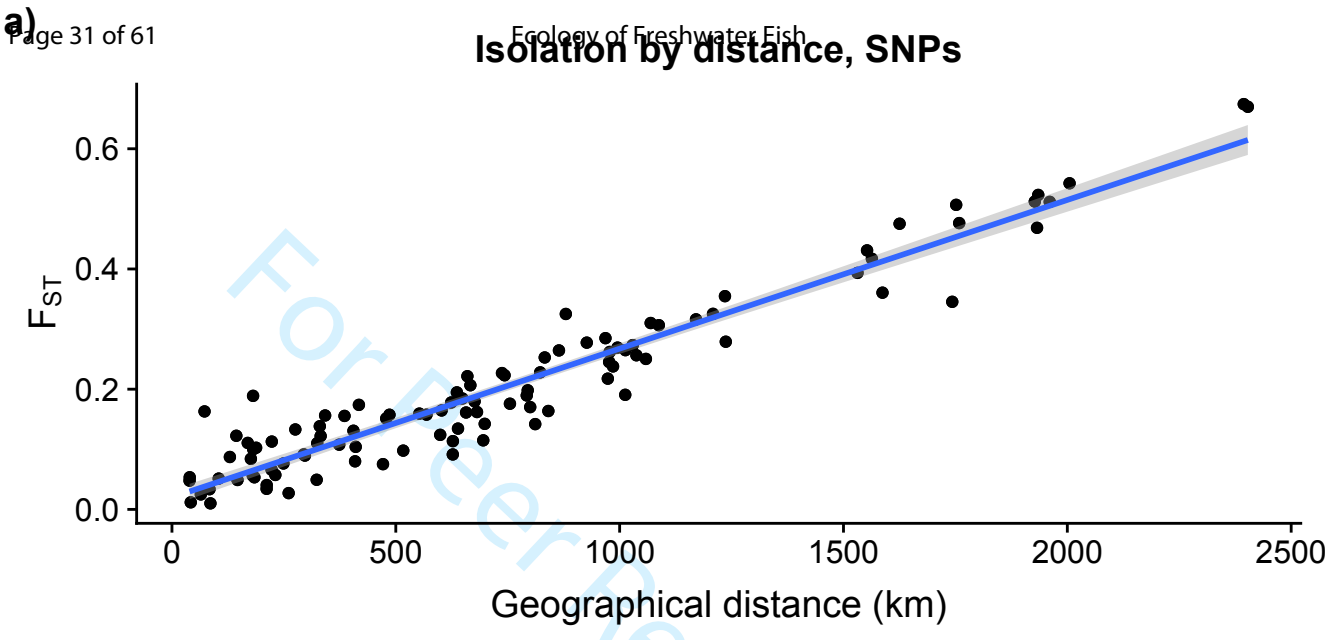

QAAN-1
Greenland
UUMM-1
UUMM-2
DISK-1
SCOR-1
SISI-1
KANG-1
MANI-1-2
NUUK-1-5
ICEL-1
Iceland
QAQO-1-2
250 km
Norway
NORW-1

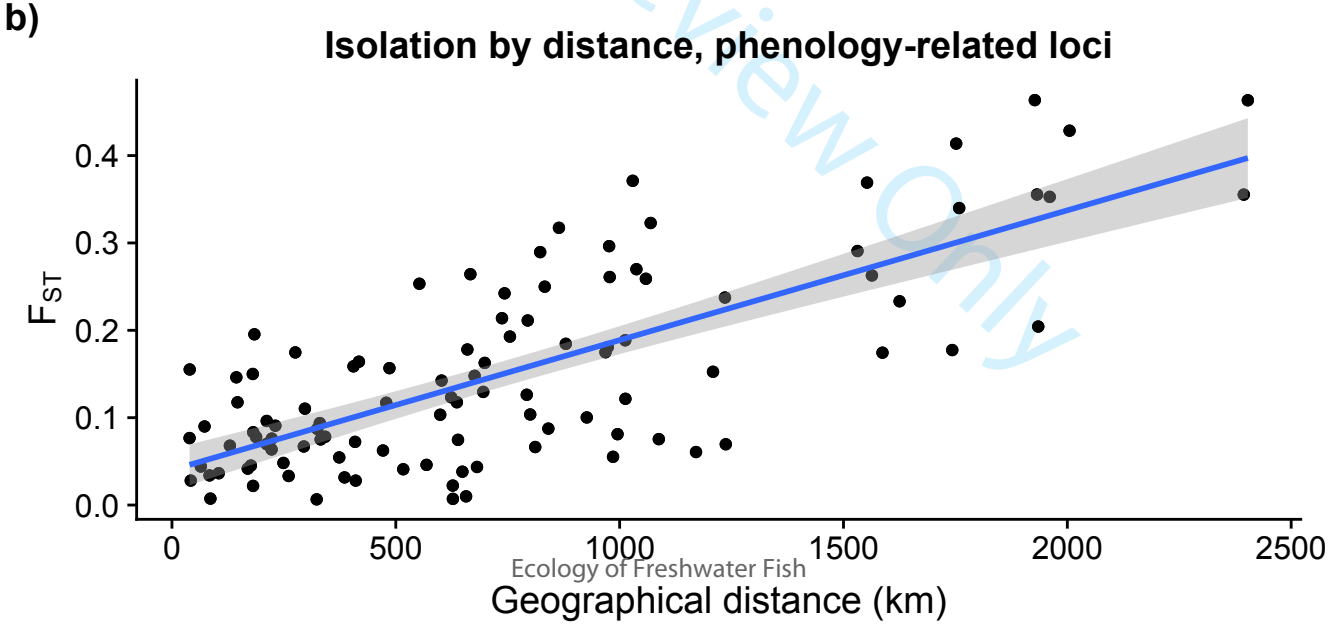
a)


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
Population
1 2 3 4 5 6 7 8 9
Cluster
Number of individuals
1
5
10
20

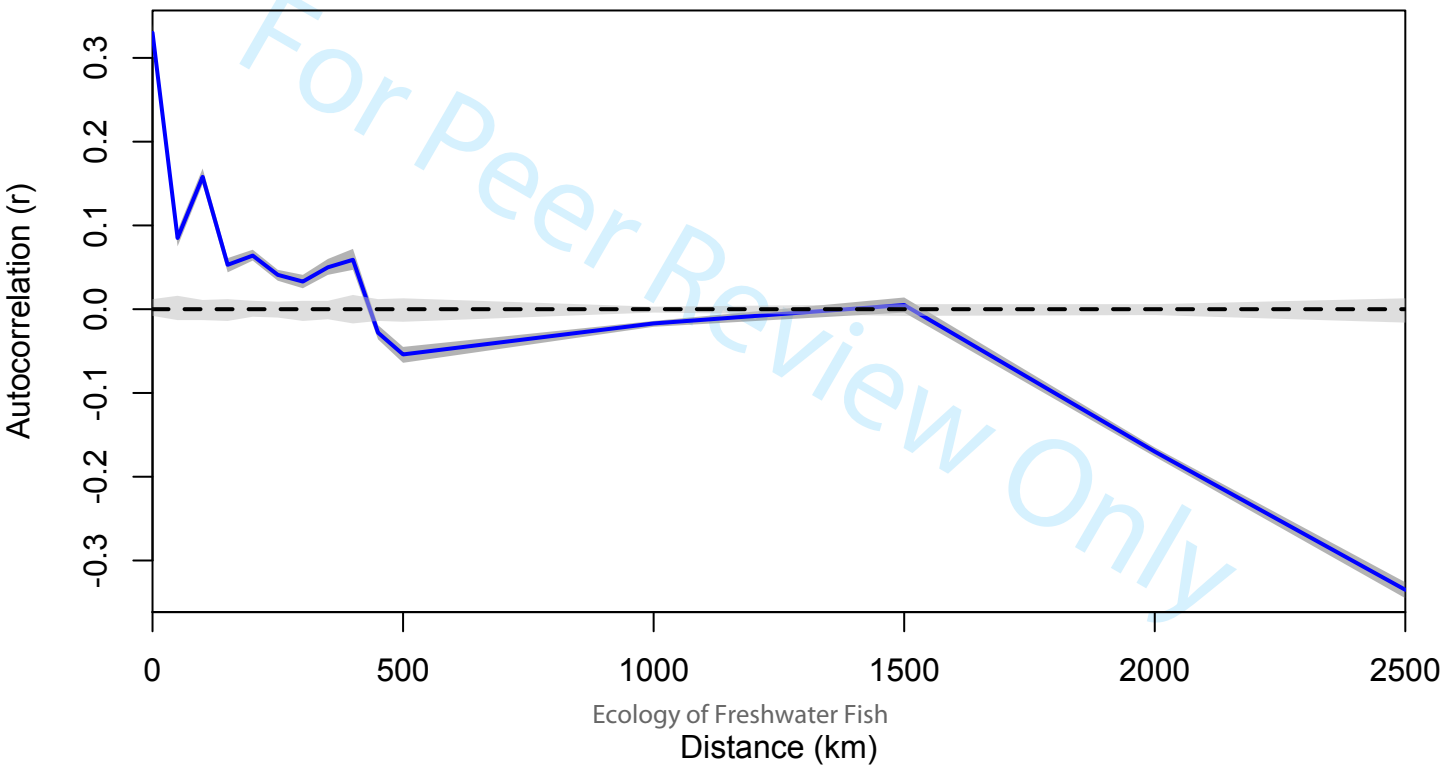
b)

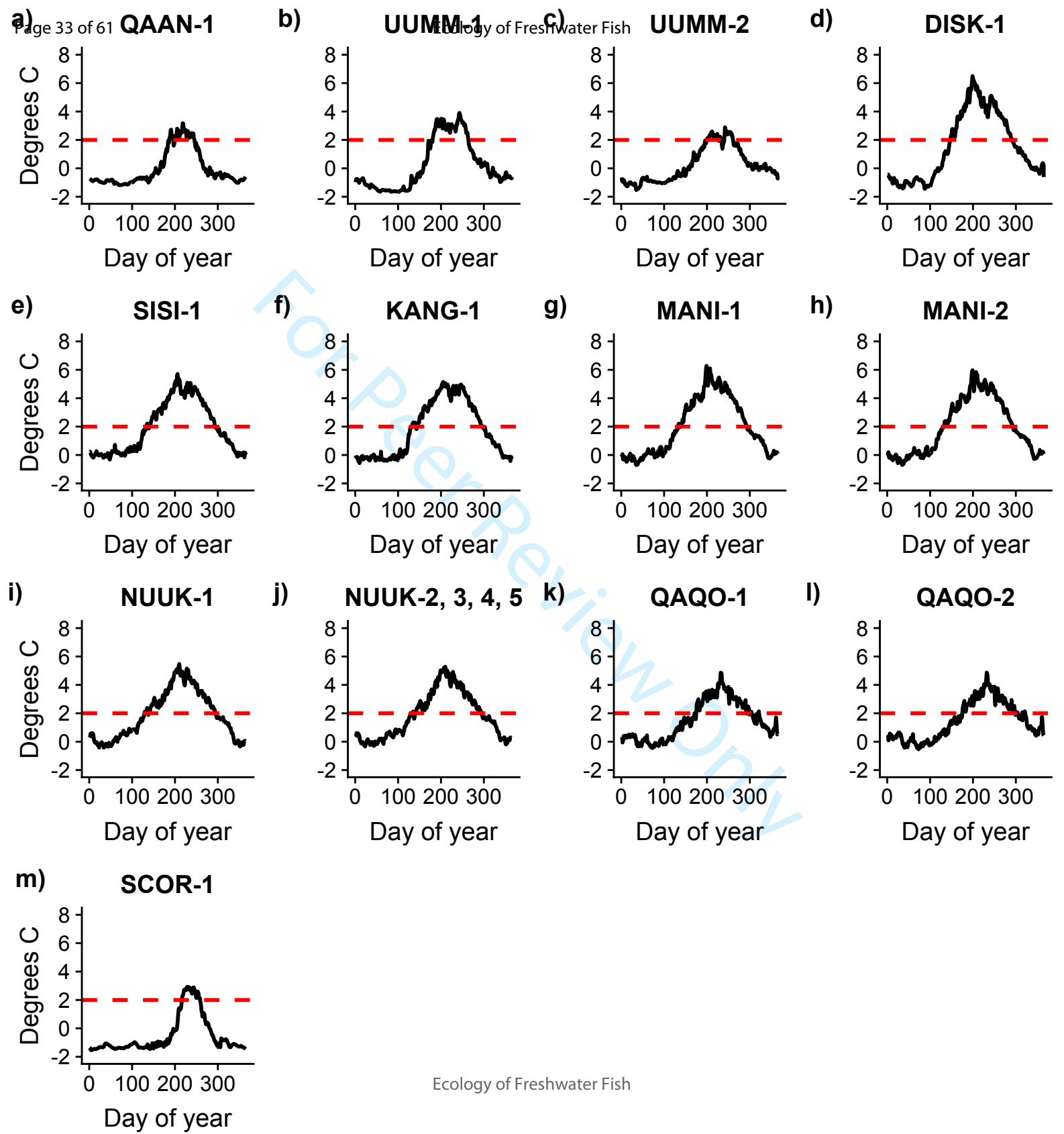

DA eigenvalues
Axis 2 (16.9% of variance)
Axis 1 (60.5% of variance)
Cluster 1
Cluster 2
Cluster 3
Cluster 4
Cluster 5
Cluster 6
Cluster 7
Cluster 8
Cluster 9





Spatial Autocorrelation





Supporting Information for

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

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.

	Family 1			Family 2		
Locus	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 *OtsClock1b*	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.

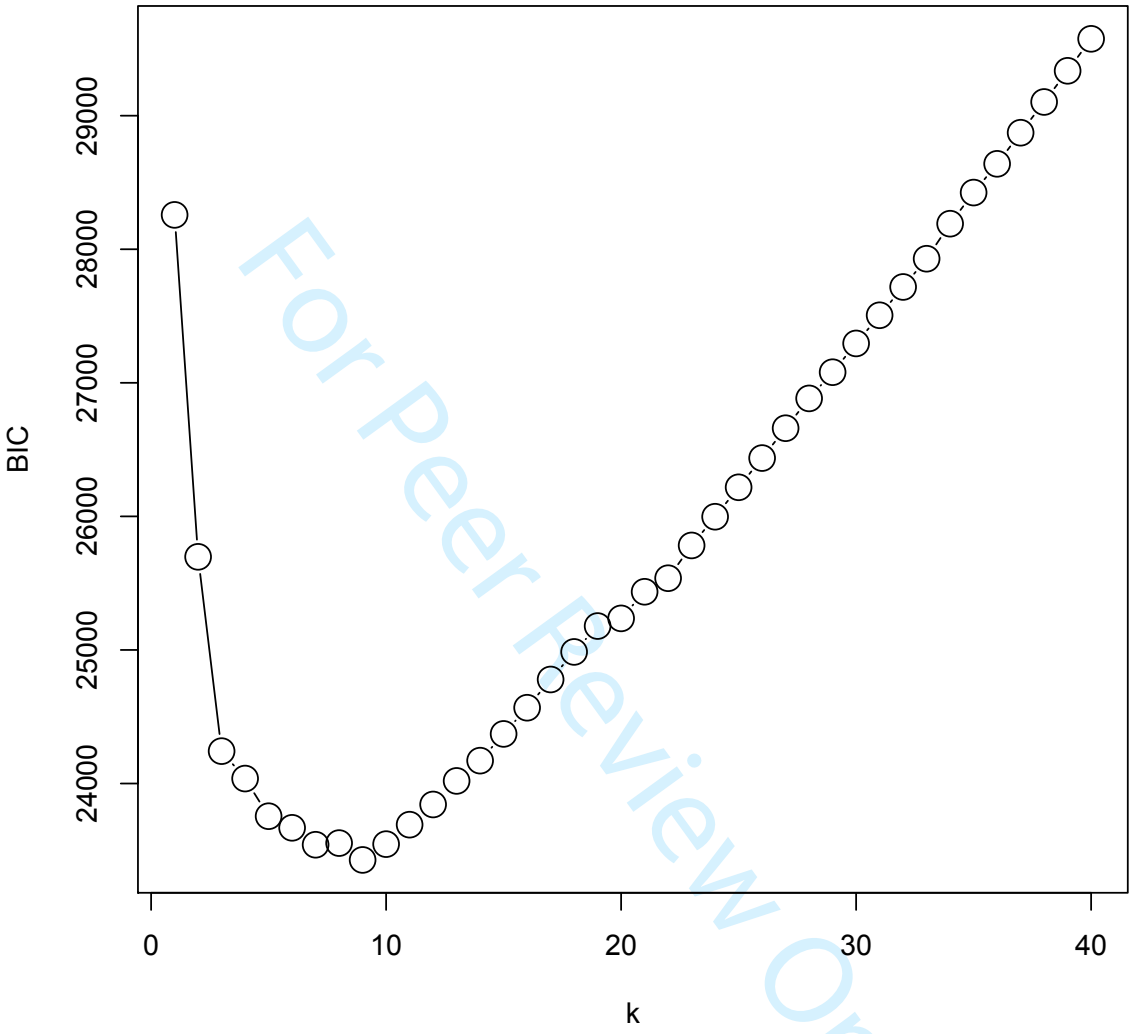


Fig. S2a. Results of F_{ST}-based outlier test (Beaumont & Nichols, 1996) involving all populations.

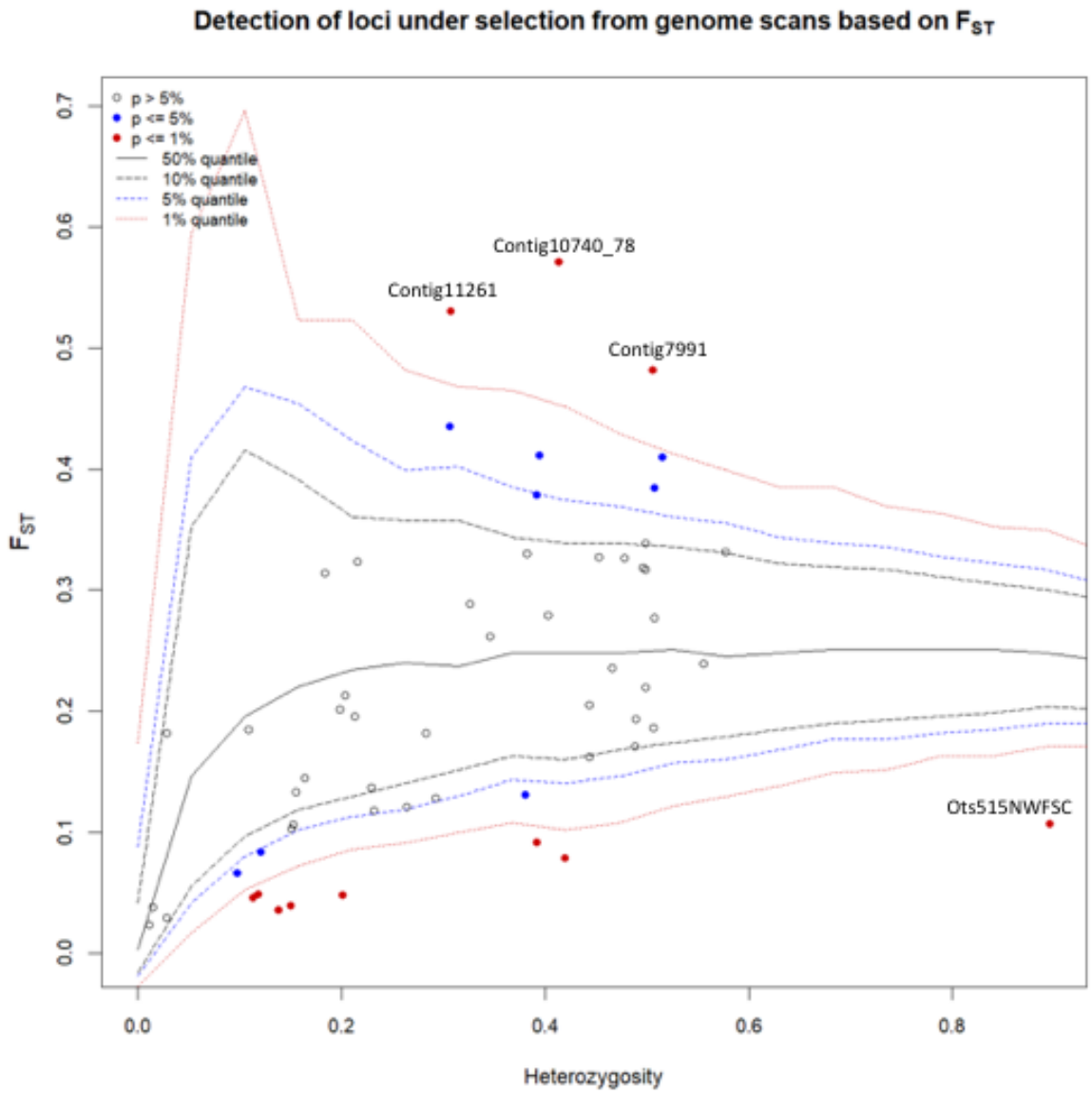


Fig. S2b. Results of hierarchical outlier test (Excoffier et al. 2009) involving Western Greenland populations (excluding QAAN-1).

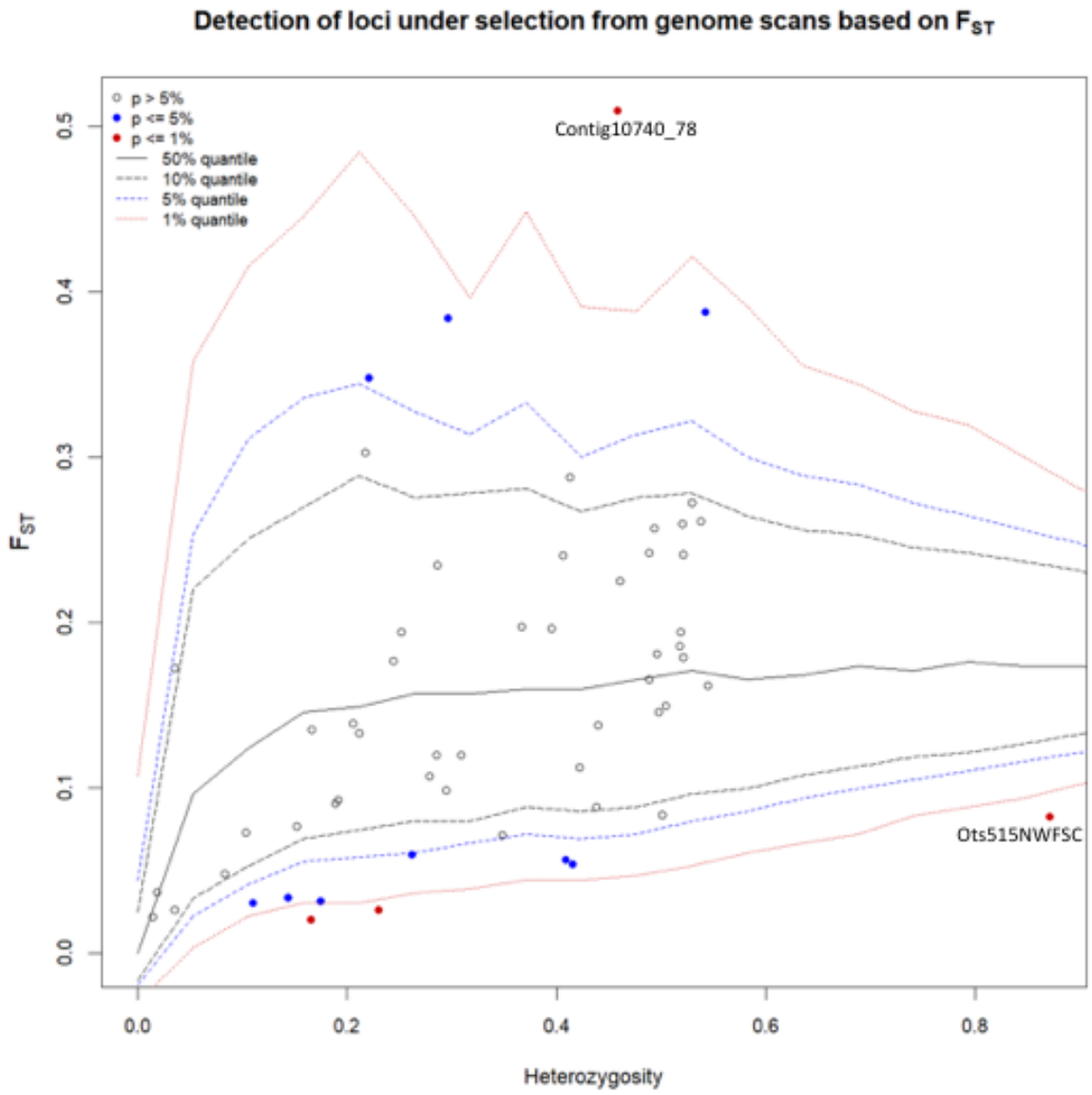


Fig. S3. Plots of association between mean allele length at *OtsClock1b* and geographical and environmental parameters for the sampled populations. Shaded areas denote 95% confidence intervals of the fitted lines. a) Mean allele length and latitude, encompassing all populations (y = 1.44x + 308.02, $R^2_{adjusted}$ = 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, $R^2_{adjusted}$ = 0.173, p = 0.0615). c) Mean allele length and end day of SST window, encompassing all anadromous populations (y = -0.20x + 459.81, $R^2_{adjusted}$ = -0.01, p = 0.365). d) Mean allele length and duration of SST window, encompassing all anadromous populations (y = -0.167x + 425.95, $R^2_{adjusted}$ = 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, $R^2_{adjusted}$ = 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, $R^2_{adjusted}$ = 0.308, p = 0.019).

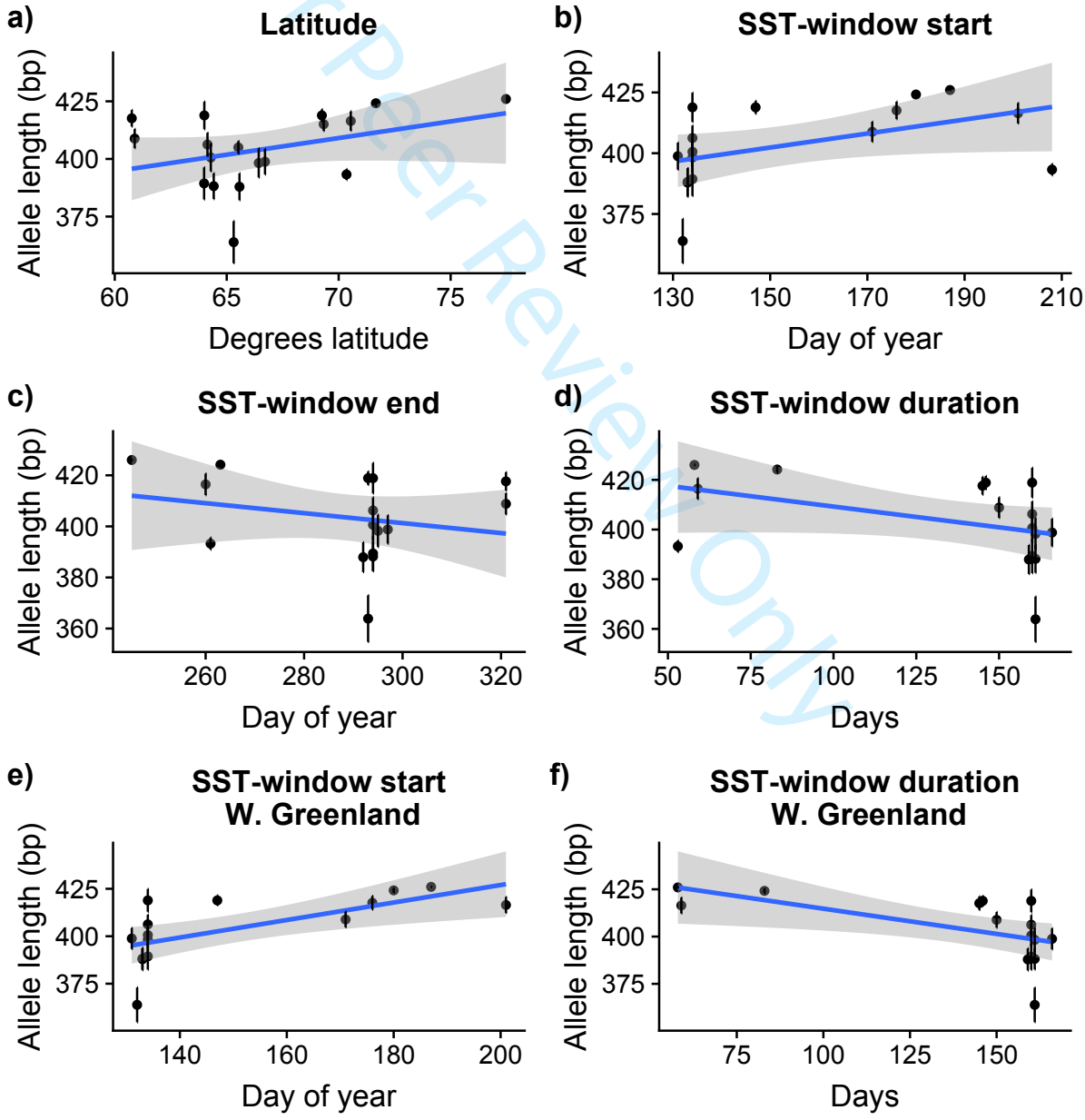


Table S2 Summary statistics

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

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

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

Contig10740_78	Jacobsen *et al* (2017)	SNP
Contig959_76	Jacobsen *et al* (2017)	SNP
Contig8978_60	Jacobsen *et al* (2017)	SNP
Contig7133_66	Jacobsen *et al* (2017)	SNP
Contig5917_74	Jacobsen *et al* (2017)	SNP
Contig4954	Jacobsen *et al* (2017)	SNP
Contig3498	Jacobsen *et al* (2017)	SNP
Contig2705	Jacobsen *et al* (2017)	SNP
Contig1525_59	Jacobsen *et al* (2017)	SNP
Contig11854_70	Jacobsen *et al* (2017)	SNP
Contig10812	Jacobsen *et al* (2017)	SNP
Contig9609	Jacobsen *et al* (2017)	SNP
Contig609_67	Jacobsen *et al* (2017)	SNP
Contig3603_79	Jacobsen *et al* (2017)	SNP
Contig2925	Jacobsen *et al* (2017)	SNP
Contig1570	Jacobsen *et al* (2017)	SNP
Contig850	Jacobsen *et al* (2017)	SNP

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

	QAAN-1 N = 18		
Total number of alleles	**Ho**	**He**	**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	-	-	-

erozygosity (He) is listed along with P-values of tests for conformance to Hardy-W

UUMM-1 N = 20			UUMM-2 N = 20		
Ho	**He**	**P**	**Ho**	**He**	**P**
0.50	0.38	0.282	0.20	0.19	1.000
0.20	0.18	1.000	0.10	0.10	1.000
0.60	0.74	0.056	0.50	0.73	0.000
0.11	0.10	1.000	0.26	0.25	1.000
0.60	0.51	0.663	0.40	0.43	1.000
0.40	0.47	0.655	0.25	0.30	0.469
0.61	0.47	0.285	0.10	0.18	0.116
0.10	0.10	1.000	0.05	0.05	1.000
0.10	0.10	1.000	0.45	0.41	1.000
0.58	0.49	0.632	0.40	0.38	1.000
0.55	0.48	0.648	0.45	0.48	1.000
0.45	0.45	1.000	0.35	0.48	0.337
0.55	0.41	0.245	0.35	0.45	0.344
0.35	0.41	0.594	0.50	0.43	0.602
0.40	0.38	1.000	0.45	0.51	0.674
0.10	0.10	1.000	0.50	0.47	1.000
-	-	-	-	-	-
0.25	0.22	1.000	0.35	0.30	1.000
0.40	0.38	1.000	0.90	0.51	0.002
0.15	0.14	1.000	0.20	0.18	1.000
0.35	0.50	0.178	0.30	0.33	1.000
0.45	0.36	0.505	0.15	0.22	0.235
0.45	0.41	1.000	0.60	0.47	0.321
0.30	0.33	1.000	0.60	0.51	0.661
0.42	0.40	1.000	0.60	0.51	0.651
0.47	0.51	1.000	0.55	0.50	1.000
-	-	-	-	-	-
0.20	0.18	1.000	0.15	0.22	0.247
0.40	0.43	1.000	0.35	0.36	1.000
0.15	0.14	1.000	0.40	0.43	1.000
0.50	0.38	0.319	0.30	0.26	1.000
0.42	0.51	0.665	0.20	0.26	0.342
0.58	0.51	0.679	0.00	0.10	0.025
-	-	-	0.05	0.05	1.000
0.37	0.37	1.000	0.05	0.05	1.000
0.05	0.05	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	0.45	0.41	1.000
0.35	0.30	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			KANG-1 N = 20		
Ho	**He**	**P**	**Ho**	**He**	**P**
0.45	0.36	0.536	0.45	0.53	0.563
0.15	0.22	0.234	0.45	0.53	0.612
0.75	0.84	0.000*	0.85	0.83	0.472
0.25	0.30	0.601	0.60	0.52	0.113
0.15	0.14	1.000	-	-	-
0.45	0.48	1.000	0.06	0.16	0.066
0.65	0.50	0.361	0.30	0.43	0.271
0.05	0.05	1.000	0.05	0.05	1.000
0.15	0.14	1.000	0.40	0.43	1.000
0.65	0.50	0.331	0.20	0.43	0.034
0.20	0.26	0.345	0.35	0.45	0.339
0.40	0.49	0.637	0.60	0.47	0.355
0.45	0.45	1.000	0.45	0.45	1.000
0.20	0.33	0.137	-	-	-
0.30	0.47	0.138	0.40	0.51	0.363
0.25	0.22	1.000	0.55	0.50	1.000
-	-	-	-	-	-
0.40	0.38	1.000	-	-	-
0.75	0.48	0.010	0.40	0.51	0.432
0.10	0.10	1.000	0.45	0.41	1.000
0.25	0.50	0.031	0.40	0.51	0.464
0.30	0.51	0.081	0.20	0.18	1.000
0.20	0.26	0.398	0.05	0.05	1.000
0.35	0.30	1.000	0.05	0.05	1.000
0.25	0.41	0.099	0.10	0.10	1.000
0.45	0.50	0.684	0.15	0.14	1.000
-	-	-	0.10	0.10	1.000
0.40	0.43	1.000	0.30	0.26	1.000
0.40	0.51	0.369	0.50	0.51	1.000
-	-	-	0.10	0.10	1.000
-	-	-	0.05	0.05	1.000
0.60	0.51	0.660	-	-	-
0.40	0.51	0.398	0.65	0.48	0.168
-	-	-	0.10	0.10	1.000
0.40	0.38	1.000	0.10	0.10	1.000
0.05	0.14	0.096	-	-	-
0.25	0.22	1.000	0.15	0.22	0.231
0.05	0.05	1.000	0.15	0.14	1.000
0.40	0.47	0.618	0.55	0.45	0.633
0.55	0.45	0.613	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

		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

	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

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
-	-	-	-	-	-
-	-	-	-	-	-
-	-	-	-	-	-
-	-	-	-	-	-
-	-	-	-	-	-
-	-	-	0.38	0.31	1.000
0.30	0.43	0.280	-	-	-