NRC Research Press

ARTICLE

# The interplay between dispersal and gene flow in anadromous Arctic char (*Salvelinus alpinus*): implications for potential for local adaptation

Jean-Sébastien Moore, Les N. Harris, Ross F. Tallman, and Eric B. Taylor



**Abstract:** Dispersal can influence the process of local adaptation, particularly when the dispersers successfully breed in the non-natal habitat. Anadromous Arctic char (*Salvelinus alpinus*) display a complex migratory behaviour that makes the distinction between breeding and nonbreeding dispersal especially important. This species does not reproduce every year, but individuals must migrate to fresh water to overwinter such that a large proportion of fish running up-river are not in breeding condition and have no potential for gene flow. We used a genetic assignment approach to identify dispersers among populations of char from Baffin Island, Canada. Estimates of dispersal varied between 15.8% and 25.5% depending on the assignment method, suggesting that Arctic char disperse at a higher rate than other salmonids. Nonbreeding individuals were more likely to use non-natal habitats than breeding individuals, thus resulting in estimates of dispersal that overestimate the potential for gene flow among populations. Finally, we parameterized a population genetic model showing that gene flow is probably sufficiently low to allow for local adaptation among populations, given realistic selection coefficients. Our results underscore the importance of understanding patterns of dispersal to appropriately evaluate their potential consequences for local adaptation and management.

**Résumé :** La dispersion a une influence importante sur l'adaptation locale, particulièrement lorsque les migrants se reproduisent dans l'habitat non-natif. L'omble chevalier anadrome (*Salvelinus alpinus*) a un comportement migratoire complexe qui rend importante la distinction entre une dispersion suivie ou non d'une reproduction. Les individus de cette espèce ne se reproduisent pas chaque année, mais doivent tous migrer en eau douce pour hiverner. Une importante proportion d'individus migrants ne sont donc pas en état de se reproduire et n'ont aucune influence sur le flux de gènes. Nous avons utilisé une approche d'assignation génétique pour identifier les individus disperseurs entre des populations d'omble chevalier de l'Île de Baffin, Canada. Les estimés de dispersion obtenus varient entre 15.8 % et 25.5 % selon la méthode d'assignation, suggérant que la dispersion est plus importante chez l'omble chevalier que chez d'autres salmonidés. De plus, les individus nonreproducteurs étaient plus susceptibles d'utiliser un habitat non-natif que les individus reproducteurs, ce qui résulte en des estimés de dispersion qui surestiment le potentiel pour le flux de gènes entre populations. Finalement, nous avons paramétré un modèle de génétique des populations qui montrent que le flux de gènes pourrait être suffisamment bas pour permettre l'évolution de l'adaptation locale à l'échelle de la rivière en supposant des coefficients de sélection réalistes. Nos résultats soulignent l'importance de comprendre les patrons de dispersion afin de proprement évaluer leurs conséquences pour l'adaptation locale et la gestion.

## Introduction

Dispersal and gene flow have a variety of important ecological and evolutionary consequences that affect the fitness of individuals and populations (Clobert et al. 2004; Garant et al. 2007). For instance, dispersal and gene flow determine the extent to which populations are genetically linked (Bohonak 1999; Waples and Gaggiotti 2006) and locally adapted (Slatkin 1987; Lenormand 2002), which in turn influences the scale over which management actions should be implemented (e.g., Storfer 1999; Fraser and Bernatchez 2001; Waples and Gaggiotti 2006). Many dispersal events, however, do not result in gene flow (Ehrlich and Raven 1969; Nosil et al. 2005), and distinguishing between dispersal events that result in gene flow from those that do not is therefore critical to predict its effects on population structure and on the evolution of local adaptation (Slatkin 1987; Garant et al. 2007).

A great deal of effort has been directed at understanding patterns of dispersal and gene flow in anadromous salmonids (Hendry et al. 2004; Dionne et al. 2008), in part because of the important implications for the management of those species (Waples 1991; Ruckelshaus et al. 2002). Anadromy refers to the behaviour where individuals hatch and grow as juveniles in fresh water, but forage as adults in the marine environment before returning to fresh water to reproduce and (or) overwinter (McDowall 1987). Anadromous salmonids tend to home to their natal freshwater habitats following marine migrations that often take them great distances from their natal habitat (Hendry et al. 2004; Quinn 2005). The homing strategy of salmonids typically leads to low gene flow among populations and is largely responsible for the high levels of genetic differentiation and local adaptation commonly observed among populations even on a small spatial scale (Taylor 1991; Fraser et al. 2011). Despite the general homing tendencies of salmonids, a component of many populations will disperse to non-natal rivers, a phenomenon referred to as "straying" (Quinn 1993). Straying is an important behaviour because it allows the colonization of new habitats and may constitute a bet-hedging strategy used in response to unpredictable habitats (Hendry et al. 2004). Straying may also result in gene flow among populations, which may reduce local adaptation (e.g.,

Received 1 March 2013. Accepted 23 June 2013.

Paper handled by Associate Editor Paloma Morán.

**J.-S. Moore* and E.B. Taylor.** Department of Zoology and Beaty Biodiversity Research Centre and Museum, The University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.
**L.N. Harris and R.F. Tallman.** Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.
**Corresponding author:** Jean-Sébastien Moore (e-mail: jsmoore@zoology.ubc.ca).
*Present address: Institut de Biologie Integrative et des Systemes, Universite Laval, 1030 Avenue de la Medecine, Quebec, QC G1V 0A6, Canada.

Dionne et al. 2008). It also leads to mixing of stocks, which can create challenges for fisheries management (Utter and Ryman 1993).

The Arctic char (*Salvelinus alpinus*) is a salmonid fish with a Holarctic distribution, and many populations at higher latitudes are anadromous (Johnson 1980; Klemetsen et al. 2003). Anadromous populations are the target of an important subsistence and commercial fishery by Inuit resource users in the Canadian Territory of Nunavut (Priest and Usher 2004; Roux et al. 2011). The commercial fishery for Arctic char is currently co-managed by the federal government and Inuit organizations (Kristofferson and Berkes 2005), but the lack of data on many of the exploited systems, combined with the logistical challenges associated with collecting such data in the high Arctic, means that many of the assumptions under which current management operates remain untested (Roux et al. 2011). For instance, each river is currently assigned a quota independent of other rivers (e.g., Harris and Tallman 2010), an approach that assumes most individuals home to their natal river every year to spawn or overwinter. Tagging studies, however, suggest that dispersal (or straying) may be fairly high in Arctic char populations compared with other salmonids (Dempson and Kristofferson 1987; Gyselman 1994). In addition, some unusual aspects of the anadromous Arctic char life cycle make distinguishing between dispersal and gene flow particularly important for this species. Many anadromous salmonids spend several years at sea before returning to fresh water to spawn (Fleming 1998; Quinn 2005). Arctic char, however, must return to fresh water yearly because they have low salinity tolerance and are not able to survive the sub-zero temperatures of the Arctic Ocean in winter (Johnson 1980; Klemetsen et al. 2003). This yearly energy expenditure associated with the migration, combined with a short feeding season (~30–100 days; Johnson 1980; Dempson and Kristofferson 1987), results in slow growth and little energy to invest in gonadal development (Dutil 1986). Consequently, Arctic char typically do not reproduce every year, and a substantial proportion of returning adults are migrating solely for the purpose of overwintering (Dutil 1986). As such, these individuals have no potential to introduce their alleles in non-natal habitats. Furthermore, patterns of tag recovery from tagging studies suggest that the individuals migrating for the purpose of overwintering may have a greater propensity to use non-natal habitats in comparison with individuals migrating for reproduction (Dempson and Kristofferson 1987; Gyselman 1994), although direct evidence for this behaviour is still lacking. Together, these observations suggest that a substantial proportion of dispersal events will not result in gene flow in anadromous Arctic char.

It is therefore necessary to distinguish between two types of dispersal in Arctic char: breeding dispersal, where a mature individual enters a non-natal habitat for the purpose of reproduction; and overwintering dispersal, where a nonbreeding individual uses a non-natal habitat to overwinter. Note that this latter form of movement does not represent dispersal according to all definitions (e.g., Howard 1960; Clobert et al. 2001; Ronce 2007), but would be considered dispersal according to other commonly accepted definitions (e.g., Bowler and Benton 2005; Garant et al. 2007).

To better understand the migratory behaviour of anadromous Arctic char and the interplay between dispersal and gene flow in determining, in part, the potential for local adaptation in this species, we conducted a microsatellite DNA survey of char from the Cumberland Sound region of Baffin Island. Our sampling scheme included samples of migrating adult fish collected as they enter fresh water during the fall migration and samples of presmolt juvenile fish still rearing in fresh water that have therefore not had an opportunity to disperse yet (i.e., they have not left their natal lakes). This was designed to test three hypotheses. First, we hypothesized that many dispersal events do not result in gene flow and predicted that under this hypothesis average genetic differentiation (i.e., as measured by $F_{ST}$) between samples of juveniles would be higher than average genetic differentiation between samples of adults from the same system, because many of these adults represent nonbreeding, overwintering adults. Second, we tested the hypothesis that overwintering fish are more likely to use non-natal habitats than breeding fish. To do so, we used genetic assignment tests to provide an estimate of total dispersal (i.e., breeding and overwintering dispersal), which we then partitioned into breeding dispersal and overwintering dispersal using information on the reproductive status of the genetically assigned fish. Third, using the same genetic assignment procedure, we tested the hypothesis that dispersers not only differ from philopatric individuals in their reproductive status, but also in other traits such as sex, age, and body size. In addition to testing these three hypotheses relating to the patterns of dispersal, we explored the potential consequences of gene flow for local adaptation in this system by parameterizing a population genetic model of the balance among migration, drift, and selection with estimates of gene flow generated from the microsatellite data.

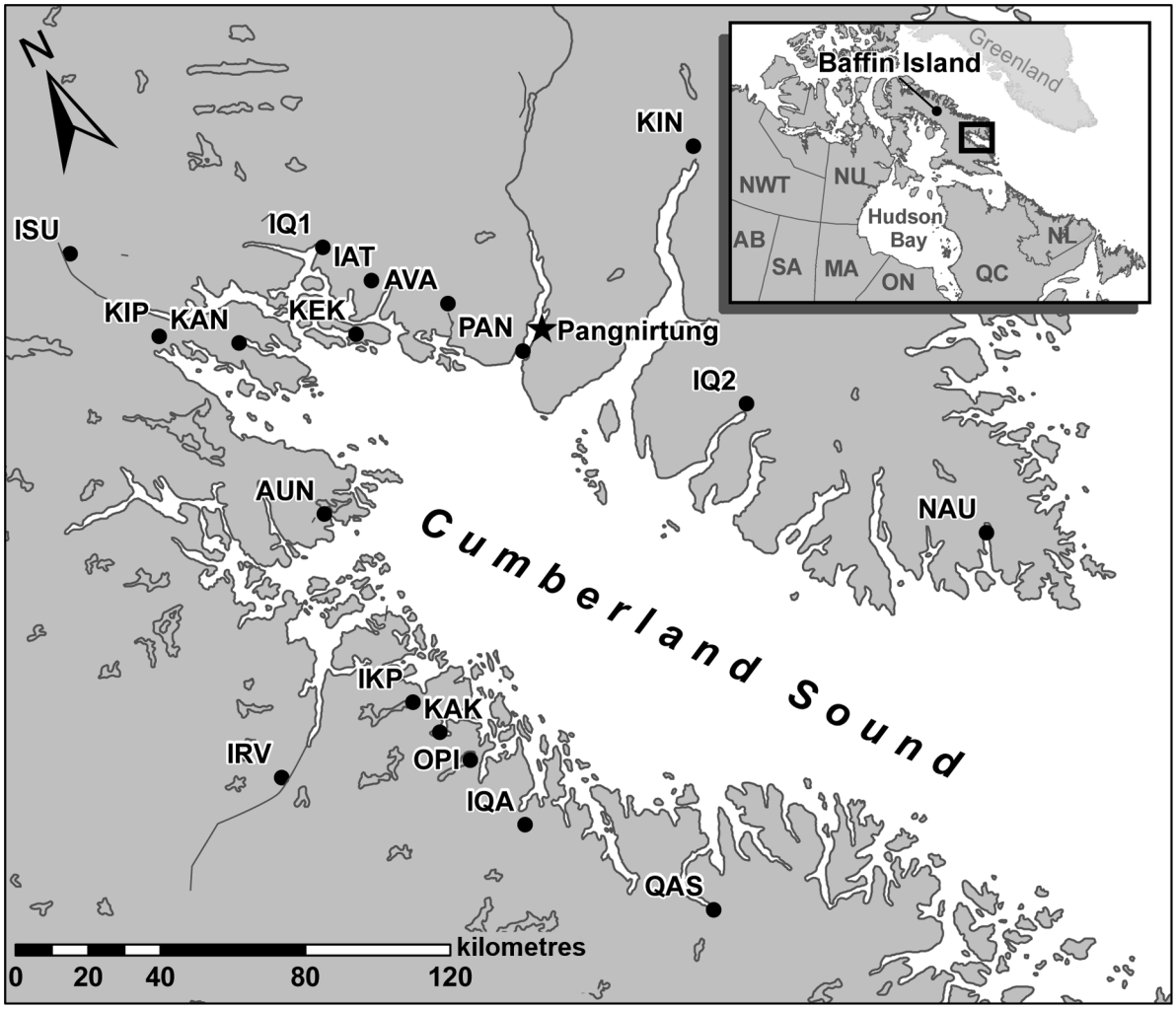
## Material and methods

### Field sampling

Arctic char were sampled from Cumberland Sound, in the southeastern part of Baffin Island, Nunavut, in Canada's eastern Arctic (Fig. 1; also refer to Table S1 in the online Supplementary Material[1]). Adult fish were collected from a total of 10 localities between 2003 and 2009, using gill nets (140 mm stretched mesh and multimesh 38–102 mm) set in salt water close to the mouth of the rivers that drain the lakes in which Arctic char spawn. Sampling was conducted from mid-July to September when fish aggregate close to those rivers prior to undergoing upstream migrations. For a few localities (QAS and IQ1), collections were made in fresh water shortly after the fish had migrated upstream because sampling was initiated after fish had already moved into fresh water. At two localities, (KIN and NAU), fish were also collected in the winter when the fish were overwintering in fresh water. Obtaining adult samples from fresh water introduces some uncertainty because it is possible that nonmigratory adults would be sampled. While such nonmigratory (or resident) individuals have been documented in a few of our sampling locations (notably QAS and IQ1), they differ markedly in morphology from migratory adults (Loewen et al. 2009) and were thus easily recognizable in the field and eliminated from the analysis. The following measurements were taken in the field: fork length (mm), body mass (g), and gonad mass (g). Sex and reproductive status (immature, overwintering — i.e., not spawning that year — or spawning) was determined based on the gonadosomatic index (GSI) of each individual, assuming that GSI should be bimodal with two nonoverlapping distributions corresponding to nonbreeding and breeding individuals (see online Supplementary Material for details[1]). Note that immature individuals are often difficult to distinguish from overwintering individuals in the field based on observation of the gonads alone. For this reason, both are analyzed as having the same reproductive status herein because dispersal of both classes cannot lead to gene flow. Fin clips were preserved in 95% ethanol for genetic analysis, and sagittal otoliths were removed and the age of most individuals was later determined in the laboratory (see Loewen et al. 2009 for full description of aging methods).

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0138.

**Fig. 1.** Map of Cumberland Sound, Baffin Island, Nunavut, Canada. Sampling locations of Arctic char (*Salvelinus alpinus*) for this study are shown with a dot and identified with a three-letter code referenced in Table S1 of online Supplementary Material[1]. The location of the nearest town, Pangnirtung, is shown with a star. The inset map shows the location of Baffin Island in North America.




Juvenile samples were collected in July 2008 and August 2009. Methods of capture differed between localities, but seine net (10 mm stretched mesh) tows were most commonly used. When seining was not possible, we used a combination of dip nets, minnow traps, and electrofishing. Whenever possible, we sampled juveniles from different areas of the rearing lake to minimize the likelihood of sampling related individuals. We sacrificed juvenile fish with an overdose of MS222, measured fork length (mm), and preserved the whole fish or a fin clip in 95% ethanol.

### Microsatellite DNA analysis

Individual genotypes were obtained at 18 microsatellite loci. Polymerase chain reaction (PCR) protocols and primer information can be found in the online Supplementary Material (Table S2[1]). The PCR products were run on an Applied Biosystems (Carlsbad, California, USA) 3100 genetic analyzer. GeneMapper Software version 3.7 (Applied Biosystems) was used to automatically score microsatellite alleles, and all scores were manually checked for quality. Ninety-six individuals were randomly selected, re-amplified at all loci, and re-genotyped to assess scoring error rates (except the DNA extraction; DeWoody et al. 2006).

MICRO-CHECKER version 2.2.3 (van Oosterhout et al. 2004) was used to test for the presence of null alleles and large allele drop-out. We used FSTAT version 2.9.3.2 (Goudet 2001) to test for Hardy–Weinberg equilibrium and genotypic disequilibrium using default values for the number of permutations. For both tests, we set the nominal significance level at 0.05 (using a Bonferroni correction for multiple comparisons). We used GENETIX version 4.05 (Belkhir et al. 2004) to generate estimates of observed heterozygosity ($H_O$) and expected heterozygosity ($H_E$) corrected for sample size. FSTAT was used to calculate allelic richness ($A_R$) and pairwise $F_{ST}$ between each sample, and significance of differences between samples were assessed with 10 000 permutations (experiment-wide $\alpha$ = 0.05 after Bonferroni correction). We used PHYLIP version 3.68 (Felsenstein 1993) to generate a neighbor-joining tree of all samples based on Cavalli-Sforza's chord measure (Cavalli-Sforza and Edwards 1967) employing 1000 bootstrap replicates to test support for each node. The tree was visualized and formatted in FigTree version 1.3.1 (Rambaut 2010).

### Comparisons between adult and juvenile samples

Sampling juvenile salmonids for the purpose of characterizing population structure is potentially problematic because of the increased risk of sampling several individuals from the same family, a phenomenon referred to as the Allendorf–Phelps effect (Waples 1998). In addition to sampling juveniles from spatially discrete locations in the lakes (whenever logistically feasible), we used the software COLONY (Wang and Santure 2009) to identify likely siblings on the basis of individual multilocus genotypes (see Supplementary Material for details, Table S4[1]). Once full-sibs were

identified ("BestML" full-sibs only), all but one randomly selected individual from each full-sib group was removed. All analyses described below were then run on the data sets with and without the full-sibs removed.

We used FSTAT to assess whether there was increased genetic differentiation among samples of juveniles compared with samples of adults. The permutation procedure was used with 10 000 permutations to test for significant differences between $F_{ST}$ for adults and juveniles. For this analysis, we used only the juvenile samples from locations for which we had an analogous adult sample. This was done to avoid the possibility that a juvenile sample without an analogous adult sample could bias the results. This should make the test more conservative because it reduces sample size and hence power.

### Genetic assignments

We used the program GeneClass2 (Piry et al. 2004) for assignment tests used to identify dispersers in the samples of adults. Before conducting the analysis, we evaluated whether we had sufficient power to detect dispersal using the juvenile samples as a reference. To do so, we followed the guidelines provided by Paetkau et al. (2004), performing a run of GeneClass2 with the juveniles samples only (i.e., self-assignment). The assignment scores from that run were used to compute values of $D_{LR}$ (mean genotype likelihood ratios) for pairs of samples. We did not look at all pairs of samples, but focused instead on those that were geographically proximate and that were identified by $F_{ST}$ estimates as being genetically similar. For those samples, $D_{LR}$ was always greater than 5, which was found to provide near maximum power by Paetkau et al. (2004). For the assignment tests, juvenile samples were used as the reference samples, and we only assigned samples of adults that had corresponding juvenile samples. All analyses were also run using the juvenile samples with the full-sibs removed as reference samples. Samples were assigned or excluded using the Bayesian computation method of Rannala and Mountain (1997) and the Monte Carlo resampling algorithm of Paetkau et al. (2004) to simulate 100 000 individuals with a 0.05 type I error rate. To reduce type I errors (i.e., individuals identified as dispersers who are actually not), we followed Hauser et al. (2006) and used the assignment score of individuals (i.e., $\text{score}_{i,l} = L_{i,l}/\Sigma L_{ij}$, where $L_{i,l}$ is the likelihood of individual $i$ belonging to sample $l$) as calculated by GeneClass2 to eliminate all individuals that had a score lower than 95%.

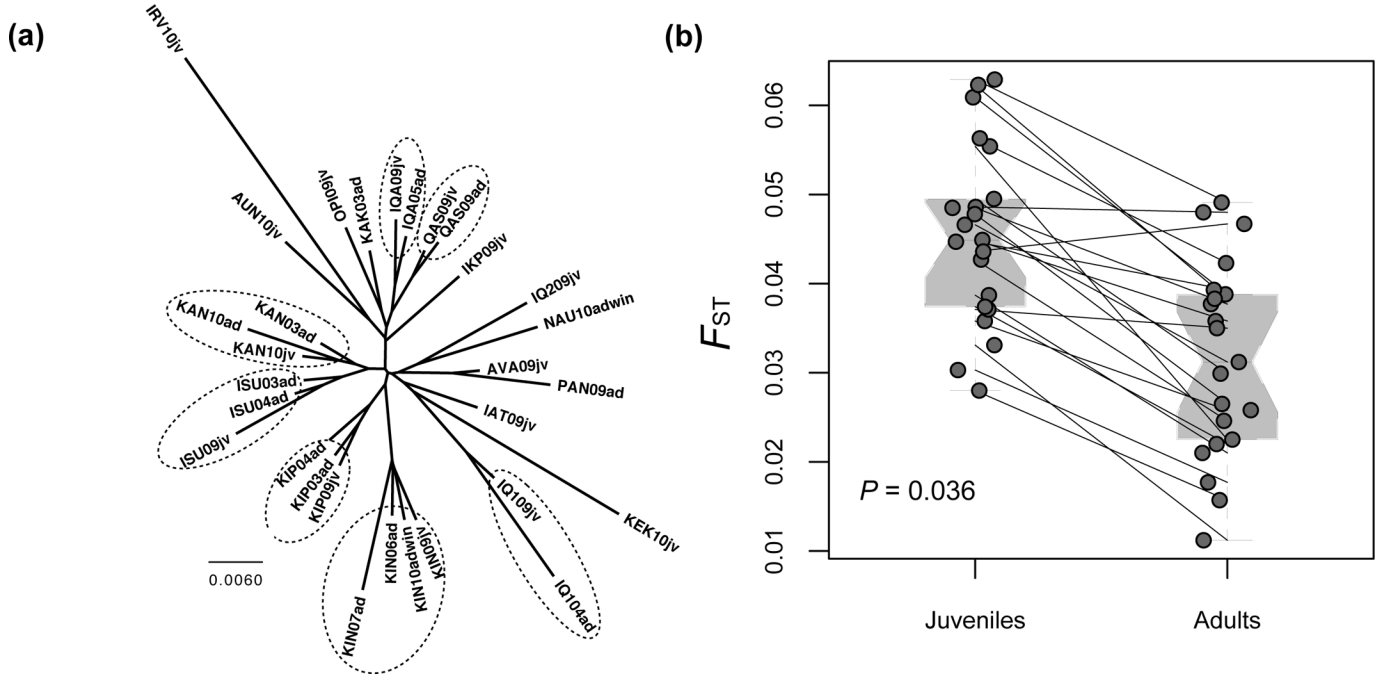
We also complemented the previous approach with assignment tests performed in STRUCTURE (Pritchard et al. 2000), which allows the identification of genetic clusters without defining populations a priori and also allows to distinguish hybrid individuals. We ran STRUCTURE on the entire data set (1290 individuals, 30 populations) under the admixture model with independent allele frequencies. We varied $K$ from 1 to 15 and ran 10 independent runs for each value of $K$ employing 100 000 burn-in and 100 000 MCMC replicates per run. The results were first visualized using STRUCTURE HARVESTER (Earl 2011), which implements the $\Delta K$ method of Evanno et al. (2005) to infer the most likely number of clusters and combines the results of many independent runs of the program for each $K$ value. Individual admixture coefficients ($Q$) were calculated for each individual after the results of the 10 independent runs for the most likely $K$ were combined in program CLUMPP (Jakobsson and Rosenberg 2007) using 1000 permutations under the LargeKGreedy algorithm. Each individual in the analysis has a $Q$ value for each of the identified genetic clusters, and the values of $Q$ range from 0.0 to 1.0, with higher values meaning that a greater proportion of this individual's genome assigns to a particular cluster. The sum of the $Q$ values for any individual across all genetic clusters adds to 1.0. We therefore eliminated putative hybrids from this analysis by removing individuals that did not have at least one $Q$ value above 0.5. All other individuals were assumed to unambiguously assign to a genetic cluster.

Based on the results of the assignment tests, adults were classified as dispersers (i.e., if the individual was assigned to a river different from where it was captured) or as philopatric (i.e., if the individual was assigned to the river from where it was captured). We then tested for differences in frequencies of dispersing versus philopatric individuals in the groups of fish classified as breeding fish (i.e., fish whose gonads were ripe when collected in the field) and nonbreeding fish (i.e., fish whose gonads were mature but resting or whose gonads were immature) using two-tailed Fisher exact tests. This procedure was repeated on the results of both the GeneClass2 and the STRUCTURE analyses. Two-tailed Fisher exact tests were also used to test for sex-biased dispersal on the results of all previously mentioned assignment tests procedures. To investigate the effect of other biological characteristics on dispersal propensity, we tested for differences in mean trait values between dispersing and philopatric individuals (from both the GeneClass2 analysis excluding individuals with low assignment score and the STRUCTURE analysis). More specifically, we looked at the effect of age (years), fork length (mm), total body mass (g), gonad mass (g), and condition factor (calculated as $K = (W \times 10^5)/L^3$, where $K$ is the condition factor, $W$ is the total body mass (g), and $L$ is the length (mm; Anderson and Neuman 1996). Only gonad mass departed from normality and was thus $\log_{10}$-transformed. We used discriminant function analysis (DFA) to test whether the biological variables predicted membership to the disperser or philopatric groups using the MASS library in R (R Development Core Team 2010) and omitting any individual for which data was missing at one or more variables. Because fork length and mass are used in the calculation of the condition factor, it is not valid to include all three variables in the DFA. We chose to exclude fork length and body mass (which are probably correlated with age) and to only include condition factor, age, and gonad mass in the DFA. Significance was assessed using Wilk's lambda. Because some traits may show an association with dispersal propensity without differing in means (for example, Gyselman 1994 found that smaller and larger Arctic char were more likely to disperse than intermediate-sized Arctic char), we also visually compared the distributions of trait values of dispersing and philopatric individuals (see Supplementary Material for details[1]).

### Potential for local adaptation

We evaluated the potential for selection to drive divergence at the scale of the river for populations of Arctic char distributed around Cumberland Sound. Although the approach advocated by Adkison (1995) has been used extensively for anadromous fishes (e.g., Hansen et al. 2002; McCairns and Bernatchez 2008), the circular nature of Cumberland Sound violates many of its assumptions. We opted for the more conservative approach of using a continent–island model, where we assume that each river receives migrants from all the other rivers (the "continent"). This simple approach probably poorly reflects the complexities of dispersal and gene flow in the present system, and we note that the goal of the current approach is heuristic. The simple model is, however, appropriate to address the present question because it conservatively assumes that gene flow comes from all rivers, not only the nearby rivers with presumably similar selective environments. The continent–island model we used is derived from the two-patch model of Yeaman and Otto (2011). According to this model, selection overcomes gene flow and drift if $s$, the selection coefficient, is larger than $(4N_em + 1)/(4N_em + 2N_e + 1)$, where $N_e$ is the effective population size, and $m$ is the rate of migration. We used the program MIGRATE-n version 3.2.15 (Beerli and Felsenstein 2001) to obtain estimates of $m$ and $N_e$. We ran the analysis only on the juvenile samples (with the sibs removed), since they should better reflect long-term gene flow than the adult samples, which may contain dispersers that will not contribute genetically to the populations they disperse to. Note that MIGRATE-n assumes that $N_e$ and $m$ remained constant over the

**Fig. 2.** Summary of population genetic structure among Arctic char (*Salvelinus alpinus*) sampling locations of Cumberland Sound. (*a*) Neighbor-joining tree of Cavalli-Sforza's chord distance, showing that paired samples of juveniles and adults from the same localities group together (encircled groups of samples). (*b*) Pairwise $F_{ST}$ values between Arctic char sampling localities. The grey circles are the actual observed pairwise $F_{ST}$ values with random jitter added to facilitate visualization. The notched box plots show the median and quartiles, and lines connect pairwise comparisons involving the same localities, but comparing juveniles (left) and adult samples (right).




last $4N_e$ generations, an assumption probably violated in the anadromous char system whose range was only recently recolonized postglacially. Recent population splitting, however, leads to inflated estimates of migration rates (P. Beerli, personal communication), which for the current application will lead to conservative estimates of the potential for selection to drive divergence. The mean values of $\theta$ and $M$ obtained from MIGRATE (averaged over all populations) were used to parameterize the model and explore whether local adaptation is likely for biologically realistic values of parameter $s$ (see Supplementary Material for details of the search strategy[1]). For diploid data, $\theta$ can be converted to $N_e$ using the following equation: $N_e = \theta/4\mu$, and $M$ can be converted to $m$ using $m = M \times \mu$, where $\mu$ is the mutation rate. Because there is no widely accepted estimate of mutation rate for microsatellites in salmonids (Steinberg et al. 2002), we varied the mutation rate between $10^{-3}$ and $10^{-5}$ for the parameter conversions. Total gene flow into each sampling location was calculated by summing the effective number of immigrants, $N_e m$, from all other samples and then dividing by the $N_e$ of the local sample.

## Results

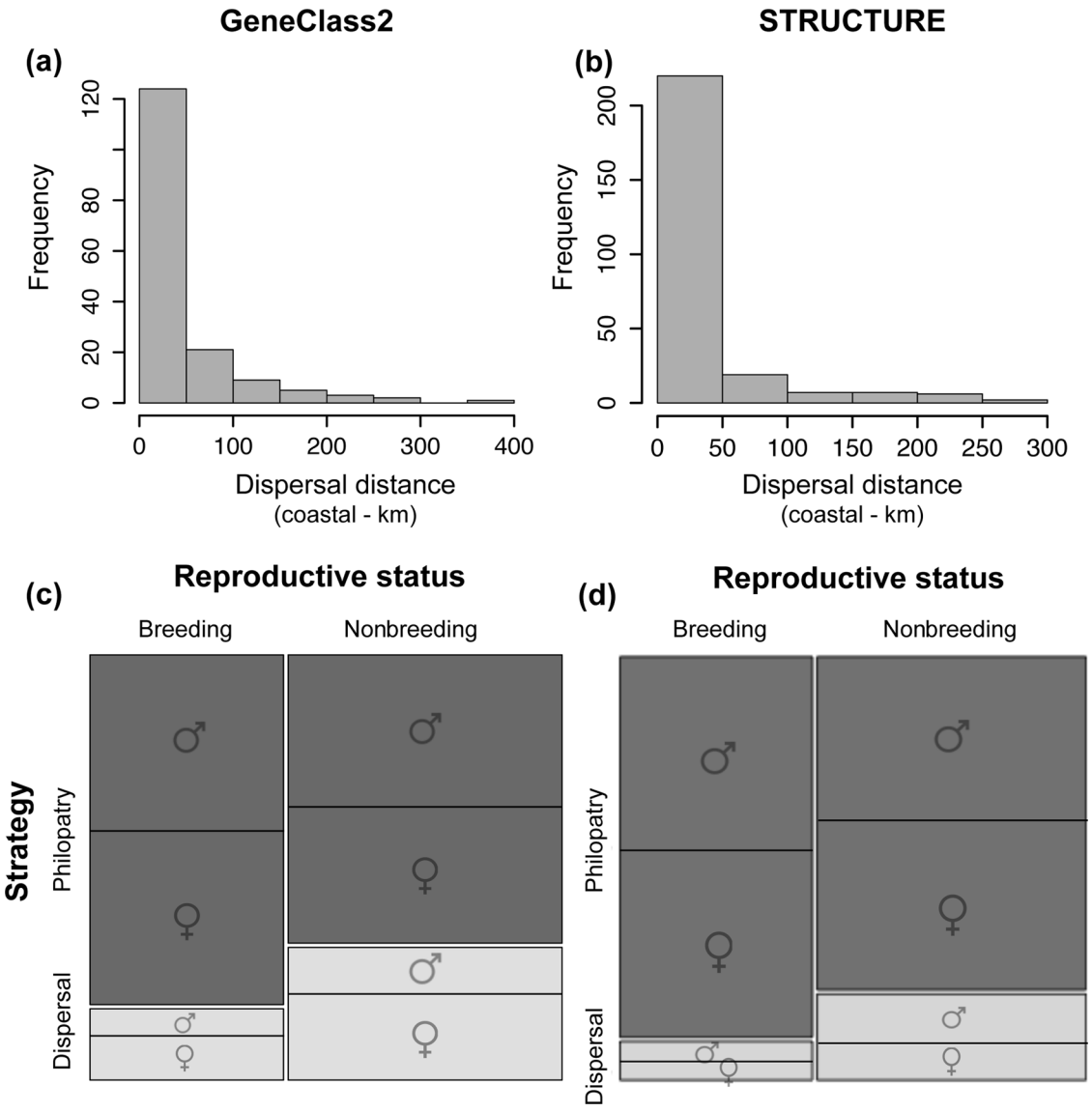
### Microsatellite polymorphism

We found high levels of polymorphisms at most of the 18 microsatellite loci examined, and the number of alleles per locus varied between 1 (for Smm21) and 56 (Sco216; average 20.4 alleles per locus). The results of the MICRO-CHECKER analysis consistently identified three loci potentially suffering from null alleles or other scoring errors: Sco109, Sco212, and Sco218. Those loci were thus eliminated (along with the monomorphic Smm21) from all subsequent analyses, leaving a total of 14 informative loci. The average scoring error rate over all loci (excluding the three aforementioned loci) was 2.0% (see Supplementary Material for details and locus-specific error rates[1]). Based on 9200 permutations, FSTAT identified 35 locus–sampling location pairs that had significant ($P < 0.05$) heterozygote deficit and four that had significant heterozygote excess. Only two locus–sampling location pairs, however, remained significant after Bonferroni correction: locus Sco202 in sample KAN03ad and Sco216 in KIP03ad, both with heterozygote deficits. Based on 2100 permutations, FSTAT identified 37 pairs of loci that were in significant genotypic disequilibrium, but none remained significant after Bonferroni correction.

We found evidence of weak, but significant, genetic differentiation among sampling locations of Arctic char distributed around Cumberland Sound. First, the neighbor-joining tree showed that paired samples of juveniles and adults from the same location tended to group together (Fig. 2*a*). This was supported by bootstrap values of more than 80% for all groupings of samples for the same site (not shown). Second, pairwise $F_{ST}$ values between localities tended to be small (global $F_{ST}$ = 0.038) but significant (Bonferroni-corrected for experiment-wide $\alpha$ = 0.05; Table S4 in the online Supplementary Material[1]). For instance, all but four pairwise comparisons between samples of juveniles were significant (average $F_{ST}$ between juveniles: 0.045). The $F_{ST}$ values also tended to be significant between samples of adults (average $F_{ST}$ = 0.029), although nonsignificant values were more common. None of the samples collected from the same site, but in different years, differed significantly, suggesting that temporal variation in population genetic structure is minimal and that comparisons of samples collected in different years is valid. Both ISU adult samples (2003–2004) and the IQA adult sample, however, differed significantly from their respective juvenile sample.

The COLONY analysis identified pairs of full-sibs in the juvenile samples (Table S5 in the online Supplementary Material[1]). While most juvenile samples were found to contain from zero to three pairs of full-sibs, three localities (i.e., ISU, KEK, AUN) contained more than 10 pairs of full-sibs each. For all three localities where many full-sibs were identified, the juveniles were difficult to collect and were thus collected from only one short suitable stretch of shoreline.

**Fig. 3.** Results of the assignment tests performed on samples of Arctic char (*Salvelinus alpinus*) with GeneClass2 and STRUCTURE. The top panels show the distributions of dispersal distances obtained with GeneClass2 (*a*) and STRUCTURE (*b*) and show the proportion of individuals classified as philopatric (dispersal distance = 0 km). The individuals classified as dispersers (i.e., all nonzero dispersal distances) tend to be classified to nearby localities. The bottom panels show mosaic plots of the reproductive status and sex of the dispersing and philopatric individuals (note that the height and width of the bars, not the area of the squares, show the proportions of individuals in each category) for the GeneClass2 (*c*) and the STRUCTURE (*d*) analyses.




The samples of juveniles were more genetically differentiated from each other than samples of adults collected from the same localities (Fig. 2*b*). The average pairwise $F_{ST}$ between samples of juveniles and adults was 0.045 (95% CI: 0.034–0.059) and 0.029 (95% CI: 0.019–0.041), respectively, and this difference was statistically significant ($P$ = 0.036). The $F_{ST}$ values remained virtually unchanged after removing putative sibs from the analysis (juveniles: $F_{ST}$ = 0.044; adults: $F_{ST}$ = 0.029), and the difference remained statistically significant, albeit slightly less so owing to the decreased sample size ($P$ = 0.044).

### Assignment tests

Out of the 359 individuals assayed using GeneClass2, a total of 192 individuals were assigned to a locality where they were captured and were inferred to be philopatric individuals. The remaining 167 individuals were classified to a locality where they were not captured and thus were inferred to be dispersers, which resulted in an initial estimate of total dispersal of 46.5%. The average assignment score over all adult samples was 83.9%, and the average probability of assignment was only 33.9%. After eliminating all individuals that had an assignment score lower than 95%, we were left with 157 individuals, 40 of which were dispersers and 117 of which were philopatric, leading to an estimate of total dispersal of 25.5%. Those dispersers were also more likely to be from geographically proximate localities (Fig. 3*a*). Interestingly, removing full-sibs from the analysis improved the probability of assignments (average maximum probability of assignment 49.0%, compared with 33.9% with the sibs included). This would occur because presence of sibs artificially increases the genetic similarity in the reference samples, thus lowering the probability of assignment even of local adults. Nevertheless, the vast majority (96.7%) of the fish identified as dispersers in this analysis are the same as those identified in the analysis from which the sibs were

**Table 1.** Results of discriminant function analysis testing for trait differences between philopatric and dispersing Arctic char (*Salvelinus alpinus*).

| | Mean value | | | | | |
|---|---|---|---|---|---|---|
| Trait | Dispersers | Philopatric | Coefficients of linear discriminants | Wilk's lambda | *F* | *P* |
| **GeneClass2** | | | | | | |
| Age (years) | 11.1 | 11.7 | 0.222 | 0.99002 | 0.35271 | 0.7873 |
| Fork length (cm) | 569.3 | 569.9 | — | | | |
| Mass (g) | 2371.4 | 2548.7 | — | | | |
| Gonad mass ($log_{10}$, g) | 0.99 | 1.13 | 0.654 | | | |
| Condition factor ($g \cdot mm^{-1}$) | 1.24 | 1.25 | 0.161 | | | |
| **STRUCTURE** | | | | | | |
| Age (years) | 11.6 | 12.0 | −0.002 | 0.97024 | 1.9632 | 0.1209 |
| Fork length (cm) | 565.7 | 574.0 | — | | | |
| Mass (g) | 2498.3 | 2513.5 | — | | | |
| Gonad mass ($log_{10}$, g) | 1.05 | 1.17 | 0.623 | | | |
| Condition factor ($g \cdot mm^{-1}$) | 1.28 | 1.22 | −6.298 | | | |

not removed. Therefore, we only report the results of the latter analysis in subsequent sections.

Each independent run of the STRUCTURE analysis for any one *K* value showed consistency in the ln*P*(*D*|*K*) values (not shown), indicating that the runs typically converged. The analysis with all the individuals returned a peak in ln*P*(*D*|*K*) value (i.e., $log_e$ probability of the data given *K*) at *K* = 11 (Fig. S3 in the online Supplementary Material[1]). Using the Δ*K* statistic, however, returned a multimodal distribution of Δ*K* values, with peaks at *K* = 2, 4, and 11 (Δ*K* values of 29.2, 24.8, and 3.1, respectively; Fig. S3 in the online Supplementary Material[1]). Such multimodal distributions of Δ*K* values are expected when hierarchical population structure is present (Evanno et al. 2005; Coulon et al. 2008). Because the level of population structure most appropriate for our current question is the population (i.e., lake) level, and because the ln*P*(*D*|*K*) criteria has been shown to perform better than the Evanno et al. (2005) method when genetic differentiation among populations is low (Waples and Gaggiotti 2006), we chose to use the value of *K* with the highest ln*P*(*D*|*K*) (i.e., *K* = 11) for all further analyses. Under this assumption, the samples of juveniles generally clustered by sampling location (Fig. S3 in the online Supplementary Material[1]), although the results also show a number of admixed individuals in each population. The adult samples, however, had a higher frequency of admixed individuals and of individuals that were assigned to a cluster that was different than the consensus cluster for that capture location (i.e., the cluster to which most other fish from that location, including juveniles, were assigned; Fig. S3 in the online Supplementary Material[1]). This was reflected in the average *Q* value (admixture coefficient) of adult fish (average *Q* = 0.53) being 15% smaller than that of juvenile fish (average *Q* = 0.68) for the cluster in which they were captured ($t$ = 7.26, df = 789, $P < 0.0001$). Elimination of all adult samples with a maximum *Q* value lower than 0.5 reduced our sample size from 359 to 259. Of the 259 individuals used in the analysis, only 41 were assigned to a genetic cluster different than that where they were caught, leading to a total dispersal estimate of 15.8%. As for the GeneClass2 analysis, the dispersers appeared to be most likely from a geographically proximate locality, although this pattern was less pronounced with this analysis (Fig. 3*b*).

### Breeding dispersal and overwintering dispersal

The distribution of GSI was clearly bimodal with two almost nonoverlapping distributions for each sexes, thus making the distinction between breeding and nonbreeding individuals relatively accurate (Fig. S1 in the online Supplementary Material[1]). All analyses conducted supported the hypothesis that overwintering fish were more likely to disperse than breeding fish. In the analysis including all individuals, we found that 69.4% of individuals assigned as dispersers were overwintering dispersers. Breeding individuals, on the other hand, were classified as philopatric more often than they were classified as dispersing (two-tailed Fisher's exact test, df = 358, $P = 0.009$). This pattern held after removing the individuals with an assignment score of less than 95% (df = 156, $P = 0.043$; Fig. 3*c*), although proportionally fewer overwintering individuals were found to disperse. This result also held when assignment tests were performed on the data set from which the full-sibs were removed (df = 358, $P = 0.012$). Finally, the results of the STRUCTURE analysis also support the conclusion that overwintering individuals are more likely to disperse, even if it generally estimated lower dispersal rates (df = 258, $P = 0.016$; Fig. 3*d*).

### Other correlates of dispersal propensity

We found no evidence of sex-biased dispersal. In the GeneClass2 analysis including all individuals, we found that 55.1% of dispersers and 45.8% of philopatric individuals were females ($P = 0.0907$). For the GeneClass2 analysis including only individuals with confident assignment, 65.0% of dispersers and 48.7% of philopatric individuals were females ($P = 0.0985$). Finally, in the analysis using STRUCTURE, 42.9% of dispersers and 50.5% of philopatric individuals were females ($P = 0.3480$). None of the other biological traits we examined could discriminate significantly between the dispersing and philopatric individuals (Table 1; Fig. S4 in the online Supplementary Material[1]).

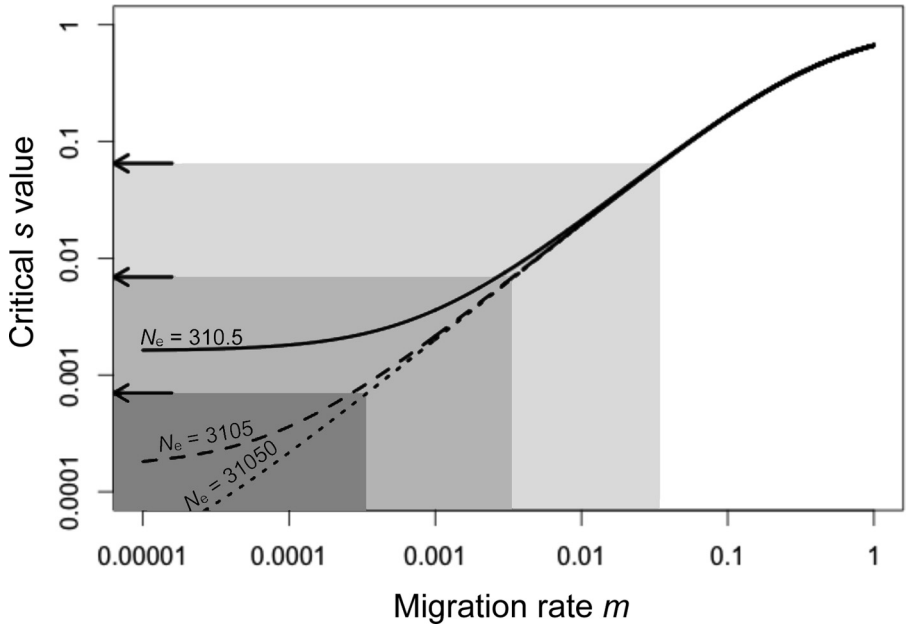
### Potential for local adaptation

Parameterization of the continent–island migration population genetic model for Arctic char suggested that local adaptation is likely for biologically realistic values of the selection coefficient *s* (Fig. 4). The MIGRATE runs returned mean (averaged over all sampling locations) $\theta$ and *M* values of 1.24 (SD = 0.39) and 1.99 (SD = 0.88), respectively (see online Supplementary Material for details[1]). Depending on the mutation rate used, this led to estimates of $N_e$ varying from 310 to 31 000 and estimates of *m* varying from 0.00034 to 0.034 (where *m* was obtained by adding the effective number of migrants coming from all samples, $N_e m$, and dividing by the local effective population size). Parameterization of the model yielded critical values for *s* (i.e., values above which local adaptation is expected) of 0.065, 0.0069, and 0.0007 assuming mutation rates of $10^{-3}$, $10^{-4}$, and $10^{-5}$, respectively.

## Discussion

To evaluate the evolutionary consequences of dispersal, it is important to resolve whether dispersal typically results in gene flow (Garant et al. 2007). The main objective of our study was to use genetic assignment to better understand the migratory behaviour of Arctic char by explicitly taking into account the reproduc-

**Fig. 4.** The relationship between the critical value of the selection coefficient (s) and the migration rate (m) for different values of the mutation rate (both axes are on a log scale). The three lines show the relationship between *s* and *m* for the three values of $N_e$ obtained from MIGRATE assuming a mutation rate of $10^{-3}$ (solid), $10^{-4}$ (dashed), and $10^{-5}$ (dotted). The arrows and shading show the calculated values of the critical *s* if both *m* and $N_e$ obtained from MIGRATE are used to parameterize the continent–island model, again depending on the mutation rate assumed: $10^{-3}$ (top), $10^{-4}$ (middle), and $10^{-5}$ (bottom). For all values of *s* above the arrows and shading, local adaptation is expected.






tive status of the dispersers, thus allowing an evaluation of the proportion of dispersal events that have the potential to result in gene flow. We found that dispersal among sampling locations was very common, more common in fact than reported in most other species of salmonids (Hendry et al. 2004). We also found, however, that a large proportion of dispersers were nonreproducing individuals using non-natal habitats for overwintering. This behaviour, whereby overwintering individuals have a greater propensity to use non-natal habitats than fish destined to spawn that year, could have important implications for the process of local adaptation in those populations and for the scale over which the commercial fishery for anadromous Arctic char should be managed.

### High dispersal in anadromous Arctic char

To measure dispersal, we used three different genetic assignment approaches (two in GeneClass2 and one in STRUCTURE) that led to considerably different estimates (varying from 15.8% to 46.5%) of the proportion of dispersers in the samples. The highest estimate, however, was generated without removing individuals with low assignment scores, and less confidence should be placed on this estimate. When the individuals with low assignment scores were removed from the GeneClass2 analysis, the estimated dispersal (25.5%) was much more comparable to the estimates generated in STRUCTURE (15.8%). Nevertheless, the absolute values of dispersal rates calculated in our study should be interpreted with caution. Furthermore, the assignment tests performed in GeneClass2 suffered from generally low assignment scores and low probabilities of assignment. In fact, 56% of all adult samples did not meet our ≥95% criterion for confident assignment. The low confidence of assignment may stem from several factors. First, the power of assignment tests increases with increasing genetic differentiation (Paetkau et al. 2004; Manel et al. 2005). The populations used in this study are only weakly differentiated (average pairwise $F_{ST}$ of 0.045 between the samples of juveniles). This could be due to recent recolonization following the last glaciation (<10 000 years ago), large effective population sizes ($N_e$) preventing accumulation of genetic differences through drift, or ongoing gene flow. Other studies, however, have achieved greater confidence in assignment despite lower levels of genetic differentiation (e.g., $F_{ST}$ 0.02 in Hauser et al. 2006). In addition, we used sample sizes and a number of loci that simulations have shown to allow for confident assignment despite low genetic differentiation (Paetkau et al. 2004). A second reason for low confidence in assignment could be that the individuals with low assignment probability come from unsampled populations (i.e., so-called "ghost" populations; Beerli 2004). We cannot fully discount this potential problem, but even if all adults with low assignment probability were in fact dispersers from unsampled populations (which seems unlikely because we sampled most populations around Cumberland Sound), they would still be dispersers, therefore not affecting our estimates of dispersal rates. Finally, low confidence in assignment may be the result of the presence of sibs in the samples of juveniles used as reference samples. The increase in average probability of assignment after the removal of sibs from the juvenile samples (the average increased from 34% to 49%) suggests that this constitutes at least part of the explanation. The proportions and identity of the dispersers, however, did not change appreciably after the removal of the sibs, suggesting the conclusions of our study are not influenced by sibling relationships.

Despite considerable differences in the estimates of dispersal rates depending on the method used, all estimates remain fairly high: in the order of 15.8%–46.5% per year. High rates of dispersal are consistent with previously published estimates from tagging studies of Arctic char. For example, Gyselman (1994) estimated a dispersal rate of 47% per year, with substantial variation among years (33%–66% per year). In another study, Dempson and Kristofferson (1987) reported rates of dispersal that varied tremendously among regions. The proportion of tagged fish that were recaptured in a different river (dispersers) varied between 0% and 17% per year among 12 different rivers in Labrador (eastern Canadian Arctic). By contrast, in the Cambridge Bay area of Canada's central Arctic, those proportions were much higher, varying between 13% and 51% per year among four rivers (Dempson and

Kristofferson, 1987). Our estimates based on genetic assignment tests therefore fall well within the range of previously reported values for Arctic char. They are, however, at the upper end of the scale of dispersal rates reported in salmonids. Indeed, a recent compilation of straying rates from tagging studies performed on salmonids (but excluding Arctic char) documented straying rates varying from 0.0% to 41.6% per year, with a median of 4.4% (Hendry et al. 2004). The studies reviewed in Hendry et al. (2004) were conducted at a variety of spatial scales, and our study was conducted on a relatively small spatial scale (maximum distance between sites <400 km), which presumably would be associated with higher dispersal among localities. Furthermore, all the species reviewed in Hendry et al. (2004) are species that only migrate for the purpose of breeding. Because we found overwintering dispersal to be higher than breeding dispersal (next section), this could partly explain why dispersal rates are generally higher in Arctic char than in other salmonids.

### Overwintering individuals have an increased propensity to disperse

We presented several lines of evidence that although total dispersal was high among sampling locations, the number of dispersal events that may result in gene flow is considerably lower. We found that the average $F_{ST}$ between pairs of juvenile samples is significantly higher than between pairs of adult samples from the same location. The weaker genetic differentiation observed among samples of adults would arise if they contained dispersing fish from non-natal populations. Greater genetic differentiation among samples of juveniles, however, suggests that dispersal of adults to other systems does not always result in gene flow. One alternative explanation for this pattern is that the juveniles sampled were more often from the same family group — a phenomenon referred to as the Allendorf–Phelps effect (Waples 1998). Our sibship reconstructions using the program COLONY, however, suggested that this alternative is unlikely. First, the number of full-sib groups in any sample was typically small. Second, when putative sibs were removed from the analysis, our findings remained unchanged. Another alternative explanation could be that genetic differentiation in juveniles increases through drift because of high variance in reproductive success of adults. While we cannot discount this alternative, we note that its effect should be fairly small given that we sampled multiple cohorts of adults and juveniles.

The lower genetic differentiation between samples of adults is consistent with our finding that a large proportion of dispersing individuals are not in reproductive condition and therefore do not contribute to gene flow. In fact, of the total number of dispersers identified by the genetic assignment tests, between 69.4% (for the analysis including all individuals) and 75.6% (for the analysis conducted in STRUCTURE) were fish whose nonreproductive status suggests that they were migrating to overwinter and have thus no potential for gene flow. These numbers are consistent across analyses, even if the analyses returned considerably different total rates of dispersal. Such a high proportion of nonbreeding fish is probably the result of three life-history characteristics of Arctic char. First, Arctic char do not breed every year (Dutil 1986). In fact, roughly two-thirds of all adult fish collected for this study were not in reproductive condition, suggesting that skipping 2 years between reproductive events may be common in Cumberland Sound Arctic char. Such “skipped breeding” is not unique to Arctic char and has been documented in many species of fish, including Atlantic salmon (*Salmo salar*; Rideout and Tomkiewicz 2011). Second, and contrary to many iteroparous species, Arctic char that skip a spawning season must return to fresh water to overwinter (Johnson 1980). This is unusual for salmonids, the great majority of them only returning to fresh water to spawn. It is not unique, however, and is a behaviour also displayed by some nonmature brown trout (*Salmo trutta*) who cannot tolerate high salinity for long periods (Larsen et al. 2008) and by the closely related Dolly Varden (*Salvelinus malma*; Armstrong 1974). Third, we have provided evidence that fish migrating to fresh water for the purpose of overwintering are more likely to utilize non-natal habitats. This unusual form of condition-dependent dispersal (Ims and Hjermann 2001) is also thought to occur in Dolly Varden (Armstrong 1974) and had been posited to occur in Arctic char (Johnson 1980), although evidence remained indirect. For instance, Gyselman (1994) operated a weir on the Nauyuk River and tagged fish on their downriver migration after spawning. He found that many postspawning tagged fish did not return the following year, but that 7.2% of the tagged fish did return 1 or 2 years later in spawning condition (Gyselman 1994), suggesting that they used a non-natal habitat in the intervening years. The evidence from our genetic assignment tests suggests that overwintering char are more likely to use non-natal habitats and that such behaviour may be widespread among anadromous Arctic char populations.

Dispersers did not differ from philopatric individuals in a number of other biological traits. First, we found no evidence of sex-biased dispersal. The promiscuous mating system of salmonids, the intense competition for females among males, and the fact that a female's reproductive success is mainly limited by her ability to produce eggs lead to the prediction that dispersal should be male-biased in salmonids (Hutchings and Gerber 2002). There are in fact several studies that have reported evidence of male-biased dispersal in other species of salmonids (Hutchings and Gerber 2002; Bekkevold et al. 2004; Fraser et al. 2004; Neville et al. 2006). The pattern, however, is not universal, and Consuegra and Garcia de Leaniz (2007) failed to find evidence for sex-biased dispersal in Atlantic salmon. Comparatively little is known about the effect of other traits on individual dispersal propensity in salmonids. One variable that has been found to be associated with dispersal propensity is age, with studies variously reporting that older (Quinn 1993) or younger (Hard and Heard 1999) fish have increased dispersal propensity. In our study, we found no evidence of trait-dependent dispersal, and none of the biological variables we examined, including age, differed between dispersing and philopatric individuals. Lack of evidence for condition-dependent dispersal in our study, and the weak and inconsistent evidence for condition-dependent dispersal in other salmonid species, is in contrast with the widespread nature of this phenomenon in other taxa (Ims and Hjermann 2001; Clobert et al. 2004; Bowler and Benton 2005).

### Potential for local adaptation

Dispersal can have important consequences for local adaptation, but dispersers need to successfully reproduce in the non-natal habitat. Our study shows that only 24% to 31% of dispersers are in reproductive condition, which, when multiplied by the total dispersal rates calculated (i.e., 15.6% to 46.5%, depending on the analysis method), led to an estimate of breeding dispersal rate of 4%–14% per year (for the analyses conducted in STRUCTURE and that conducted in GeneClass2 including all individuals, respectively). While this is considerably lower than total dispersal (16%–46% per year), it still has the potential to translate into rates of gene flow high enough to prevent local adaptation. It is unlikely, however, that all breeding dispersers will successfully reproduce in the non-natal environment. Indeed, heterogeneous habitats can lead to selection against migrants, and many studies have found evidence for this process in salmonids (Tallman and Healey 1994; Hendry et al. 2000; Dionne et al. 2008) and other taxa (for a review, see Nosil et al. 2005). While we do not have evidence for selection against migrants in this system, the generally lower rates of gene flow calculated with MIGRATE (0.034% to 3.4%) suggest that breeding dispersers may indeed have lower reproductive success than local fish. More work would be necessary to under-

stand the cause of this discrepancy between the rates of breeding dispersal and gene flow.

The estimates of gene flow generated by MIGRATE were also used to parameterize a population genetic model of the balance among selection, gene flow, and drift (Adkison 1995; Yeaman and Otto 2011). Similar approaches have been used extensively in other studies of anadromous fishes as a tool to explore the potential for local adaptation (Hansen et al. 2002; McCairns and Bernatchez 2008). The goal of such analyses is to demonstrate that local adaptation is a possible outcome given biologically realistic parameter values, not to demonstrate the existence of local adaptation. Our results suggest that local adaptation in Cumberland Sound Arctic char is possible, given that selective environments are sufficiently heterogeneous. The model suggested that depending on the mutation rate assumed, selection coefficients ranging from 0.0007 to 0.065 may be sufficient to drive local adaptation. A review of estimates of the strength of *s* on major quantitative trait loci in nature suggests that values ranging from 0.01 to 0.05 are most typical (Morjan and Rieseberg 2004). All but the highest estimate of *s* derived from the parameterization, therefore, could potentially lead to local adaptation under biologically realistic conditions. In addition, the highest critical *s* value we obtained assumed a mutation rate ($10^{-3}$) that is probably higher than that of most salmonid microsatellites (Steinberg et al. 2002). This approach makes several assumptions that are likely violated in Cumberland Sound. Indeed, the MIGRATE analysis, which assumes equilibrium conditions, is potentially problematic in the present case because the populations used were only recently established following the last glaciation (<8000 years ago). Furthermore, the model that we parameterized makes many simplifying assumptions regarding the spatial scale of gene flow. The assumptions violated both in the MIGRATE analysis and in the simple model, however, are likely to lead to underestimated potential for local adaptation and therefore make our conclusions conservative (discussed in the Materials and methods section). In short, the parameterization of the population genetic model is a decidedly exploratory approach. The results do suggest, however, that local adaptation is a possibility that should be explored in more detail in anadromous Arctic char, especially given how prevalent local adaptation is in other anadromous salmonids (Taylor 1991; Fraser et al. 2011).

### Management implications

Our work has a few important implications for the management of the commercial fishery for anadromous Arctic char in Nunavut. First, the genetic assignment tests, while they did not allow a precise quantification of the amount of dispersal, still suggest that dispersal is high and should be considered in management. Second, we show that while dispersal is high, gene flow remains fairly low. This introduces an interesting challenge for management: how to reconcile the more regionally integrated approach suggested by the dispersal estimates with the fact that gene flow is low enough that each river may represent an independently evolving, distinct genetic unit (Fraser and Bernatchez 2001)? An appropriate compromise may be to continue managing the fishery on a river-by-river basis, but to use information on dispersal when specific conservation actions are required. For example, if a population showed evidence of declining abundance, it may be important to reduce fishing pressure on nearby populations in addition to reducing pressure on the focal population. More precise estimates of dispersal, using telemetry or genetic assignment aided by new sequencing technologies, would be useful in implementing such a management approach.

## Acknowledgements

This study was made possible by the participation of the Pangnirtung Hunters and Trappers Association, who offered help in the field and shared their extensive knowledge of Arctic char with the authors. More specifically, we thank P. Qappik, J. Maniapik, S. Sowdloapik, P. Kilabuk, J. Akpailaluk, J. Ishulutak, T. Nauyuk, J. Shoapik, N. Shoapik, J. Kakee, and D. Nakashuk. Help with the logistics and in the field was also provided by S. Wiley and M. Toyne. We thank R. Bajno for insights in the lab and L. Bernatchez, V. Castric, O. Gaggiotti, A. Hendry, J. Mee, and M. Whitlock for useful comments on the study. S. Yeaman derived the continent–island model used to evaluate the potential for local adaptation. M. Hansen and six anonymous reviewers provided useful comments on an earlier version of the manuscript. Funding for the fieldwork was provided by the Polar Continental Shelf, Indian and Northern Affairs Canada (through two Northern Scientific Training Program scholarships awarded to JSM), the Natural Sciences and Engineering Research Council of Canada (NSERC, through a Northern Research Internship awarded to JSM and a Discovery Grant awarded to EBT), and from Fisheries and Oceans Canada. JSM was supported by an NSERC Canada Graduate Scholarship, a Bourse de Doctorat en Recherche from the Fond Québécois sur la Nature et les Technologies, and a Four Year Scholarship from The University of British Columbia.

## References

Adkison, M.D. 1995. Population differentiation in Pacific salmons: local adaptation genetic drift, or the environment? Can. J. Fish. Aquat. Sci. **52**(12): 2762–2777. doi:10.1139/f95-865.

Anderson, R., and Neuman, R.M. 1996. Length, weight, and associated structural indices. *In* Fisheries techniques. *Edited by* B.R. Murphy and R.M. Neuman. American Fisheries Society, Bethesda, Maryland.

Armstrong, R.H. 1974. Migration of anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. J. Fish. Board Can. **31**(4): 435–444. doi:10.1139/f74-071.

Beerli, P. 2004. Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. Mol. Ecol. **13**: 827–836. doi:10.1111/j.1365-294X.2004.02101.x. PMID:15012758.

Beerli, P., and Felsenstein, J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. Proc. Nat. Acad. Sci. **98**: 4563–4568. doi:10.1073/pnas.081068098. PMID:11287657.

Bekkevold, D., Hansen, M.M., and Mensberg, K.L.D. 2004. Genetic detection of sex-specific dispersal in historical and contemporary populations of anadromous brown trout *Salmo trutta*. Mol. Ecol. **13**: 1707–1712. doi:10.1111/j.1365-294X.2004.02156.x. PMID:15140113.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N., and Bonhomme, F. 2004. GENETIX 4.05, logiciel sous Windows pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000. Université de Montpellier II, Montpellier.

Bohonak, A.J. 1999. Dispersal, gene flow, and population structure. Quart. Rev. Biol. **74**: 21–45. doi:10.1086/392950. PMID:10081813.

Bowler, D.E., and Benton, T.G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. **80**: 205–225. doi:10.1017/S1464793104006645. PMID:15921049.

Cavalli-Sforza, L.L., and Edwards, A.W.F. 1967. Phylogenetic analysis: models and estimation procedures. Am. J. Hum. Genet. **19**: 233. doi:10.2307/2406616.

Clobert, J., Wolff, J.O., Nichols, J.D., Danchin, E., and Dhondt, A.A. 2001. Introduction. *In* Dispersal. *Edited by* J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols. Oxford University Press, Oxford.

Clobert, J., Ims, R.A., and Rousset, F. 2004 Causes, mechanisms and consequences of dispersal. *In* Ecology, genetics and evolution of metapopulation. *Edited by* I. Hanski and O. Gaggiotti. Elsevier Academic Press. pp. 307–335.

Consuegra, S., and Garcia de Leaniz, C. 2007. Fluctuating sex ratios, but no sex-biased dispersal, in a promiscuous fish. Evol. Ecol. **21**: 229–245. doi:10.1007/s10682-006-9001-7.

Coulon, A., Fitzpatrick, J.W., Bowman, R., Stith, B.M., Makarewich, C.A., Stenzler, L.M., and Lovette, I.J. 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida scrub-jay (*Aphelocoma cirulescens*). Mol. Ecol. **17**: 1685–1701. doi:10.1111/j.1365-294X.2008.03705.x. PMID:18371014.

Dempson, J.B., and Kristofferson, A.H. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. *In* Common strategies of anadromous and catadromous fishes. *Edited by* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper. American Fisheries Society Symposium. pp. 340–357.

Dewoody, J., Nason, J.D., and Hipkins, V.D. 2006. Mitigating scoring errors in microsatellite data from wild populations. Mol. Ecol. Notes, **6**: 951–957.

Dionne, M., Caron, F., Dodson, J., and Bernatchez, L. 2008. Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. Mol. Ecol. **17**: 2382–2396. doi:10.1111/j.1365-294X.2008.03771.x. PMID:18430145.

Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia, **4**: 945–955.

Earl, D.A. 2011. Structure Harvester v0. 3 [online]. Available from: http://taylor0.biology.ucla.edu/structureHarvester/ [accessed 1 March 2013].

Ehrlich, P.R., and Raven, P.H. 1969. Differentiation of populations. Science, **165**: 1228–1232. doi:10.1126/science.165.3899.1228. PMID:5803535.

Evanno, G., Regnaut, S., and Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. **14**: 2611–2620. doi:10.1111/j.1365-294X.2005.02553.x. PMID:15969739.

Felsenstein, J. 1993. PHYLIP: phylogenetic inference package, version 3.5 c.

Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Can. J. Fish. Aquat. Sci. **55**(S1): 59–76. doi:10.1139/d98-009.

Fraser, D.J., and Bernatchez, L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Mol. Ecol. **10**: 2741–2752. doi:10.1046/j.0962-1083.2001.01411.x. PMID:11903888.

Fraser, D.J., Lippé, C., and Bernatchez, L. 2004. Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). Mol. Ecol. **13**: 67–80. doi:10.1046/j.1365-294X.2003.02038.x. PMID:14653789.

Fraser, D.J., Weir, L.K., Bernatchez, L., Hansen, M.M., and Taylor, E.B. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity, **106**: 404–420. doi:10.1038/hdy.2010.167. PMID:21224881.

Garant, D., Forde, S.E., and Hendry, A.P. 2007 The multifarious effects of dispersal and gene flow on contemporary adaptation. Funct. Ecol. **21**: 434–443. doi:10.1111/j.1365-2435.2006.01228.x.

Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9. 3).

Gyselman, E.C. 1994. Fidelity of anadromous Arctic char (*Salvelinus alpinus*) to Nauyuk Lake, N.W.T., Canada. Can. J. Fish. Aquat. Sci. **51**(9): 1927–1934. doi:10.1139/f94-194.

Hansen, M.M., Ruzzante, D.E., Nielsen, E.E., Bekkevold, D., and Mensberg, K.L.D. 2002. Long-term effective population sizes, temporal stability of genetic composition and potential for local adaptation in anadromous brown trout (*Salmo trutta*) populations. Mol. Ecol. **11**: 2523–2535. doi:10.1046/j.1365-294X.2002.01634.x. PMID:12453237.

Hard, J.J., and Heard, W.R. 1999. Analysis of straying variation in Alaskan hatchery chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. Can. J. Fish. Aquat. Sci. **56**(4): 578–589. doi:10.1139/f98-199.

Harris, L.N., and Tallman, R.F. 2010. Information to support the assessment of Arctic Char, *Salvelinus alpinus*, from the Isuituq River system, Nunavut. DFO Can. Sci. Adv. Sec. Sci. Res. Doc. 2010/063:vi+37.

Hauser, L., Seamons, T.R., Dauer, M., Naish, K.A., and Quinn, T.P. 2006. An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (*Onchorhynchus mykiss*) in Forks Creek, Washington, USA. Mol Ecol **15**: 3157–3173.

Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., and Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science, **290**: 516–518. doi:10.1126/science.290.5491.516. PMID:11039932.

Hendry, A.P., Castric, V., Kinnison, M.T., and Quinn, T.P. 2004. The evolution of phylopatry and dispersal: homing versus straying in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford.

Howard, W.E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. **63**: 152–161. doi:10.2307/2422936.

Hutchings, J.A., and Gerber, L. 2002. Sex-biased dispersal in a salmonid fish. Proc. R. Soc. B Biol. Sci. **269**: 2487–2493. doi:10.1098/rspb.2002.2176.

Ims, R.A., and Hjermann, D. 2001. Condition-dependent dispersal. *In* Dispersal. *Edited by* J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols. Oxford University Press, Oxford. pp. 203–216.

Jakobsson, M., and Rosenberg, N.A. 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics, **23**: 1801–1806. doi:10.1093/bioinformatics/btm233. PMID:17485429.

Johnson, L. 1980. The Arctic charr. *In* Charrs: salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Dr. W. Junk bv Publishers, The Hague. pp. 15–98.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* L.: a review of aspects of their life histories. Ecol. Freshw. Fish, **12**: 1–59. doi:10.1034/j.1600-0633.2003.00010.x.

Kristofferson, A.H., and Berkes, F. 2005. Adaptive co-management of Arctic char in Nunavut Territory. *In* Breaking ice: renewable resource and ocean management in the Canadian north. *Edited by* F. Berkes, R. Huebert, H. Fast, M. Manseau, and A. Diduck. University of Calgary Press, Calgary, Canada.

Larsen, P., Nielsen, E., Koed, A., Thomsen, D., Olsvik, P., and Loeschcke, V. 2008. Interpopulation differences in expression of candidate genes for salinity tolerance in winter migrating anadromous brown trout (*Salmo trutta* L.). BMC Genet. **9**: 12. doi:10.1186/1471-2156-9-12.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends Ecol. Evol. **17**: 183–189. doi:10.1016/S0169-5347(02)02497-7.

Loewen, T.N., Gillis, D., and Tallman, R.F. 2009. Ecological niche specialization inferred from morphological variation and otolith strontium of Arctic charr *Salvelinus alpinus* L. found within open lake systems of southern Baffin Island, Nunavut, Canada. J. Fish Biol. **75**: 1473–1495.

Manel, S., Gaggiotti, O.E., and Waples, R.S. 2005. Assignment methods: matching biological questions with appropriate techniques. Trends Ecol. Evol. **20**: 136–142. doi:10.1016/j.tree.2004.12.004. PMID:16701357.

McCairns, R.J., and Bernatchez, L. 2008. Landscape genetic analyses reveal cryptic population structure and putative selection gradients in a large-scale estuarine environment. Mol. Ecol. **17**: 3901–3916. doi:10.1111/j.1365-294X.2008.03884.x. PMID:18662229.

McDowall, R.M. 1987. Evolution and the importance of diadromy: the occurence and distribution of diadromy in fishes. Am. Fish. Symp. **1**: 1–13.

Morjan, C.L., and Rieseberg, L.H. 2004. How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. Mol. Ecol. **13**: 1341–1356. doi:10.1111/j.1365-294X.2004.02164.x. PMID:15140081.

Neville, H.M., Isaak, D.J., Dunham, J.B., Thurow, R.F., and Rieman, B.E. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. Mol. Ecol. **15**: 4589–4602. doi:10.1111/j.1365-294X.2006.03082.x. PMID:17107485.

Nosil, P., Vines, T.H., and Funk, D.J. 2005. Reproductive isolation caused by natural selection against immigrants from divergent habitats. Evolution, **59**: 705–719. doi:10.1554/04-428. PMID:15926683.

Paetkau, D., Slade, R., Burden, M., and Estoup, A. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol. Ecol. **13**: 55–65. doi:10.1046/j.1365-294X.2004.02008.x. PMID:14653788.

Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L., and Estoup, A. 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. J. Hered. **95**: 536–539. doi:10.1093/jhered/esh074. PMID:15475402.

Priest, H., and Usher, P.J. 2004. Final Report: Nunavut Wildlife Harvest Study 1996–2001, prepared for the Nunavut Wildlife Management Board. p. 816.

Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics, **155**: 945–959. PMID:10835412.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**: 29–44. doi:10.1016/0165-7836(93)90038-9.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. UBC Press.

Rambaut, A. 2010. FigTree. Version 1.3. 1 [online]. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. Available from http://tree.bio.ed.ac.uk/software/figtree.

Rannala, B., and Mountain, J.L. 1997. Detecting immigration by using multilocus genotypes. Proc. Nat. Acad. Sci. **94**: 9197–9201. doi:10.1073/pnas.94.17.9197. PMID:9256459.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Austria (01/19).

Rideout, R.M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: more common than you might think. Mar. Coast. Fish. **3**: 176–189. doi:10.1080/19425120.2011.556943.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst. **38**: 231–253. doi:10.1146/annurev.ecolsys.38.091206.095611.

Roux, M.J., Tallman, R.F., and Lewis, C.W. 2011. Small-scale Arctic charr *Salvelinus alpinus* fisheries in Canada's Nunavut: management challenges and options. J. Fish Biol. **79**: 1625–1647. doi:10.1111/j.1095-8649.2011.03092.x. PMID:22136243.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: What science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**: 665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science, **236**: 787–792. doi:10.1126/science.3576198. PMID:3576198.

Steinberg, E.K., Lindner, K.R., Gallea, J., Maxwell, A., Meng, J., and Allendorf, F.W. 2002. Rates and patterns of microsatellite mutations in pink salmon. Mol. Biol. Evol. **19**: 1198–1202. doi:10.1093/oxfordjournals.molbev.a004177. PMID:12082138.

Storfer, A. 1999. Gene flow and endangered species translocations: a topic revisited. Biol. Conserv. **87**: 173–180. doi:10.1016/S0006-3207(98)00066-4.

Tallman, R.F., and Healey, M.C. 1994. Homing, straying, and gene flow among seasonally seperated populations of Chum salmon (*Oncorhynchus keta*). Can. J. Fish. Aquat. Sci. **51**(3): 577–588. doi:10.1139/f94-060.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture, **98**: 185–208. doi:10.1016/0044-8486(91)90383-I.

Utter, F., and Ryman, N. 1993. Genetic markers and mixed stock fisheries. Fisheries, **18**: 11–21. doi:10.1577/1548-8446(1993)018<0011:GMAMSF>2.0.CO;2.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., and Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol. Ecol. Notes, **4**: 535–538. doi:10.1111/j.1471-8286.2004.00684.x.

Wang, J., and Santure, A.W. 2009. Parentage and sibship inference from multilocus genotype data under polygamy. Genetics, **181**: 1579–1594. doi:10.1534/genetics.108.100214. PMID:19221199.

Waples, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Mar. Fish. Rev. **53**: 11–22.

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J. Hered. **89**: 438–450. doi:10.1093/jhered/89.5.438.

Waples, R.S., and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol. Ecol. **15**: 1419–1439. doi:10.1111/j.1365-294X.2006.02890.X.

Yeaman, S., and Otto, S.P. 2011. Establishment and maintenance of adaptive genetic divergence under migration, selection, and drift. Evolution, **65**: 2123–2129. doi:10.1111/j.1558-5646.2011.01277.x. PMID:21729066.