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Genetic analysis of sympatric migratory ecotypes of Arctic charr *Salvelinus alpinus*: alternative mating tactics or reproductively isolated strategies?

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Three populations of Arctic charr *Salvelinus alpinus* from southern Baffin Island were previously identified to display variable migratory phenotypes, with an anadromous component of the population and another remaining resident in fresh water. In this study, 14 microsatellite markers were used to help distinguish between two alternative hypotheses to explain the co-existence of the two ecotypes: that the two ecotypes originate from a single population and are the result of a conditional mating tactic or that the migratory ecotypes are reproductively isolated populations utilizing alternative migratory strategies. In two of the three replicate systems, F_{ST} values between the resident and anadromous individuals were non-significant, while they were significant in a third sampling location. Bayesian clustering analysis implemented in structure, however, failed to identify any within-location clustering in all three sampling locations. It is concluded from these analyses that the life-history ecotypes are most likely conditional mating tactics, rather than reproductively isolated populations. Other evidence in favour of the alternative mating tactic hypothesis is briefly reviewed, and implications for management of those populations are discussed.

Key words: anadromy; Baffin Island; life history; microsatellites; reproductive isolation; salmonids.

INTRODUCTION

Many populations of anadromous salmonids display variable life history, such that a section of the population matures at an early age opting to forego migrations to marine habitats, while another section undergoes anadromous migrations (Fleming, 1998; Hendry *et al.*, 2004). Such dimorphisms have traditionally been understood under the framework of conditional mating tactics (Hutchings & Myers, 1994; Gross, 1996; Thorpe *et al.*, 1998). Under this framework, one genotype is able to give rise to the two alternative mating tactics (residency *v*. anadromy) and the decision to follow a tactic is conditional on the individual's status (most commonly its size or

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growth rate in salmonids; Hendry *et al.*, 2004) such that the tactic will maximize the individual's fitness given its status (Gross, 1996). There are considerable empirical data that supports this interpretation of mating dimorphism in salmonids (Thomaz *et al.*, 1997; Thorpe *et al.*, 1998; Hendry *et al.*, 2004; Thériault *et al.*, 2007*a*).

An alternative explanation for intra-population variation in migratory behaviour is that it could represent two alternative, genetically fixed strategies (Gross, 1996). According to this model, differences in migratory behaviour are the result of a genetic polymorphism, and are maintained either because of frequency-dependent selection or because the two behaviours are expressed by two reproductively isolated populations (Gross, 1996). There is no evidence for the former mechanism in salmonids, but there are well-documented cases of reproductively isolated populations co-existing sympatrically, exhibiting different migratory strategies in sockeye salmon *Oncorhynchus nerka* (Walbaum 1972) (Taylor *et al.*, 1996; Wood & Foote, 1996); Atlantic salmon *Salmo salar* L. 1758 (Verspoor & Cole, 1989; Tessier & Bernatchez, 2000) and rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) (Docker & Heath, 2003).

The Arctic charr *Salvelinus alpinus* (L. 1758) displays variation in migratory behaviour throughout its range, with populations at the southern and northern extremes of the range being more likely to reside in fresh water year-round (*i.e.* resident populations), and populations at intermediate latitudes being more likely to be anadromous if access to marine habitats exists (Johnson, 1980). Anadromy, however, can also vary within a population and *S. alpinus* populations composed of anadromous and resident individuals have been identified in Norway (Nordeng, 1983; Rikardsen & Elliott, 2000) and in many parts of the Canadian Arctic (Reist, 1989; Babaluk *et al.*, 1997; Loewen *et al.*, 2009). Some evidence exists arguing that life-history variation in *S. alpinus* populations conforms to the alternative mating tactics framework. For example, in a population of *S. alpinus* from northern Norway that exhibited variable life history, resident parents were able to produce anadromous offspring and *vice versa*, suggesting that the behaviour is not completely genetically fixed (Nordeng, 1983).

In south-east Baffin Island, in Canada's Nunavut territory, three populations of *S. alpinus* are known to display variable migratory phenotypes (Loewen *et al.*, 2009, 2010; Fig. 1). Loewen *et al.* (2009) showed that in Qinngu, Iqaluggarjuit and Qasigigiat Lakes, anadromous individuals co-existed with individuals that matured at a much smaller size and did not migrate to the marine environment. Otolith strontium profiles showed that the small-maturing fish spent all their lives in the freshwater environment, except in Qasigigiat, where the small-maturing fish probably used the tidal habitat (Loewen *et al.*, 2009). Small-maturing fish were also found to differ from non-mature fish of similar size in a variety of morphological traits (*e.g.* eye diameter, pectoral fin and pelvic fin lengths), growth patterns and mean age (Loewen *et al.*, 2010). Furthermore, Loewen (2008) found that the sex ratio of the resident component of the population was heavily skewed towards males. This observation is consistent with the precocious male life-history strategy commonly observed in salmonids (Fleming, 1998; Fleming & Reynolds, 2004). The fact that precocious females were observed at all (Loewen, 2008), however, raises the possibility that the resident segment of the population is reproductively isolated from the anadromous segment.

In this paper, data from 14 microsatellite markers are used to test for the presence of genetic differentiation among migratory ecotypes of Baffin Island *S. alpinus* in

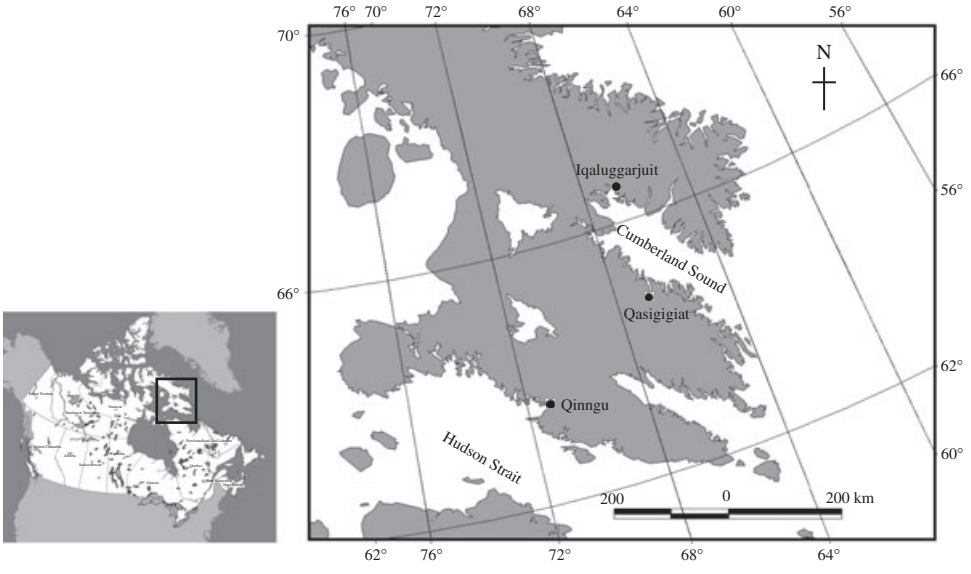

FIG. 1. Map showing the location of the three lakes with the sympatric migratory ecotypes of *Salvelinus alpinus* in south-eastern Baffin Island: Iqaluggarjuit, Qasigiat and Qinngu Lakes.

order to help evaluate two alternative hypotheses explaining the co-existence of the forms. The conditional mating tactic hypothesis makes the prediction that within each population, the resident and anadromous forms should not be genetically differentiated. Alternatively, the reproductively isolated ecotype hypothesis makes the prediction that within each population, the resident and anadromous forms should be at least in part genetically differentiated. This last prediction, however, only holds if the two forms have been reproductively isolated for enough time for neutral genetic differences to accumulate by genetic drift. The use of microsatellites, one of the fastest mutating markers available (Ellengren, 2000), for this study decreases the likelihood of this last explanation.

MATERIALS AND METHODS

FIELD SAMPLING

Loewen *et al.* (2009) provide extensive details regarding the study area and the field collection methods. In short, specimens of *S. alpinus* were collected from three lake systems in southern Baffin Island: Qinngu Lake close to the community of Kimmirut on the Meta Incognita Peninsula, and Qasigigiat and Iqaluggarjuit Lakes, both close to the community of Pangnirtung in the Cumberland Sound area (Fig. 1 and Table I). Sampling was conducted from late-August to mid-September from 2003 to 2009 when most anadromous individuals had migrated back to fresh water to overwinter and spawn. Fish were captured with multimesh (38–102 mm stretched mesh), 38 mm stretched mesh and 140 mm stretched mesh gillnets. For each fish collected in the field, fork length (L_F; mm), round mass (g), sex and maturity were recorded and the sagittal otoliths were removed and preserved for age and isotope analysis. The non-migratory nature of the small-maturing fish during the 2002 to 2005 sampling years were confirmed using otolith microchemistry (strontium distributions) described by Loewen *et al.*

TABLE I. Sampling locations with geographic co-ordinates and sample sizes for each *Salvelinus alpinus* ecotype per year for each location

Sampling location	Geographical co-ordinates		Year	Sample size	
	Latitude (N)	Longitude (W)		Resident	Anadromous
Iqaluggarjuit	66° 43·2′	66° 34·7′	2002	4	41
			2004	18	47
			2009	11	0
Qasigigiat	66° 19·1′	64° 37·5′	2003	12	33
			2004	8	30
			2009	6	42
Qinngu, Blandford Bay	63° 3·01′	71° 18·0′	2004	6	0
			2005	15	29

(2009). The migratory behaviour of the fish sampled in 2009, however, was not confirmed with otolith microchemistry. Given that all small-maturing fish in the study by Loewen *et al.* (2009) had strontium profiles consistent with freshwater residency, all the small-maturing fish sampled in 2009 were considered residents. The size cutoff used to define small-maturing fish was 400 mm L_F, as described by Loewen *et al.* (2009).

MICROSATELLITE DNA ANALYSIS

Individual genotypes were obtained at 18 microsatellite loci combined in four multiplexes (Table II). For each locus, the forward primer was labelled with a fluorescent dye, and the reverse primer was pig-tailed to reduce stutter and facilitate genotyping (Brownstein *et al.*, 1996). Polymerase chain reaction (PCR) amplifications were carried out in 10 µl volume reactions (see Table II for details). The PCR cycles were as follows: an initial denaturation step of 10 min at 95° C, 35 cycles of denaturation (45 s at 94° C), annealing (45 s at 55° C) and extension (45 s at 72° C), and a final extension cycle of 30 min at 72° C. The PCR products were run on an Applied Biosystems (www.appliedbiosystems.com) 3100 genetic analyser. GeneMapper 3.7 (Applied Biosystems) was then used to automatically score microsatellite alleles, and all scores were then manually checked for quality.

Basic descriptive statistics were calculated for each sample using the Microsatellite Toolkit (Park, 2001): number of alleles (N_A), observed heterozygosity (H_O) and Nei's (1987) unbiased expected heterozygosity (H_Z) controlling for sample size. FSTAT version 2.9.3.2 (Goudet, 2001) was used to test for Hardy–Weinberg equilibrium (HWE) and genotypic disequilibrium using default values for the number of permutations. For both tests, the nominal significance level was set at 0·05 (using a Bonferroni correction for multiple comparisons). FSTAT was used to calculate allelic richness (A_R, *i.e.* number of alleles controlling for sample size). Genetic differentiation between samples was also computed in FSTAT using Weir & Cockerham's (1984) θ estimator of pair-wise F_{ST} between each sample, and significance was assessed with 10 000 permutations (experiment-wide $\alpha = 0{\cdot}05$ after Bonferroni correction). The data set was first analysed with each sampling year kept separate. None of the F_{ST} values between years within sampling location, however, were significant and the years were therefore combined for all subsequent analyses. Analyses of molecular variance (AMOVA) were conducted in Arlequin 3.0 (Excoffier *et al.*, 2005) to test for the presence of hierarchical population structure. The hierarchical levels of population structure were first defined with the sampling locations (Qinngu, Qasigigiat and Iqaluggarjuit) as the groups, and the life-history ecotypes as the populations within groups. A second analysis was conducted with the ecotypes as the groups and the sampling locations as the populations within groups. A factorial correspondence analysis (FCA) was conducted in Genetix 4.05 (Belkhir *et al.*, 2004) to identify genetic discontinuities among samples.

TABLE II. Details of the primers and polymerase chain reactions (PCR) used for each of the four multiplexes to assess genetic variation of resident and anadromous *Salvelinus alpinus*

Multiplex	Locus	Dye	Reference	Primer (μM)	$MgCl_2$ (mM)	dNTPs (μM)	Taq*
mpAC1	*sco200*	VIC	DeHaan & Ardren (2005)	0·40	1·50	200	1·00
	smm22	NED	Crane *et al.* (2004)	0·40			
	sco220	6-FAM	DeHaan & Ardren (2005)	0·50			
	sco215	PET	DeHaan & Ardren (2005)	0·30			
mpAC2a†	*sco212*	6-FAM	DeHaan & Ardren (2005)	0·50	2·00	200	0·50
	sco218	VIC	DeHaan & Ardren (2005)	0·50			
	sfo18	NED	Angers *et al.* (1995)	0·20			
mpAC2b†	*sco202*	PET	DeHaan & Ardren (2005)	0·20	1·50	200	0·50
	smm21	VIC	Crane *et al.* (2004)	0·16			
mpAC3	*omm1128*	VIC	Rexroad *et al.* (2001)	0·16	2·00	200	0·50
	smm24	NED	Crane *et al.* (2004)	0·20			
	otsG253b	VIC	Williamson *et al.* (2002)	0·12			
	ssosl456	6-FAM	Slettan *et al.* (1995)	0·50			
	omm1105	PET	Rexroad *et al.* (2001)	0·20			
mpAC4	*otsG83b*	6-FAM	Williamson *et al.* (2002)	0·50	2·00	200	1·00
	smm17	NED	Crane *et al.* (2004)	0·16			
	sco109	VIC	Shaklee (2003)	0·50			
	sco216	PET	DeHaan & Ardren (2005)	0·40			

*AmpliTaq Gold DNA polymerase with gold buffer and $MgCl_2$ solution from Applied Biosystems.
†mpAC2a and mpAC2b were combined post-PCR for genotyping.

FCA is a multivariate approach for categorical variables (here diploid genotypes at different loci), which identifies a number of orthogonal axes that best explain variation in the data. Variation in individual genotypes was visualized along the first three axes explaining the most variation in the FCA.

The Bayesian clustering algorithm implemented via Structure 2.3.2 (Pritchard *et al.*, 2000) was used to determine the most likely number of genetic clusters among samples. The main advantage of the Structure algorithm is that it allows the identification of genetic discontinuities among samples without having to specify the sampling locations, or ecotypes, *a priori*. The algorithm accomplishes this by grouping together samples to maximize HWE and linkage equilibrium within a genetic cluster. Because the null hypothesis to be falsified with this analysis is that of panmixia, the algorithm was modified to maximize the likelihood of finding any genetic discontinuities in the samples. The LOCPRIOR model (Hubisz *et al.*, 2009) implemented via Structure 2.3.2 allows for sample group information to be used to aid in the clustering process. It does so by using the location of origin of each individual as a prior in the Bayesian algorithm. This model has been found to detect genetic structure at lower levels of divergence than the regular model, but does not detect the structure when it is not present (Hubisz *et al.*, 2009). Structure was run with the LOCPRIOR model under the admixture and correlated allele frequency conditions, with 250 000 burn-in and 500 000 Markov chain Monte Carlo (MCMC) replicates. K values (*i.e.* numbers of genetic clusters) ranging from one to 10 were tested, and 20 independent runs were conducted under each K value. The most likely number of genetic cluster was determined using the *post hoc* ΔK method advocated by Evanno *et al.* (2005). The software CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007) was used to combine the results of the 20 independent runs for the most likely K under the Greedy algorithm with 1000 replicates, and the results of the Structure analysis were visualized using Distruct 1.1 (Rosenberg, 2004). Structure was also run using the same conditions but without the LOCPRIOR model (Fig. S1, Supporting Information).

TABLE III. Summary statistics of microsatellite variation for each ecotypes of *Salvelinus alpinus* per sampling location. The data were analysed first for each year separate, but the years were found not to differ and were thus combined in all subsequent analyses. Number of alleles (N_A), allelic richness (A_R, *i.e.* number of alleles corrected for differences in sample size, only calculated for the 'years combined' samples), observed heterozygosity (H_O) and Nei's (1987) unbiased expected heterozygosity (H_Z) are shown

Sampling location	Life-history ecotype	Year	Years separate			Years combined			
			N_A	H_O	H_Z	N_A	H_O	H_Z	A_R
Iqaluggarjuit	Anadromous	2002	12·71	0·74	0·80	15·29	0·72	0·81	10·71
		2004	12·79	0·71	0·82				
	Resident	2002	4·79	0·74	0·83	11·79	0·74	0·81	10·61
		2004	9·64	0·70	0·81				
		2009	8·57	0·78	0·81				
Qasigigiat	Anadromous	2003	10·14	0·82	0·79	14·50	0·79	0·79	9·76
		2004	11·29	0·78	0·79				
		2009	12·14	0·77	0·78				
	Resident	2003	7·86	0·78	0·78	11·07	0·77	0·79	10·26
		2004	8·36	0·82	0·83				
		2009	5·29	0·68	0·70				
Qinngu	Anadromous	2005	10·93	0·65	0·75	10·93	0·65	0·75	9·82
	Resident	2004	5·86	0·74	0·76	9·93	0·77	0·78	9·84
		2005	8·86	0·78	0·78				

When hierarchical population structure is present, the Structure programme often identifies only the higher level of structure (Coulon *et al.*, 2008). To ensure that within-sampling location population structure is not obscured by higher-level structure, the Structure analysis was repeated for each sampling location separately. The LOCPRIOR model was used again, with life-history ecotypes as the specified population of origin. All other run parameters were identical to the analysis for all sampling locations simultaneously (*i.e.* admixture and correlated allele frequencies models, with 250 000 burn-in and 500 000 MCMC replicates, with K ranging from one to 10 tested in 20 independent runs). The Evanno *et al.* (2005) method was used again, and CLUMPP and DISTRUCT were used to combine and visualize the results according to the parameters specified above.

RESULTS

Two of the 18 microsatellite loci scored were monomorphic across all samples (*smm21* and *omm1128*) and were thus removed from all analyses. The remaining 16 loci were highly polymorphic (Table III) and the number of alleles per locus ranged from four (for *sco215*) to 77 (for *sco216*; mean = 22·6). After correction for multiple comparisons (adjusted $\alpha = 0{\cdot}0002$), four loci showed heterozygote deficits in at least one sampling location (here defined as samples of one ecotype collected in 1 year in one sampling location): *sco218* in five, *sco109* in three, *sco202* in one and *sco212* in one sampling location. Loci *sco218* and *sco109* have been found to be problematic in other datasets as well (J.-S. Moore, unpubl. data) and may suffer from null alleles or large allele dropouts. Those loci were therefore removed from

TABLE IV. Semi-matrix of pair-wise F_{ST} (Weir & Cockerham, 1984) values between all sampling locations (abbreviated with first three letters) and ecotypes ('res' for residents and 'anad' for anadromous) of *Salvelinus alpinus*

	IQAanad	IQAres	QASanad	QASres	QINanad	QINres
IQAanad	0	0·004	0·027*	0·025*	0·075*	0·064*
IQAres		0	0·031*	0·026*	0·068*	0·068*
QASanad			0	−0·001	0·079*	0·072*
QASres				0	0·079*	0·072*
QINanad					0	0·039*
QINres						0

*Significant population differentiation after correction for multiple comparisons (adjusted $\alpha = 0{\cdot}003$).

all subsequent analyses, leaving a total of 14 informative markers. Twelve pairs of loci displayed significant linkage disequilibrium before correction for multiple comparisons, but only two remained significant after correction: *sco200* × *sco216* and *Smm22* × *Sfo18*.

Various measures of genetic differentiation revealed significant population structure variation among the samples. Values of F_{ST} between Qinngu and the two Cumberland Sound sampling locations varied between 0·064 and 0·079 and were all significant after correction for multiple comparisons (adjusted $\alpha = 0{\cdot}003$; Table IV). The two Cumberland Sound sampling locations were also significantly differentiated, but F_{ST} values were smaller, ranging from 0·025 to 0·031 (Table IV). Genetic differentiation between ecotypes was not significant in Qasigigiat ($F_{ST} = -0{\cdot}001$) and in Iqaluggarjuit ($F_{ST} = 0{\cdot}004$), but was significant between ecotypes in Qinngu ($F_{ST} = 0{\cdot}039$). The AMOVA with sampling locations as groups found that genetic diversity among populations explained 94% of the variance, while sampling location explained 4·88% of the variance ($P > 0{\cdot}05$), and ecotypes only 0·47% ($P < 0{\cdot}05$) (Table V). When groupings were defined by ecotypes, among-ecotype differentiation explained −1·74% of the variation ($P > 0{\cdot}05$) while sampling locations explained 5·44% of the variation ($P < 0{\cdot}001$).

TABLE V. Results of the two analyses of molecular variance (AMOVA) conducted on the three *Salvelinus alpinus* sampling locations

Groupings	Source of variation	d.f.	Sum of squares	% Variance explained	*P*-value
By sampling location	Among sampling locations	2	72·3	4·88	>0·05
	Between ecotypes within sampling location	3	13·2	0·47	<0·05
	Within ecotypes	598	1915·3	94·65	<0·001
By ecotype	Among ecotypes	1	5·4	−0·06	>0·05
	Between sampling locations within ecotype	4	80·1	0·18	<0·001
	Within sampling locations	598	1915·3	3·20	<0·001

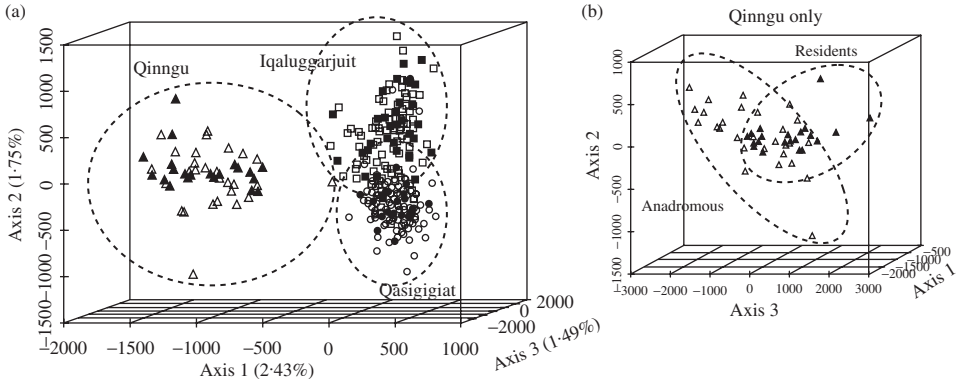

FIG. 2. Results of the factorial correspondence analysis (FCA) conducted on the three *Salvelinus alpinus* sampling locations (△, ▲, individuals from Qinngu; ○, ●, individuals from Qasigigiat; □, ■, individuals from Iqaluggarjuit). (a) Clustering of all the samples along the three most important axes of variation (△, ○, □, anadromous individuals; ▲, ●, ■, resident individuals). (b) Results of the same FCA, with only the Qinngu sampling locations shown. The axes have been re-organized to help visualization of the slight differentiation between anadromous and resident individuals along axis 3 in Qinngu.

The results of the FCA are in general agreement with the F_{ST} values and the AMOVA (Fig. 2). The three most important axes explained only 5·67% of the variation, with axes 1, 2 and 3 explaining 2·43, 1·74 and 1·49% of the variation [Fig. 2(a)], respectively. Because the amount of variation explained is small, the results should be interpreted with caution. There is a clear distinction between Qinngu and the two Cumberland Sound sampling locations along axis 1, while the two Cumberland Sound locations are separated, albeit to a lesser extent, along axis 2 [Fig. 2(a)]. Within sampling locations, resident and anadromous individuals are essentially indistinguishable, especially in Qasigigiat and Iqaluggarjuit. In Qinngu, however, there is a slight differentiation between ecotypes along axis 3 [Fig. 2(b)]. This result is consistent with the significant F_{ST} values between ecotypes in Qinngu.

The results of the Structure analysis suggested that ecotypes are not genetically differentiated. Both the ΔK method (Evanno *et al.*, 2005) and the ln Prob$K$|data method (Pritchard *et al.*, 2000) concluded that the most likely number of genetic clusters in the data was three [Fig. 3(a), (b)]. This was also true for the analysis done without the LOCPRIOR model (Fig. S1, Supporting Information). Examination of the individual assignment probability to each cluster revealed that each sampling location was differentiated from the others (although the two locations from the Cumberland Sound were not strongly differentiated), but that sympatric ecotypes within sampling locations were not differentiated [Fig. 3(c)]. Those results were also supported by the Structure analyses conducted at each sampling location separately (Fig. 4). In Qasigigiat, the most likely number of genetic cluster was one according to the ln Prob$K$|data method [Fig. 4(a)]. Because ΔK is not defined for $K = 1$, it is concluded that there is no population structure within Qasigigiat based on the ln Prob$K$|data method alone. In contrast, the most likely number of genetic clusters in the other two populations according to both methods was two [Fig. 4(a)]. While population structure was identified in both locations, the individuals did not cluster according to life-history ecotype [Fig. 4(b)].

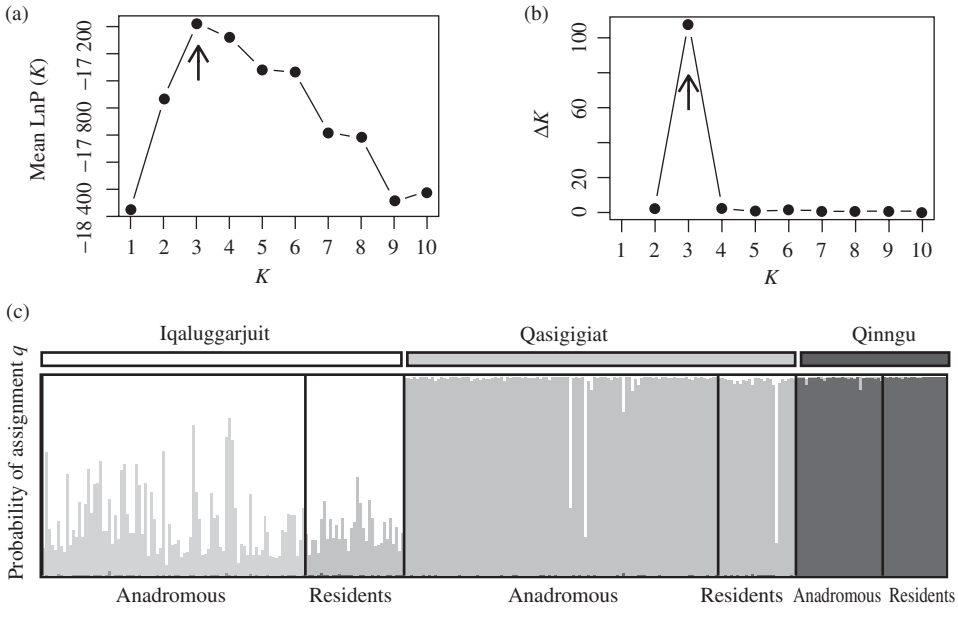

FIG. 3. Results of the structure analysis on all *Salvelinus alpinus* sampling locations. (a) Mean ln probability of the data given each value of K (*i.e.* number of genetic cluster). ↑, the most likely number of genetic clusters (3) according to this method (Pritchard *et al.*, 2000). (b) Values of ΔK (Evanno *et al.*, 2005) for each value of K. ↑, the most likely number of genetic clusters (3) according to this method. (c) Probability of assignment (q) to each of the three genetic clusters for each individual.

DISCUSSION

Sympatric migratory ecotypes are commonly observed in salmonids (Wood & Foote, 1996; Fleming, 1998; Fleming & Reynolds, 2004; Hendry *et al.*, 2004). The co-existence of these phenotypes is generally explained under the framework of alternative mating tactics or of reproductive isolation between genetically fixed mating strategies (Gross, 1996). In this study, analysis of microsatellite DNA data was used to help distinguish between these two alternative hypotheses in polymorphic populations of *S. alpinus* from southern Baffin Island (Loewen *et al.*, 2009). Using the genetic results obtained in this study along with other sources of available evidence, the migratory ecotypes from those three South Baffin localities probably represent a case of alternative mating tactics. Implications of such an interpretation for fisheries management are discussed.

LACK OF GENETIC DIFFERENTIATION IN CUMBERLAND SOUND ECOTYPES

The results of all analyses suggest a lack of genetic differentiation between resident and anadromous fish in the two Cumberland Sound sampling locations. First, F_{ST} values between ecotypes were not significantly different from zero, and an FCA showed that both ecotypes were indistinguishable along the first three axes of divergence. The results of the AMOVA are ambiguous and challenging to interpret. When

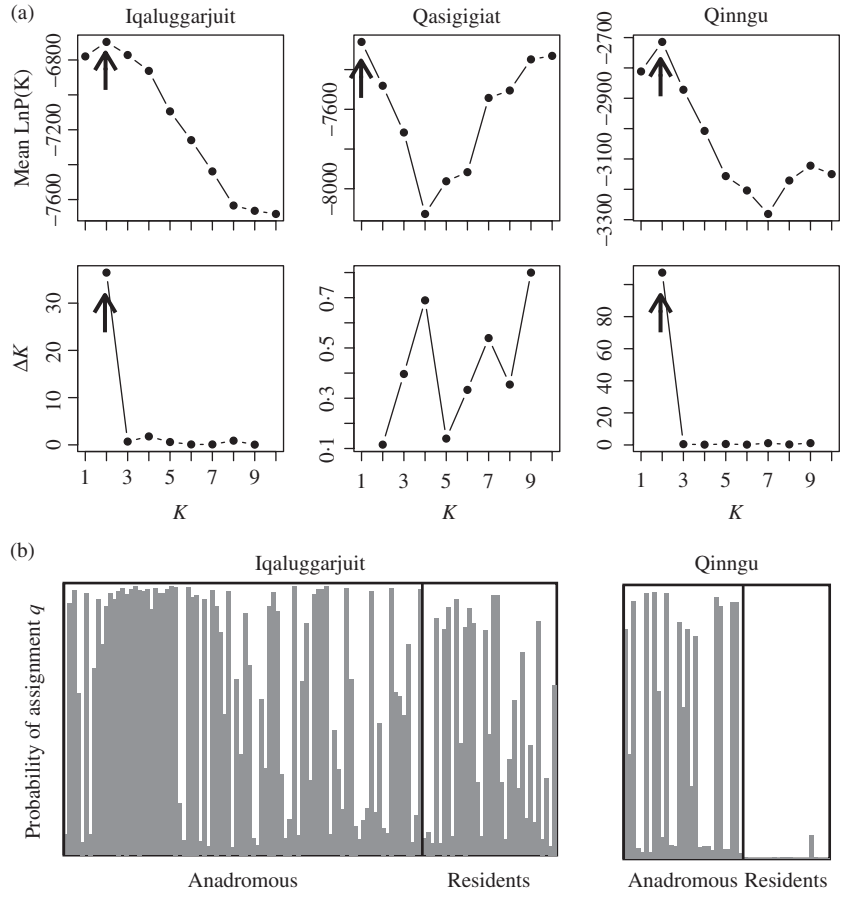

FIG. 4. Results of the structure analysis on single *Salvelinus alpinus* sampling locations. (a) Mean ln probability of the data (top) and delta K (bottom; Evanno *et al.*, 2005) values for each value of K (*i.e.* number of genetic cluster) in each sampling location. ↑, the most likely number of genetic clusters according to each method (Pritchard *et al.*, 2000; Evanno *et al.*, 2005). Note that because ΔK is not defined for $K = 1$, there is no ↑ for most likely ΔK in Qasigigiat. (b) Probability of assignment (q) to each of the three genetic clusters for each individual. This is shown only for two sampling locations, because the most likely number of genetic clusters (K) in Qasigigiat was one.

groupings were defined by sampling location, differences between ecotypes explained a significant amount of genetic variation, but this may be due to the presence of small amounts of genetic differences between the ecotypes in the Qinngu sampling location. When groupings were defined by ecotypes, differences among ecotypes were not significant, but differences among sampling locations were, which is more consistent with the F_{ST} values. Finally, the Structure analysis failed to identify the presence of genetic clusters within sampling locations, further suggesting that the ecotypes are not genetically differentiated. When each sampling location was analysed separately, the Structure analysis identified the population structure but it did not correlate with life-history ecotype. An alternative explanation would be that the ecotypes are indeed reproductively isolated, but that the divergence is too recent for genetic drift to have

led to the accumulation of significant genetic differences between the forms. This possibility is considered unlikely given that microsatellites are fast evolving loci that accumulate differences rapidly because of a high mutation rate (Ellengren, 2000). Furthermore, available estimates of N_e for the Cumberland Sound populations are not exceptionally large (*c*. 3000) and should leave ample room for drift to act on allele frequencies (Moore *et al.*, 2013). In summary, the lack of genetic differentiation suggests that the resident and anadromous sympatric ecotypes are not reproductively isolated within those lakes.

PRESENCE OF WEAK GENETIC DIFFERENTIATION IN QINNGU

Contrary to the observation of genetic homogeneity in the two Cumberland Sound sampling locations, the two sympatric ecotypes from Qinngu were found to be weakly genetically differentiated in some analyses. Indeed, the pair-wise F_{ST} value between the ecotypes was significantly different from zero, and the AMOVA suggested that ecotypes explained a significant amount of the genetic variation, presumably only in Qinngu. Finally, the FCA results show that there is moderate clustering of the ecotypes in Qinngu along the third axis of variation. The Structure results, on the contrary, do not support the presence of genetic differences between the ecotypes. Four alternative (but not necessarily mutually exclusive or exhaustive) interpretations of these results are possible.

First, it is possible that the presence of significant genetic differentiation is simply an artefact of the small sample size or of the analysis methods used. The number of samples analysed from Qinngu is indeed quite small (residents: $n = 21$; anadromous: $n = 29$), and it is possible that a few outlier individuals would have a disproportionate effect on average allele frequencies within sample, and therefore bias estimates of genetic differentiation. The FCA does indeed suggest that less than five individuals are responsible for most of the differentiation between ecotypes [Fig. 2(b)]. When analysed with methods that define populations *a priori* (the AMOVA and the F_{ST} analysis), the presence of a few outlier individuals could then bias the results towards finding more genetic differentiation. The Structure analysis, however, does not rely on *a priori* definition of populations, and did not identify significant genetic discontinuity between the two ecotypes in Qinngu (Fig. 3). This was true even if the analysis was conducted with a Bayesian prior favouring clustering among ecotypes (Hubisz *et al.*, 2009), and therefore suggests that the data do not support the presence of genetic differentiation among ecotypes.

Second, the Qinngu sampling site differs from the other two sites by the presence of a large lake upstream of the smaller lake where the samples for this study were collected (Loewen *et al.*, 2009; no samples were collected from the upper lake). The two lakes are connected, and anadromous *S. alpinus* are known to utilize the upper lake for spawning. Migration from the ocean to the upper lake, however, requires that they first pass through the lower lake. It is therefore possible that spawning site fidelity leads to genetic differentiation between the individuals spawning in the lower and upper lakes. Sampling of anadromous individuals in the lower lake at the time of the upstream migration (Loewen *et al.*, 2009) would lead to the capture of some individuals from this other putative upstream population. If all the resident individuals sampled, however, originate from the lower lake, this would lead to a pattern of

apparent genetic differentiation between ecotypes, when it is in fact the result of genetic differentiation between spawning aggregations. The results of the Structure analysis conducted on Qinngu alone are consistent with this hypothesis. Indeed, Structure identified many anadromous individuals that belong to a second genetic cluster, while all resident individuals belong to a single cluster [Fig. 4(b)]. Samples of anadromous individuals known to originate in the upper and lower lakes would be required to test this hypothesis more formally. A related explanation would be family-biased sampling in the non-migratory ecotype, *i.e*. the sampling of related individuals that would make them appear more genetically similar. This can be an important problem in genetic studies of salmonids, especially when non-mature individuals are collected in their freshwater phase (the so-called Allendorf–Phelps effect; Waples, 1998). This hypothesis, however, was formally evaluated using sibship reconstruction analyses in a previous study involving the present sampling locations (Moore *et al.*, 2013) and was found to have a minimal impact on patterns of genetic differentiation.

Third, it is possible that the two ecotypes from Qinngu are reproductively isolated and therefore represent incipient species utilizing two alternative, genetically fixed reproductive strategies. This interpretation seems implausible, especially given the strongly male-biased sex ratio observed in the non-migratory ecotype (Loewen *et al.*, 2010).

Fourth, genetic differences observed between ecotypes could result from assortative mating or selection against hybrids if the migratory tactics are partly genetically determined. Available evidence suggests that migratory ecotypes in the genus *Salvelinus* often have a heritable component. In northern Norway, anadromous parents produced both anadromous and resident offspring but were more likely to produce anadromous offspring (and *vice versa* for resident parents; Nordeng, 1983). Thériault *et al.* (2007*a*) used genetic pedigree reconstructions in natural conditions to demonstrate the presence of a considerable additive genetic variance component for migratory traits in polymorphic populations of brook tout *Salvelinus fontinalis* (Mitchill 1814) (Thériault *et al.*, 2007*a*). This could then lead to the accumulation of genetic differences between morphs, but only if a certain degree of assortative mating or selection against hybrids existed (Schluter, 2002). There is some evidence from other polymorphic populations of *S. alpinus* that small-maturing forms and large-maturing forms mate assortatively (Jonsson & Hindar, 1982; Gíslason *et al.*, 1999). This evidence, however, comes only from sympatric lacustrine populations. There is no direct evidence of selection against hybrids in polymorphic populations of *S. alpinus*, but Jonsson & Jonsson (2001) have suggested that patterns of morphological variation are consistent with this hypothesis (Snorrason *et al.*, 1994; Forseth *et al.*, 2003). Again, however, all evidence comes from sympatric, landlocked ecotypes. In summary, this fourth interpretation appears unlikely.

EVIDENCE FOR ALTERNATIVE MATING TACTICS

The existence of alternative mating tactics in salmonids is well supported by empirical evidence (Fleming, 1998; Fleming & Reynolds, 2004; Hendry *et al.*, 2004). In *S. alpinus*, there is also extensive evidence of alternative mating tactics but most examples are from European populations (Nordeng, 1983; Svenning *et al.*, 1992; Rikardsen & Elliott, 2000; Klemetsen *et al.*, 2003). Populations of *S. alpinus* with variable migratory phenotypes from the North American Arctic, however, have

received less attention. Indeed, while variable migratory phenotypes have been documented in a few locations (Reist, 1989; Babaluk *et al.*, 1997), the ecological and evolutionary mechanisms driving the co-existence of the two phenotypes remain elusive.

Loewen *et al.* (2010) suggested that the polymorphism observed in the South Baffin localities could be best understood under the framework of alternative migratory tactics, but that genetic evidence would strengthen this conclusion. This study provides such evidence, and concludes that, at least in the two Cumberland Sound sampling locations, the two migratory ecotypes are not reproductively isolated. This is consistent with evidence from other populations of salmonids with variable migratory phenotypes where resident and anadromous individuals do not show significant genetic differences (Hindar *et al.*, 1991; Thériault *et al.*, 2007*a*). It is also consistent with the results of Reist (1989) who showed that migratory ecotypes of *S. alpinus* from the western Canadian Arctic did not differ significantly at two allozyme markers.

The heavily male-biased sex ratio observed also constitutes evidence in support of alternative mating tactics. Given the differences in selective pressures associated with vastly different gamete size in both sexes, it is expected that males will predominate in the resident component of the population (Fleming & Reynolds, 2004). Larger body sizes can help males secure females during competition for mates (Fleming & Reynolds, 2004), but smaller non-migratory males often successfully fertilize eggs by utilizing a sneaking tactic (Myers & Hutchings, 1987; Thériault *et al.*, 2007*b*). In most salmonid species, therefore, the resident tactic appears to be restricted to males, and reports of females utilizing this tactic are rare [a few examples for *S. salar* are given by Power (1969) and Prouzet (1981)]. This, however, is not the case in the South Baffin Island sampling locations, where female resident fish are observed despite being considerably less common than their male counterparts: the sex ratio is *c*. 20:1 in favour of males (Loewen *et al.*, 2010). This is consistent with observations from European populations of *S. alpinus* with alternative mating tactics. In the Salangen River system, the sex ratio of males to females is *c*. 4:1 (Nordeng, 1983). Female residents are also observed in the partially migrating populations of *S. alpinus* in lakes Storvatn and Rungavatn in northern Norway (Rikardsen & Elliott, 2000). The increased prevalence of females utilizing the resident tactic in *S. alpinus* relative to other salmonids is intriguing but has received little attention. This observation indeed suggests that the balance between the costs and benefits of migration for female *S. alpinus* differ from that of other salmonids (Hendry *et al.*, 2004).

Despite the available evidence suggesting that the migratory ecotypes of southern Baffin Island are indeed alternative mating tactics, it should be noted that direct evidence is still lacking. The strongest test for such a hypothesis would be to observe the offspring of anadromous parents developing into resident individuals, or anadromous offspring developing from resident parents. Such observations have been made in European populations of *S. alpinus* (Nordeng, 1983), and in hatchery populations from Labrador (Papst, 1994), but not from the present sampling locations. Alternatively, the observation of resident individuals switching to an anadromous tactic later in life would also constitute strong evidence in favour of the alternative mating tactic. Resident individuals have indeed been shown to switch to the anadromous tactic later in life in some *S. alpinus* populations (Nordeng, 1983; Rikardsen & Elliott, 2000). The observation that the resident fish from all three South Baffin lakes were on average younger than anadromous individuals (Loewen *et al.*, 2010) suggests that it may indeed be the case. Such patterns, however, could also be the result

of increased mortality or faster senescence in the resident fish, although mortality may be expected to be higher for anadromous fish facing more severe predation and fishing pressures in the marine environment.

IMPLICATIONS FOR FISHERIES MANAGEMENT

Jonsson & Jonsson (2001) suggested that sympatric *S. alpinus* morphs should be managed as separate species. The genetic results of this study argue instead that the sympatric ecotypes of Baffin Island *S. alpinus* are not separate populations, but instead are two components of the same population. Independent management of the two ecotypes is thus unwarranted. Anadromous *S. alpinus* populations of southern Baffin Island are currently the target of subsistence fishing by the Inuit from the communities of Kimmirut and Pangnirtung (Nunavut Wildlife Management Board, 2004). In addition, the anadromous stocks of *S. alpinus* from the Cumberland Sound support a small-scale commercial fishery (Roux *et al.*, 2011). Assuming that the sympatric ecotypes do indeed constitute a case of alternative mating tactics, it can probably be safely assumed that the resident component of the population reproduces and thus contributes demographically to the overall population. Indeed, small-maturing males have been shown to mate and reproduce with anadromous females in many populations of salmonids (Myers & Hutchings, 1987; Thériault *et al.*, 2007*b*; Johnstone *et al.*, 2013). If, however, the resident component of the population has a tendency to produce more resident offspring, this could reduce their contribution to the recruitment of the fishery, which targets anadromous individuals only, and could therefore have negative economic consequences for the fishery (Myers, 1984). Mating with residents would still contribute to maintaining genetic diversity in the populations (Johnstone *et al.*, 2013; Moore & Fraser, 2013). Furthermore, the presence of variation in life-history traits between exploited populations (*i.e.* biocomplexity) has been shown to have a positive effect on their long-term viability, the so-called port-folio effect (Hilborn *et al.*, 2003; Schindler *et al.*, 2010) and the maintenance of this diversity should also be a priority for management.

An interesting possibility is that increased fishing pressure on the anadromous component of the population may over the long-term increase the relative fitness of the resident tactic thus resulting in a higher frequency of this tactic in the population. Fisheries-induced evolutionary changes are now well documented in a large number of species (Stokes & Law, 2000; Hutchings & Fraser, 2008), including salmonids (Quinn *et al.*, 2007; Hard *et al.*, 2008). In the case of migratory tactics, theory shows that the frequency of alternative mating phenotypes in a given population represents an evolutionary stable continuum determined by the relative fitness of the two tactics (Hutchings & Myers, 1994). Fishing for the anadromous individuals exclusively, by increasing the costs of marine migrations, would thus increase the relative fitness of the resident tactic. Modelling work suggests that after 100 years of fishing pressures targeting exclusively the anadromous component of the population, the probability of migrating could decrease significantly in *S. fontinalis* populations (Thériault *et al.*, 2008). In conclusion, exploitation of anadromous *S. alpinus* in South Baffin Island could have long-term consequences for the relative frequency of the two ecotypes.

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Supporting Information

Supporting Information may be found in the online version of this paper:
Figure S1. Results of the structure analysis conducted on all samples together without using the LOCPRIOR option. (a) Mean ln probability of the data given each value of K (*i.e*. number of genetic cluster). (b) Values of ΔK (Evanno *et al.*, 2005) for each value of K., the most likely number of genetic clusters (3) according to this method. (c) Probability of assignment (q) to each of the three genetic clusters for each individual.

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