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SHORT COMMUNICATION

The ghost of hybrids past: fixation of arctic charr (*Salvelinus alpinus*) mitochondrial DNA in an introgressed population of lake trout (*S. namaycush*)

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Abstract

Complete fixation of arctic charr (*Salvelinus alpinus*) mitochondrial DNA (mtDNA) was observed in a southern Québec population of lake trout (*S. namaycush*). This introgressed population otherwise appeared to be normal with regard to lake trout morphology and three species-diagnostic microsatellite loci. Arctic charr do not occur in the area, suggesting that the hybridization event was prehistoric. Of several possible hypotheses, the most plausible explanation for this aberrant population is that hybridization occurred *in situ* soon after deglaciation, with repeated backcrossing of hybrids with lake trout. Fixation of *S. alpinus* mtDNA in the population may have occurred either by chance (drift) or selection, although indirect evidence and data from similarly introgressed brook trout (*S. fontinalis*) populations in the region suggest that selection favouring the *S. alpinus* mitochondrial type and/or associated nuclear genes may have been involved.

Keywords: introgression, mitochondrial DNA, *Salvelinus*, selection, zoogeography

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Introduction

The potential evolutionary significance of introgressive hybridization has received increased attention in recent years. Although long considered insignificant, particularly among animals, this phenomenon is increasingly being recognized as a significant source of novel genetic variation and a potent evolutionary force (Arnold 1992; Harrison 1993). Among vertebrates, hybridization and introgression are most common in fishes, particularly among species living in or proximal to recently deglaciated regions (Hubbs 1955; Verspoor & Hammar 1991). Cases of reticulate evolution, where introgression has had long-term effects on the recipient species' genetic structure, are especially interesting (Dowling & deMarais 1993; Taylor & Hebert 1993). In particular, systems showing mitochondrial introgression and fixation are rare, and take on additional significance given the current controversy surrounding the possible non-neutrality of mitochondrial variants (Ballard & Kreitman 1994; Rand *et al*. 1994).

Bernatchez *et al*. (1995) recently reported a population of brook trout (*Salvelinus fontinalis*) in southern Québec which is completely introgressed for arctic charr (*S. alpinus*) mitochondrial DNA (mtDNA). Subsequent work has documented similar occurrences in nearby populations of *S. fontinalis*, and suggests that this interspecific mitochondrial replacement may have selective consequences (Glémet *et al*. 1997). Here we report another instance of interspecific mitochondrial replacement in southern Québec, in a population of lake trout (*S. namaycush*) which is fixed for *S. alpinus* mtDNA.

Materials and methods

Seven fish were initially collected by angling from Lac des Chasseurs in southern Québec (48°13' N, 67°52' W) in 1992 as part of a broad-scale genetic survey of lake trout populations in eastern North America (Wilson & Hebert 1996) (Fig. 1). Forty fish were subsequently obtained in 1995 from the Québec Ministère de l'Environnement et de la Faune (MEF) station in Rimouski. Fish were characterized as lake trout by MEF personnel, based on external morphology (body colouration, head shape, etc.) as described in Scott & Crossman (1973). No meristic analyses were initially conducted, as the fish appeared to be normal lake

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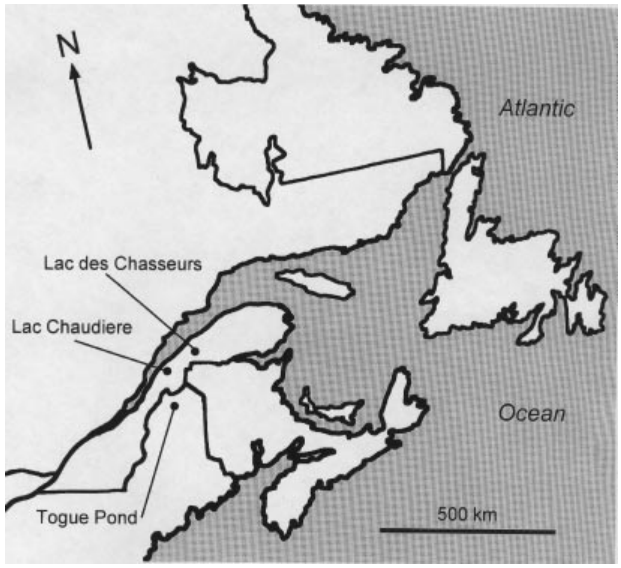

Fig. 1 Map of southern Quebec and adjoining areas, showing location of Lac des Chasseurs and source populations for *Salvelinus alpinus* (Lac Chaudiere, Quebec) and *S. namaycush* (Togue Pond, Maine).

trout. Arctic charr have never been recorded in this lake (C. Banville, MEF Rimouski, personal communication).

For the initial seven specimens, mitochondrial DNA (mtDNA) was extracted from liver tissue as described by Wilson & Hebert (1996). The entire mtDNA molecule was digested with five restriction enzymes (*Ava*I, *Bam*HI, *Dra*I, *Hin*dIII, and *Xba*I). The resulting DNA fragments were separated on 1.2% agarose gels, stained with ethidium bromide, and visualized under ultraviolet light. All of these enzymes show diagnostic differences between lake trout and arctic charr (Wilson & Hebert 1993, 1996; Wilson *et al*. 1996).

For the remaining fish, total DNA was obtained from muscle tissue as described by Bernatchez *et al*. (1992). A 2.5 kb portion of the mitochondrial ND-5/6 region was amplified via the polymerase chain reaction (PCR) using primers described by Cronin *et al*. (1993). PCR was carried out using reactant concentrations as described by these authors and the thermal profile utilized by Bernatchez *et al*. (1995). Amplified DNA was digested with two restriction enzymes (*Hae*III and *Rsa*I) that show diagnostic fragment patterns for lake trout and arctic charr within the ND-5/6 region (L. Bernatchez, unpublished data). DNA fragments were run out on 1–1.5% agarose gels for 1–3 h, stained with ethidium bromide and photographed under UV light.

Microsatellite analyses were carried out using three loci (SFO-11, SFO-12, and SFO-18) that are diagnostic between lake trout and arctic charr (Angers & Bernatchez 1996), in order to determine the species identity with respect to the nuclear genome of the Lac des Chasseurs fish. The criterion of diagnosability for each locus was determined by the complete or virtual lack of intraspecific variation for those loci based on geographically remote populations of each species and the observation of nonoverlapping allelic size classes between the two species in all cases. For example, at SFO-12, two Arctic charr populations from northeastern North America and Europe were fixed for the same allele (225) whereas only two alleles (259 and 261) were observed among lake trout populations. Loci were amplified as described in Angers *et al*. (1995) and Angers & Bernatchez (1996), with the exception that ^{35}S-labelled dATP was used for band detection. Microsatellites were run on 6% acrylamide gels at 1950 V for 1.5–3 h, then exposed to X-ray film for 1–2 days. For comparative purposes, lake trout and arctic charr from the region were included in the mtDNA and microsatellite analyses. Arctic charr DNA was used from fish collected from Lac Chaudière in southern Québec (47°50' N, 71°20' W). Lake trout samples came from Togue Pond, Maine (46°56' N, 70°07' W).

Results

Morphology

All fish collected from Lac des Chasseurs were identified as lake trout (*Salvelinus namaycush*) based on their external appearance. Body colouration (dark green with numerous small yellow spots), head shape, and general morphology of these fish matched that of typical lake trout (Scott & Crossman 1973). Detailed morphometric analyses were not carried out on subsequently collected samples, as these were obtained via creel census from local fishermen.

mtDNA

All fish from Lac des Chasseurs possessed a single mtDNA haplotype which matched the common arctic charr haplotype in southern Québec (Table 1). The initial seven fish showed fragment patterns from digestion of the entire mtDNA molecule that corresponded with arctic charr populations from southern Québec and New Brunswick (Wilson *et al*. 1996), and were very distinct from eastern populations of lake trout (Wilson & Hebert 1996). For subsequently collected fish, RFLP screening of amplified DNA from the mitochondrial ND-5/6 region determined species-diagnostic fragment patterns for lake trout and arctic charr with *Hae*III and *Rsa*I (Table 1). PCR amplification and digestion with these restriction enzymes showed that all 47 fish collected from Lac des Chasseurs had fragment patterns identical to the pattern observed for arctic charr from Lac Chaudière (Table 1).

Table 1 Restriction fragment patterns (in kb) generated from digestion of total mtDNA and PCR-amplified ND-5/6 mitochondrial DNA for fish from Lac des Chasseurs, as well as allopatric samples of *Salvelinus namaycush* and *S. alpinus*. Presence (1) or absence (0) of fragment patterns are indicated. Sample sizes are provided in brackets

Enzyme	Fragment sizes									LC	SA	SN
Total mtDNA digests										(7)	(24)	(11)
*Ava*I	6.79	2.79	2.18	1.28	0.98	0.87	0.65			1	1	0
	5.49	2.68	2.22	1.68	1.52	1.36	1.10	0.60	0.57	0	0	1
*Bam*HI	15.50	1.30								1	1	0
	9.48	7.32								0	0	1
*Dra*I	7.38	3.49	3.25	2.29						1	1	0
	7.05	5.35	3.30							0	0	1
*Hin*dIII	5.14	3.96	3.45	2.25	1.76	0.26				1	1	0
	9.10	2.24	1.96	1.76	1.48	0.26				0	0	1
*Xba*I	13.50	3.20								1	1	0
	8.11	5.35	3.18							0	0	1
ND-5/6 fragment										(47)	(10)	(10)
*Hae*III	0.60	0.60	0.56	0.35	0.35					1	1	0
	0.70	0.57	0.56	0.18						0	0	1
*Rsa*I	1.44	1.08								1	1	0
	1.29	1.08								0	0	1

LC, Lac des Chasseurs; SA, *S. alpinus*; SN, *S. namaycush*.

Microsatellites

Fish from Lac des Chasseurs displayed microsatellite alleles within the expected size range for lake trout (Angers & Bernatchez 1996) at all three loci examined (Table 2). Alleles observed for SFO-11 and SFO-18 were the same size for Lac des Chasseurs fish and lake trout from Togue Pond, and were recognizably distinct from alleles observed in arctic charr from Lac Chaudière (Table 2). In addition, the Lac des Chasseurs population was polymorphic at SFO-12, possessing two alleles (259 and 263) within the size range observed in other lake trout populations and very distinct from the only allele (225) found at this locus in Arctic charr thus far (Angers & Bernatchez 1996) (Table 2).

Discussion

Our results clearly show that interspecific replacement of *Salvelinus namaycush* mtDNA with that from *S. alpinus* has occurred in the Lac des Chasseurs population. Although the presence of the *S. alpinus* haplotype in this population could potentially be accounted for by the paraphyletic retention of an ancestral haplotype or convergent evolution, these explanations are highly improbable. Both *S. alpinus* and *S. namaycush* show maximum levels of intraspecific divergence in the order of 1% or less among North American populations (Wilson & Hebert 1996, 1997; Wilson *et al*. 1996), and Nearctic and Palearctic populations of *S. alpinus* differ by less than 2% (Wilson *et al*. 1996). No shared haplotypes were detected between the two species in these surveys. These low intraspecific divergence values are typical of freshwater and anadromous fishes which occur in formerly glaciated regions (Billington & Hebert 1991). In contrast, mitochondrial divergence between *S. alpinus* and *S. namaycush* has been estimated at approximately 3% (Grewe *et al*. 1990).

Furthermore, as geographical variation among haplotypes occurs in both species, it is highly improbable that the locally retained paraphyletic haplotype should match the local *S. alpinus* haplotype so closely. Of the five restriction enzymes used to screen the entire mtDNA molecule of the initial seven fish, all are diagnostic between the two species (Wilson & Hebert 1996; Wilson *et al*. 1996), and three (*Ava*I, *Bam*HI, and *Hin*dIII) detect geographical variation within North American populations of *S. alpinus* (Wilson *et al*. 1996). The haplotype detected within the Lac des Chasseurs fish exactly matches the local *S. alpinus* haplotype for the restriction enzymes used, based on RFLP screening of the entire mtDNA molecule and the PCR-amplified ND-5/6 fragment, making symplesiomorphic retention or convergent evolution unlikely.

All other potential explanations involve introgressive hybridization between *S. alpinus* and *S. namaycush*, with subsequent backcrossing between hybrids and *S. namaycush*. The occurrence of F_1 hybrids across the parent species' current contact zone indicates that hybridization between these species is not uncommon (Hammar *et al*. 1989; Wilson & Hebert 1993). In addition, bidirectional introgression within northern populations shows that hybrids are nonsterile and capable of breeding with both parent species (Wilson & Hebert 1993).

Table 2 Microsatellite loci and allele sizes (in bases) for Lac des Chasseurs fish, *Salvelinus namaycush* and *S. alpinus*, using designations from Table 1. Sample sizes (in brackets) and allele frequencies are indicated for each taxon

		Frequency		
Locus	Allele	LC	SA	SN
		(20)	(12)	(12)
SFO-11	122	0	1.00	0
	124	1.00	0	1.00
SFO-12	225	0	1.00	0
	259	0.85	0	1.00
	263	0.15	0	0
SFO-18	161	0	1.00	0
	173	0.95	0	1.00
	175	0.05	0	0

The absence of similar chimeric populations of either species in the region (Wilson & Hebert 1996; Wilson *et al*. 1996) suggests that the Lac des Chasseurs population is descended from hybrids formed *in situ* following the post-Wisconsinan deglaciation during the late Pleistocene or early Holocene. Both arctic charr and lake trout occur in lakes in southern Quebec, New Brunswick and New England, although southern populations of *S. alpinus* are largely limited to lakes that were isolated soon after deglaciation (Scott & Crossman 1973; Dumont 1982). Although *S. alpinus* is not found in Lac des Chasseurs or its drainage (C. Banville, Rimouski MEF, personal communication), it is probable that the species colonized the area soon after deglaciation (Dumont 1982), followed later by lake trout. *S. alpinus* is one of the first species to occupy habitats following glacial retreat (Power *et al*. 1973; Hammar 1987), but is readily displaced by more temperate species such as lake trout at lower latitudes (Kircheis 1980; Fraser & Power 1989). The high degree of disturbance within recently deglaciated habitats would have increased the probability of hybridization between both species (Hubbs 1955), particularly if founding populations were small (Wilson *et al*. 1985).

A viable hypothesis is that *S. alpinus* mitochondrial fixation occurred via founder effects or drift following hybridization. If founding populations of both *S. alpinus* and *S. namaycush* were small, or if the Lac des Chasseurs population remained at low numbers for several generations, fixation could have occurred quite rapidly (Avise *et al*. 1984). The possibility of low founder numbers and/or restricted population size is indirectly supported by the low microsatellite allelic diversity within this population, and by low levels of mtDNA diversity among natural populations of both parent species from areas outside those inundated by proglacial lakes during retreat of the Wisconsinan glaciers (Wilson & Hebert 1996, 1997; Wilson *et al*. 1996).

An alternate hypothesis is that hybrids may have been favoured under periglacial conditions, due to selective advantages in having the *S. alpinus* mitochondrial type or associated nuclear genes. If so, as lake trout displace arctic charr from temperate populations without evidence of hybridization (Kircheis 1980; Fraser & Power 1989), it seems probable that any selective advantages for hybrids would have been operative under past rather than present conditions. Furthermore, it is probable that mitochondrial introgression was widespread before the transition to modern conditions occurred. Recent work with brook charr (*S. fontinalis*) has revealed that at low temperatures (6 °C), naturally introgressed brook charr with *S. alpinus* mtDNA show a threefold increase in metabolic scope for activity over genetically pure *S. fontinalis* from neighbouring populations, which may have provided a selective advantage in early postglacial environments (Glémet *et al*. 1997). Experimental hybridization of *Drosophila* species has also demonstrated that interspecific mitochondrial replacement can occur at the population level within several generations (Aubert & Solignac 1990), although the operative selective mechanisms have yet to be determined.

Other evidence is suggestive that the interspecific mitochondrial replacement observed in this population may have resulted from a combination of selective processes and historical demographic circumstances. In northern Canada, all but one of the natural F_1 *S. namaycush* × *S. alpinus* hybrids observed by Wilson & Hebert (1993) possessed lake trout mtDNA, indicating matings between female *S. namaycush* and male *S. alpinus*. In addition, no introgression of *S. alpinus* mtDNA into *S. namaycush* was observed among Arctic populations, despite limited introgression of nuclear genes. Wilson & Hebert (1993) attributed this strong directional bias to differences in egg size between the two parent species, and speculated that hybrids resulting from crosses between female *S. alpinus* and male *S. namaycush* might suffer a high incidence of caudal deformities due to the smaller volume of *S. alpinus* eggs. Deliberate crosses between species with differing egg volumes have long been known to have reduced success (Day 1884), particularly when the female species produces smaller eggs. Although effects of maternal egg volume on progeny survivorship from crosses between *S. alpinus* and *S. namaycush* have not been examined, crosses between male *S. namaycush* and female *S. fontinalis* result in high mortality due to embryonic deformities (Berst *et al*. 1980). If some selective advantage was associated with having *S. alpinus* mitochondria and/or associated nuclear genes in early hybrid and backcross generations, this may have overcome the developmental and selective penalties normally imposed by this directional cross.

No strong conclusions can be made regarding the extent or lack of nuclear introgression in this population, as only three microsatellite loci were used. However, the external appearance of the Lac des Chasseurs fish (indistinguishable from typical lake trout) differs strongly from F_1 *S. namaycush* × *S. alpinus* hybrids, which are morphologically intermediate between the two parent species (Wilson & Hebert 1993). This, together with the microsatellite data, suggests that nuclear introgression has not been extensive.

Although the mechanism responsible for the fixation of *S. alpinus* mtDNA in this population has not yet been determined, it seems probable that the observed interspecific mitochondrial replacement resulted from either drift, selection or possibly both following a post-Wisconsinan hybridization event. This and similar instances of reticulate evolution provide rare opportunities for examining cytonuclear interactions, particularly for nuclear genes associated with mitochondrial functions. With increasing evidence of interspecific mitochondrial replacement (e.g. Dowling & Hoeh 1991; Bernatchez *et al*. 1995) and possible non-neutrality of mitochondrial variants (Aubert & Solignac 1990; Ballard & Kreitman 1994; Rand *et al*. 1994), it may be necessary to re-examine current interpretations of geographical patterns of mtDNA diversity within species. Future studies examining the potential significance of introgressive hybridization should also consider not only nuclear and mitochondrial introgression, but also potential interactions and coevolution between these two genomes.

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Both authors are interested in the evolutionary biology of salmonids, aquatic conservation biology, and the effect of Pleistocene glaciations on phylogeographic structure of fishes. L.B.'s general research interests are in the understanding of patterns and processes of organismal and molecular evolution, as well as their significance to conservation issues. C.C.W. is doing a postdoctoral fellowship in Australia on the evolutionary ecology of interspecific hybrids in *Daphnia*.
