

Ecology, Evolution, and Conservation of Lake-Migratory Brook Trout: A Perspective from Pristine Populations

DYLAN J. FRASER*¹ AND LOUIS BERNATCHEZ

Departement de Biologie, Université Laval, Quebec City, Quebec G1K 7P4, Canada

Abstract.—Reintroduction or rehabilitation plans for fish populations in many systems (e.g., lakes) are complicated by limited data on ecological and genetic characteristics before human disturbances occurred. While no two lakes have identical physical and biological characteristics, a growing body of empirical evidence nevertheless indicates that parallel patterns of population structuring may evolve within northern temperate fish species. Examining the population structuring in undisturbed lakes of similar physical and biological characteristics may thus provide insight into the probable historical extent and causes of both population structuring and connectivity in human-impacted lakes. Here, we review research on the population structuring and evolution of migratory brook trout *Salvelinus fontinalis* in a relatively undisturbed, postglacial lake (Mistassini Lake, Quebec). We provide information on lake habitat use, the morphology and life history characteristics of populations, diets, lakewide genetic population structure, seasonal migration characteristics between spawning and feeding areas, population evolutionary histories, and the prevalence of lake spawning. The biology of Mistassini Lake brook trout has a compelling number of similarities with what is known about that of the “coaster” form in Lake Superior and lake-migratory brook trout elsewhere. Our review also has several implications for the rehabilitation of coaster populations with respect to (1) clarifying the degree of natural connectivity between populations; (2) predicting the likelihood of recolonization of vacant habitats; (3) choosing candidate source populations for translocations; and more broadly, (4) understanding the spatial scale of probable local adaptation. Mistassini Lake therefore provides a useful case study that applies to lake-migratory trout elsewhere. We hope that our research will stimulate managers and biologists working on similar systems with pronounced human disturbances to consider the interplay between ecology and evolution in future conservation efforts.

Understanding the processes that lead to population diversity (structuring) within species is essential to maintaining species viability and adaptability as well as to adopting appropriate rehabilitation strategies (Utter 1981; Waples 1991; Moritz 1999; Fraser and Bernatchez 2001; Moritz 2002). Conservation biologists recognize that population diversity evolves, broadly speaking, along two major axes. Divergent natural selection can lead to adaptive differences among populations, or populations with independent evolutionary histories may accumulate unique genetic differences that are not replaceable within human lifetimes (Figure 1; reviewed in Fraser and Bernatchez 2001; Moritz 2002). Recognition of how these two axes might interact within a given system (e.g., lakes, rivers) is useful for conservation strategies because it can provide vital information on why some populations share more attributes of their ecology and genetics than others.

Studies aiming to characterize intraspecific popula-

tion structure are often conducted on systems already impacted by human disturbances. This is problematic for the rehabilitation or restoration of populations because baseline data on population structuring, and the processes that have led to it, may be limited or unclear. For instance, estimates of genetic differentiation in disturbed systems provide no direct information about these parameters in the past (Waples 1991). Habitat fragmentation may isolate populations and result in highly reduced gene flow among populations that were once connected (Caizergues et al. 2003; Meldgaard et al. 2003; Yamamoto et al. 2004). In contrast, artificial supplementation (e.g., stocking) can lead to the mixing of previously genetically distinct populations (Hansen 2002). These issues are significant because the extent of gene flow between populations is often used to define conservation units or decide which extant populations should be used as sources in the rehabilitation of extirpated populations (Moritz 1999; Fraser and Bernatchez 2001).

Although no two systems will have identical physical and biological characteristics, a growing body of empirical evidence indicates that parallel patterns of population structuring may evolve within many northern temperate fish species after postglacial colonization of separate lakes (McPhail 1993; Taylor

* Corresponding author: dylan.fraser@dal.ca

¹ Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada.

Received October 17, 2005; accepted February 22, 2007

Published online July 10, 2008

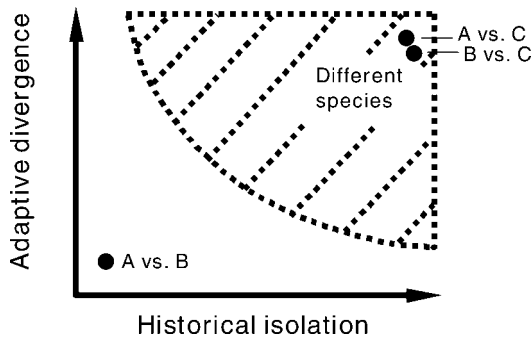


FIGURE 1.—Conceptual depiction of the evolution of population diversity on two axes: (1) adaptive divergence, where divergent natural selection leads to adaptive variation among populations in, for example, phenotypic and life history traits; and (2) historical isolation (encompassing the evolutionary history of populations), where populations that are historically isolated over time accumulate unique genetic differences (modified from Moritz 2002; see also Fraser and Bernatchez 2001). A wide body of theory predicts that adaptive divergence does not necessarily require genetic isolation (e.g., divergence in the face of gene flow) but that genetic differences may arise between historically isolated populations without divergent selection (Endler 1977). Consider a species composed of three populations (A, B, and C). Where both axes of divergence operate together (the area within the dashed lines), as in the interpopulation comparisons between populations A and C or B and C, the different populations would essentially be considered separate species by most taxonomists. Conversely, populations A and B have not been historically isolated and exhibit little adaptive differentiation between them. For conservation purposes, a long-term strategy would thus be to focus efforts on protecting components of populations A or B and C. Short-term rehabilitation might also be guided by a consideration of both axes and would probably vary with the population. As one example, if translocations of individuals from outside populations were deemed necessary for the rehabilitation of population A, population B would be a better source than C.

et al. 1996; Pigeon et al. 1997; Waples et al. 2004). The examination of population structuring in undisturbed lakes of similar physical and biological characteristics may therefore provide insight into the probable historical extent and causes of both population structuring and connectivity in lakes affected by human activities.

Such a comparison is particularly useful for lake-migratory brook trout *Salvelinus fontinalis* in eastern North America. Currently, several organizations are involved in the rehabilitation and reintroduction of “coaster” populations within Lake Superior, where a history of human activities has led to the dramatic decline or extirpation of many populations and where historical biological data on the species are limited (Newman et al. 2003; Ridgway 2008, this issue; Sloss

et al. 2008, this issue; Wilson et al., in press). However, a few other large-lake systems in eastern North America have lake-migratory brook trout that are very similar to the coaster form in Lake Superior. Moreover, some of these systems have evaded pronounced human disturbances.

One such system is Mistassini Lake in northern Quebec (50°25'N, 73°53'W). Here, there has been no introduction of exotic fish species, and thus far, major human development (roads, towns), heavy exploitation, hydroelectric development, logging, and mining around the lake have been minimal. Given these characteristics, the primary objectives of this article are twofold. First, we review the population structuring of lake-migratory brook trout in undisturbed Mistassini Lake. Our review is based on a series of ongoing research studies on the ecology, evolution, and genetics of this form of brook trout within the lake. We specifically place this review in the context of the two major axes of divergence outlined above that are relevant for conservation purposes—that is, adaptive divergence and historical isolation. Second, we consider the conservation implications of evaluating population structuring and connectivity in an undisturbed system such as Mistassini Lake. We address this in the context of both the rehabilitation of lake-migratory brook trout in Lake Superior and the populations of fishes with analogous life cycles in other systems that may have been affected by human activities.

Study Site

Like other systems harboring lake-migratory brook trout (e.g., Lakes Superior, Nipigon) Mistassini Lake is a large, oligotrophic postglacial lake (2,150 km²) located in the boreal forest ecoregion (Figure 2). The Mistassini Lake watershed is the source for the Rupert River, which ultimately drains into James Bay. The lake is divided into two deep basins (100–170 m) by a distinctive island chain (Figure 2). The two basins have lengths of approximately 150 km and widths ranging from 6 to 15 km. The only human settlement on the lake is the Cree First Nations community of Mistissini (population, 3,000 circa 2000), with road access to the lake via the community or a provincial wildlife reserve at Penicouane Bay; the 51st latitudinal parallel divides the lake into Cree and provincial management territories (Figure 2). Traditionally, local Crees conducted a subsistence harvest of brook trout. There are also three seasonal, fly-in recreational fishing camps on the lake (Figure 2).

The fish community in Mistassini Lake and nearby Lake Albanel (Figure 2), which also contains lake-migratory brook trout, is dominated by lake trout

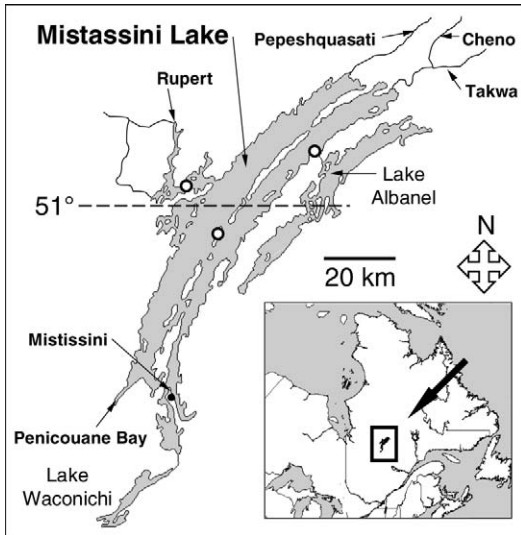


FIGURE 2.—Map of Mistassini Lake showing the rivers used for spawning by brook trout (outflow: Rupert River; inflows: Pepeshquasati, Cheno, and Takwa rivers). Access points to the lake are through the town of Mistissini and Penicouane Bay. The small white circles represent seasonal fishing camps on the lake. Public access to the lake is limited from the south end of the lake to the 51st parallel. The area above the 51st parallel is solely Cree First Nations territory.

S. namaycush, lake whitefish *Coregonus clupeaformis*, walleye *Sander vitreus*, long-nose sucker *Catostomus catostomus*, and white sucker *C. commersoni*, although other coldwater species are present, including northern pike *Esox lucius*, cisco *Coregonus artedii*, and burbot *Lota lota* (Flick 1977; Cree Trapper's Association of Mistissini [CTA], personal communication). Flick (1977) conducted 86 gill nettings of Lake Albanel in the summer and found that brook trout contributed only 3% of the total number of fish. A commercial fishery for lake trout and whitefish in the early 1960s in Mistassini Lake also reported low incidental catches of brook trout (DuBois 1967).

General Biology of Mistassini Lake Brook Trout

What is known about the biology of brook trout in Mistassini Lake is analogous to the information available for other anadromous salmonid fishes and lake-migratory brook trout in other lakes, including coasters from Lake Superior. Their life cycle involves the fall spawning of adults and the rearing of juveniles in lake inflows, primarily the Pepeshquasati and Cheno rivers (see discussion below on a third inflow, the Takwa River), and the lake's outflow, the Rupert River (Figure 2), with seasonal migrations to lake feeding areas for growth and maturation. We treat the

possibility that brook trout may spawn within Mistassini Lake itself in the discussion below.

The inflows used for spawning are some of the largest tributaries of Mistassini Lake. Juveniles stay within rivers for 1–2 years before migrating to the lake, stay in the lake for another 1–4 years, then return to natal rivers to spawn and complete the life cycle. An exception to this pattern is outflow trout; some of those individuals appear to be permanent residents of the outflow (Fraser 2005). Most sexually mature trout on spawning grounds are 3–6 years old (representing the number of completed winter seasons; Fraser et al. 2004). Ages 4 and 5 predominate among spawning trout in the inflow spawning populations, whereas fish in the outflow spawning populations are typically 3–4 years old. The maximum age we detected for any spawning or lake-caught individual was 8 years (Fraser 2005). Together, these ages are consistent with age-classes typically seen in other migratory brook trout populations from similar latitudes (Flick 1977; Dutil and Power 1980; Power 1980). Most spawning trout average 480–550 mm in length (mass, 1.3–2.5 kg), similar to that of north shore Lake Superior coasters (Newman et al. 2003).

Like the feeding migrations of coasters in Lake Superior, the intralake feeding migrations of Mistassini brook trout predominantly occur in coastal areas, especially from May through July (see also Mucha and Mackereth 2008, this issue). Trout move to deeper waters in July and August, but generally remain close to coastal areas (D. Fraser, personal observations; CTA, personal communication); the winter movements of Mistassini Lake trout are unknown. Mistassini Lake brook trout are opportunistic feeders, their diets varying with the time of year and food availability. Trout captured in May and June typically contain a variety of terrestrial and aquatic invertebrates in their stomachs (e.g., *Coleoptera*, *Diptera*, *Hemiptera*, *Ephemeroptera*, and *Hymenoptera*; Flick 1977) as well as snails (unidentified species; D. Fraser, personal observations). Trout captured later in the summer often show more fish remains in their stomachs (identifiable species: cisco and logperch *Percina caprodes*), and even mice *Peromyscus* spp. when captured in spawning rivers (Flick 1977; CTA, personal communication; D. Fraser, personal observations). To date, no research has addressed whether the diet of Mistassini Lake brook trout varies with age.

Ecology, Evolution, and Population Structuring

Most migratory brook trout return to their natal river to spawn (White 1942; O'Connor and Power 1973). Such a tendency encourages the development of genetically distinct populations in individual rivers

(Castric and Bernatchez 2003) and was our expectation a priori for trout spawning in different inflows and the outflow of Mistassini Lake. A molecular genetic analysis based on 10 microsatellite loci of adult trout collected on spawning grounds in each river over three consecutive years (2000–2002) confirmed this expectation (Fraser et al. 2004). Furthermore, genetic differences among rivers were shown to be temporally stable over the same time period.

Particularly noteworthy were the more pronounced genetic differentiation (i.e., higher F_{ST}) and reduced gene flow (i.e., lower migration rate [m], as defined by Wright 1951) between the outflow (Rupert) and inflow (Pepeshquasati and Cheno) populations ($F_{ST} = 0.10$ versus 0.02; $m = 0.007$ versus 0.015; Fraser et al. 2004). If these patterns of genetic differentiation reflected limited dispersal capabilities of trout between different rivers, we might have expected a pattern of isolation by distance, wherein genetic differentiation would increase with the distance separating populations (Castric and Bernatchez 2003). However, a first indication that factors other than limited dispersal among rivers might explain the population structuring in Mistassini Lake was that the distance between the outflow and closest inflow (Pepeshquasati) approximated that between inflows. Moreover, intralake dispersal does not appear to be inhibited, because trout can be found up to 140 km from their natal river mouths in either lake basin (Figure 3).

Subsequent research has found that the outflow and inflow trout groups do not originate from a common ancestor but from two different ancestral populations (Fraser and Bernatchez 2005b). Changes in the direction of discharge of Mistassini Lake from the southwest to west occurred during its postglacial formation (7,000–8,000 years ago; Bouchard 1981), and there is a correspondence between these changes and the directions by which each ancestral group apparently colonized the lake (Figure 4). Although some gene flow between ancestral groups occurred upon colonizing Mistassini Lake and continues to occur, outflow and inflow trout maintain themselves as separate genetic entities. In fact, genetic differentiation between outflow and inflow groups is greater than between inflow trout and trout originating from Lake Albanel, despite barriers to gene flow between the two lakes (Flick 1977; Fraser and Bernatchez 2005b).

Several lines of indirect evidence support the proposition that natural selection related to the migratory life cycle has played an important role in maintaining genetic isolation between the two groups and in generating the overall patterns of population structuring within Mistassini Lake. Besides the spatial isolation of spawning grounds in each river and

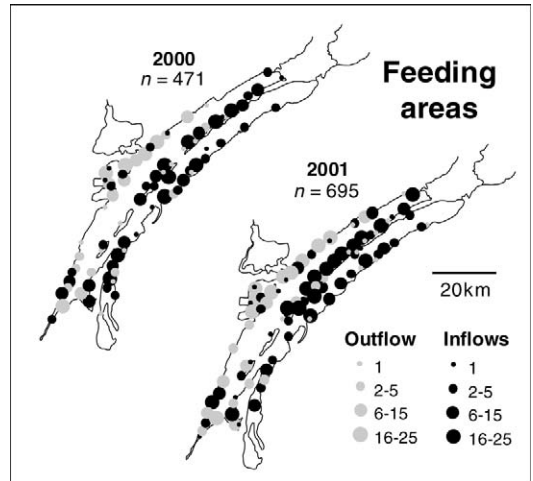


FIGURE 3.—A spatial representation of the number of individuals captured in summer fisheries within the feeding areas of Mistassini Lake that were assigned to spawning populations of lake-migratory brook trout based on multilocus genotype assignment tests (10 microsatellite loci) modified from Fraser and Bernatchez (2005a). Inflow populations are denoted in black because their spatial distributions did not differ from one another in either year.

differences in age-at-maturity, the outflow and inflow trout return to rivers and spawn at different times of year. Both of these events occur earlier in the Cheno and Pepeshquasati (inflow) populations, and qualitative observations suggest that the difference in spawning time is approximately 2–3 weeks at the level of the outflow versus inflows (Fraser 2005; CTA, personal communication). The differences probably relate in part to the fact that outflows from large lakes cool more slowly in the fall than do inflows because the temperature of outflows is moderated by water from the lake (Burger et al. 1997; Carmack et al. 1979).

Mistassini Lake brook trout populations also differ in their space use within feeding areas. We used the distinct genetic signal found within individual rivers to subsequently assign individuals captured throughout the lake in the summer fishery to their most probable population of origin, using individual assignment tests (details in Fraser and Bernatchez 2005a). Over two consecutive summers (2000–2001), outflow trout utilized the areas along the north shore of the lake around the Rupert River mouth, the large bay to the west of the mouth of the Rupert River, and the southwest region of the lake (Figure 3). Conversely, in both years, inflow trout (Pepeshquasati and Cheno) were typically found along the distinctive island chain and southern shores of the lake (Figure 3). Importantly, this spatial segregation in feeding areas is related to the

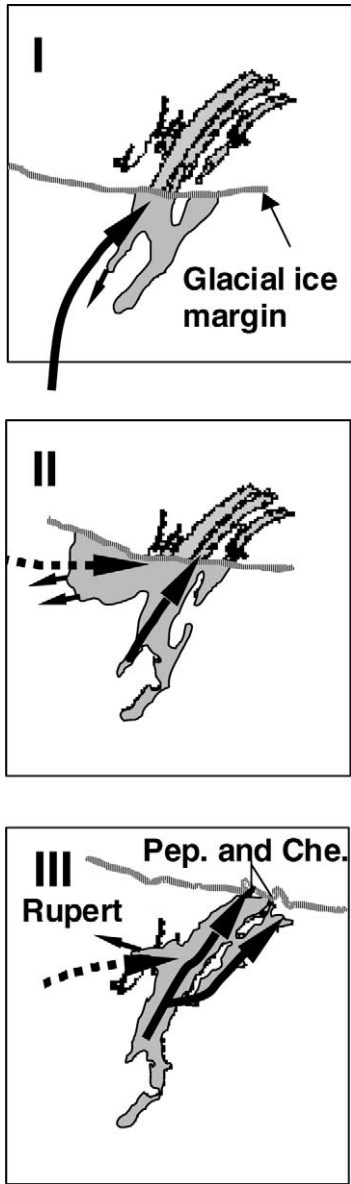


FIGURE 4.—Colonization history of lake-migratory brook trout in Mistassini Lake. The sequential reconstruction of the lake following glacial recession is indicated by steps I–III (approximately 7,000–8,000 years ago; modified from Bouchard 1981 and Fraser and Bernatchez 2005b). The gray lines indicate the locations of the glacial ice margin at the different steps. The small arrows represent the directions of discharge at the different steps (note the change from south to west as the lake grows). The large black arrows represent the probable direction and timing of colonization by the outflow population’s ancestral group (dashed lines) and the inflow populations’ ancestral group (solid lines) based on their phylogeographic relationships with populations from surrounding drainages (details in Fraser and Bernatchez 2005b). River abbreviations in step III are as follows: Pep. = Pepeshquasati River, Che. = Cheno River, Rupert = Rupert River.

use of different coastal habitats (represented by littoral zone substrate; Fraser and Bernatchez 2005a). Furthermore, the distance that individuals migrate within feeding areas is longer for inflow trout than outflow trout (~70 km versus ~20 km). Once entering rivers, inflow trout also migrate upstream to spawning grounds at much greater distances and elevations than outflow trout (~35–75 km versus ~0–15 km, 50–150 m versus –10–0 m). These differences in migration distance and difficulty are notable because populations with longer migrations (i.e., inflow trout) are expected to show adjustments in body shape that compensate for the energy costs that such migrations can incur (Fraser and Bernatchez 2005a and references therein). Accordingly, inflow trout have more streamlined body forms with longer posterior regions (caudal peduncle length), traits known to improve swimming efficiency for long migrations in other salmonids (Taylor and McPhail 1985; Taylor and Foote 1991).

The above discussion shows that phenotypic and life history trait differences related to migration among brook trout populations in a pristine environment (Mistassini Lake) are negatively associated with the amount of gene flow between populations. Differences relate to divergent feeding areas and spawning grounds that outflow and inflow populations occupy (e.g., migration distance and body form; spatial segregation in feeding areas and differential habitat use). Where such relationships exist between phenotypic divergence and gene flow, as well as environmental factors, divergent natural selection is strongly implicated in divergence (Endler 1977; Smith et al. 1997). Furthermore, geographic distance and gene flow are not correlated, implying that limited dispersal and genetic drift have not been important causes of differentiation. Although the genetic basis for trait differences has not been confirmed for Mistassini Lake populations per se, variation in other phenotypic traits (growth, disease resistance, and embryonic development) has a strong genetic basis in brook trout, including in other populations from the Rupert River drainage (Perry et al. 2004a, 2004b). Additionally, traits differences described above have a genetic component in other migratory salmonid fishes (Taylor and McPhail 1986; Skulason et al. 1993; Quinn et al. 2000). Together, these data provide indirect evidence that outflow and inflow trout are adapted locally to their respective feeding areas and spawning grounds.

On the other hand, the Mistassini Lake populations have multiple origins, so one cannot completely discount the possibility that ancestral groups had some preexisting differences that facilitated their colonization of certain lake areas. Again, there was a correspondence between directional outflow changes

during lake formation and the colonization of ancestral brook trout groups to the lake. Therefore, the nature and timing of colonization may have impacted the way that evolution could proceed among population groups within Mistassini Lake. For instance, the spatial distributions of populations within feeding areas were not easily separated from the likely colonization routes of their ancestors (Figure 3 versus Figure 4; Fraser and Bernatchez 2005b). Altogether, the main implication here is that both unique historical events and natural selection have probably helped to shape the phenotypic and genetic diversity observed between Mistassini Lake brook trout populations today.

Results and Discussion

Implications for Lake-Migratory Brook Trout Conservation and Rehabilitation in Other Lakes

Rehabilitation must consider adaptive divergence and evolutionary history.—The presence of phenotypically and genetically distinct migratory brook trout populations within Mistassini Lake provides an additional example of a general phenomenon observed in several northern temperate freshwater fish species (Taylor 1999; Bernatchez 2004). If lake-migratory brook trout in other lakes (e.g., Lake Superior coasters) likewise do not represent a single, panmictic population, this has important ramifications for conservation initiatives. First, divergent populations within a lake represent different components of the biodiversity of brook trout. It is thus important to recognize and maintain these components, to ensure that the long-term potential of brook trout to respond to any environmental changes is maximized. Second, it is relevant to recognize population differences in the short-term to facilitate appropriate rehabilitation strategies.

Research on migratory brook trout in Mistassini Lake shows the importance of ancestral origin in structuring existing populations in relation to geological history. Dynamic changes in the direction of discharge such as those that occurred during the formation of Mistassini Lake are known to have also occurred in many other large, postglacial lakes (Taylor 1999; Behrmann-Godel et al. 2004), including Lake Superior (this volume). The work of Danzmann et al. (1998) supports the proposition that Lake Superior coasters have multiple ancestors; they reported the presence of mitochondrial DNA haplotypes from multiple ancestral groups of brook trout that had evolutionary histories spanning several hundred thousand years before secondary contact. Ancestral groups in Lake Superior might have maintained some degree of reproductive isolation after secondary contact with

one another, as they have in Mistassini Lake (Fraser and Bernatchez 2005b). If so, managers or others involved in rehabilitation efforts should consider that populations with such long, independent evolutionary histories may have been exposed to contrasting environments and may have accumulated unique genetic differences or incompatibilities. For example, reduced embryonic survival relative to pure forms (outbreeding depression) has been reported for hybrids between two lineages of whitefish that evolved separately during the last glaciation events (Lu and Bernatchez 1998). This suggests that if coasters originated from multiple ancestral groups and maintained their genetic distinction in sympatry (after colonizing Lake Superior), fish from one ancestral group will not necessarily replace or facilitate the rehabilitation of a declining or extirpated population that originated from a different ancestral group in the same lake. It further implies that any hybridization between ancestral groups, either before supplementation (recruitment of young to stock in the wild) or after supplementation (interbreeding between groups when one group is stocked into another group's environment), could have negative effects on further recovery.

Research on Mistassini Lake also shows that environmental gradients related to habitat structure are important in promoting adaptive differences in lake-migratory brook trout. As a result, the geographical proximity of one river to another cannot be used by itself as a proxy for the degree of local adaptation (adaptive divergence) between trout inhabiting them (e.g., the case of Rupert–Pepeshquasati versus Pepeshquasati–Cheno in Mistassini Lake). If Lake Superior coasters function much like Mistassini Lake lake-migratory brook trout, such information is relevant for rehabilitation where certain scientific data are lacking. For instance, in the absence of data on the extent of genetic distinctiveness of trout in different vicinities (e.g., rivers), decisions concerning which extant trout to use for rehabilitation or reintroductions must also carefully consider additional, comparative information relating to potential adaptive differences in habitat use, migratory behavior, and life history characteristics.

Rehabilitation requires consideration of a suite of habitats in both spawning and feeding areas.—Our research shows interrelationships between the spawning grounds and feeding areas that different lake-migratory brook trout populations utilize, in terms of their habitat use, migration distances, body morphologies, and life histories—interrelationships that are probably important for population persistence. If similar relationships exist elsewhere (e.g., coasters in Lake Superior), then lake habitats (feeding areas of subadults and adults) are also critical to local

adaptation of lake-migratory brook trout. Consequently, conservation and rehabilitation efforts should not focus solely on habitat within spawning rivers. In addition, if coasters are not a single population, then knowledge of the extent of spatial use of remaining populations within feeding areas will provide invaluable information on the potential for recolonization of vacant or extirpated habitats, as well as basin-wide information of lake habitat use. If coasters from different rivers in Lake Superior have (or had) different spatial distributions within feeding areas, as Mistassini Lake populations do, it might also be informative to demarcate their existing spatial boundaries to protect individuals from specific regions for conservation purposes.

Rehabilitation must maintain natural connectivity patterns and identify key source populations.—Our data suggest that dispersal of lake-migratory brook trout is prevalent between interconnected groups of populations inhabiting different rivers (e.g., inflows). If coasters or similar forms exhibit or historically exhibited such behavior in other lakes, this information may be important for their recovery. For example, although divergent natural selection may lead to phenotypic differences and a reduction of gene flow between outflow and inflow trout populations in Mistassini Lake, smaller differences in selective regime and higher gene flow are probably responsible for the similarities between inflow populations. A third northeast inflow, Takwa, is also used for spawning in Mistassini Lake, although the abundance of spawning trout in Takwa appears to be much lower than that in other inflows, particularly Pepeshquasati (Fraser et al. 2004). Takwa trout are genetically distinct from trout in their sister river Cheno but are not genetically distinct from Pepeshquasati trout, despite the latter river being further away from Takwa (Figure 2; Fraser et al. 2004). One possible explanation for these unusual patterns of genetic differentiation is that greater gene flow from especially Pepeshquasati and Cheno to Takwa (than vice versa) has an impact on the genetic structuring in Takwa (detailed in Fraser et al. 2004).

From a conservation perspective, such connectivity patterns in a pristine system provide insights into population persistence, key source populations (e.g., Pepeshquasati), and the possibility for recolonization of extirpated habitats by lake-migratory brook trout. Management resources may not be available at the finest levels of population structuring (typically individual rivers in salmonids), so an approach focusing on the prioritization of conservation efforts within groups of interconnected populations may be more appropriate (see also Waples 1991; Youngson et al. 2003; Fraser et al. 2007a, 2007b). Fraser et al.

(2004) also provided evidence for male-biased dispersal among inflows. Not only does this further support the premise that inflow populations are demographically connected, it also suggests that if dispersal rates in other systems (e.g., Lake Superior) are sex biased the recolonization rates of extirpated habitats may be lower than expected (Fraser et al. 2004). Consequently, if deemed necessary, translocations of sufficient numbers of both sexes between closely related rivers may also be useful to quicken the recolonization process through supplementation and to maintain genetic variability within metapopulations that was fulfilled by dispersers in the past.

What might historical levels of abundance have been like?—Although no quantitative assessments of the abundance of Mistassini Lake populations have been undertaken, we have some idea of the relative abundance of these populations based on temporal estimates of effective population sizes (N_e) within the outflow and each inflow. Point estimates of N_e among inflow and outflow populations ranged from approximately 350 to 1000 (details in Fraser et al. 2004). Given the commonly reported ratio of N_e/N (0.1–0.2) in other salmonid fishes with analogous migratory life cycles (e.g., Heath et al. 2002; Shrimpton and Heath 2003), each spawning population of Mistassini Lake brook trout might be on the order of a few to several thousand individuals, with the largest population (Pepeshquasati) perhaps being on the order of 10,000 individuals. Our point estimates should be taken with some caution because of their wide confidence intervals (Fraser et al. 2007a). The ratio of N_e/N is also known to vary considerably among salmonid populations (e.g., Shrimpton and Heath 2003), so the cost of using N_e estimates as surrogates for N must be recognized. Nevertheless, if lake-migratory brook trout in other systems (e.g., coasters in Lake Superior) had historically similar N_e values before human impacts, the implication here is that lake-migratory brook trout are probably not “overly abundant” even in their natural state.

What is the possibility of lake-spawning trout?—Lake spawning of migratory brook trout is known in some lakes (Lake Superior: Newman et al. 2003; Lake Nipigon: Ricker 1932; Wilson et al., in press), and this possibility cannot be entirely dismissed in Mistassini Lake. However, available genetic data suggest that the vast majority of trout within Mistassini Lake originate from the spawning rivers we sampled (Fraser and Bernatchez 2005a). A number of local First Nations brook trout “experts” ($n = 20$) have also indicated that they have not seen brook trout spawning in the lake (Fraser et al. 2006). Based on the number of individuals that could be confidently excluded from

our sampled populations (Fraser and Bernatchez 2005a), we estimate that up to 5–15% could be associated with lake spawning.

For the rehabilitation of coasters, we think it also important to consider the ancestral origins of any lake-spawning trout. In Mistassini Lake, for example, we speculate that lake-spawning trout originate from the outflow (Rupert) ancestor. As potential spawning habitats, outflows share more similar characteristics with the lake than inflows do (less current, deeper water, similar temperatures). Outflow trout are also deeper-bodied than inflow trout, a body form known to facilitate the use of lake-spawning areas in other salmonid fishes (Hendry 2001). Additionally, when genotypes of all individuals sampled in feeding areas are clustered into multivariate space (a factorial component analysis), inflow-assigned trout have less variance than outflow-assigned trout (data not shown). Thus, if some trout spawn in the lake but have been assigned incorrectly to our source populations sampled within rivers (outflow and inflows), they more likely originate from the outflow ancestor. Interestingly, in a parallel context, three genetically isolated morphotypes of migratory brown trout *Salmo trutta* inhabit Lough Melvin, Ireland; the only morphotype known to spawn in the lake also utilizes the outflow for breeding (Ferguson and Taggart 1991). Overall then, to improve chances of successful rehabilitation of coasters, the choice of source population for rehabilitation should again consider the evolutionary history of populations, in relation to the likely processes that have led to their habitat divergence within Lake Superior.

Migratory behavior within feeding areas must be considered.—Another point that we believe may have relevance to the conservation of other lake-migratory forms of salmonid fishes (e.g., coasters) is the observation that Mistassini Lake trout have a tendency to form small schools (consisting of 3–12 individuals) within feeding areas. Fraser et al. (2005) provided evidence that such schools are nonrandom in their genetic composition, many schools being formed of individuals from the same population or even partially composed of members from the same family (i.e., full- or half-siblings). These results were obtained for inflow populations (Pepeshquasati and Cheno) even though their spatial distributions overlap strongly within feeding areas in the lake.

The tendency for migratory brook trout to form small schools in feeding areas is not limited to Mistassini Lake (it also occurs, for example, in Lake Nipigon; R. Swainson, Ontario Ministry of Natural Resources, personal communication), although analyses of the genetic composition of schools in other lakes have not been conducted. Nevertheless, we suggest that

because of the general susceptibility of migratory brook trout to fishing pressure (Flick 1977; Power 1980; Curry et al. 2003), precautions should be made to prevent the complete exploitation of these social groups. Indeed, such exploitation could ultimately lead to the erosion of genetic variability within populations or affect group behaviors that are important for survival and the completion of the life cycle in these trout (see Fraser et al. 2005). For sectors of Lake Superior where coaster angling is still permitted, management strategies might therefore find it worthwhile to implement harvest restrictions that prevent the harvesting of multiple individuals from the same schools.

A lakewide perspective on conservation and rehabilitation is beneficial.—Our research also suggests that a lakewide perspective on conservation is important for success with migratory forms of fish such as coasters in lakes. If coaster brook trout in Lake Superior and related forms in other lakes also have high mobility, then movements of trout between spawning grounds and feeding areas—trout that originate from different rivers and that probably are genetically distinct populations—may overlap multiple management jurisdictions. In Mistassini Lake, for example, the current management system divides the lake arbitrarily along the 51st latitudinal parallel between First Nations and provincial wildlife reserve territories. This is in the completely opposite direction of the biological reality of feeding areas of different populations (Figure 2 versus Figure 3). Human-defined management areas are also a fact of life in other lakes, such as Lake Superior (e.g., state, provincial, and federal agencies). Because such divided management systems will probably continue, each jurisdiction must recognize that activities in one region may have consequences for the successful protection, reintroduction, or rehabilitation of coaster populations elsewhere.

General Implications

If Mistassini Lake had been substantially disturbed by human activities, it is unlikely that we would have been able to detect the same patterns of population structuring and connectivity. For instance, stocking of all populations from a common strain could have erased the historical signal of population structuring as well as any evidence of phenotypic divergence between inflows and outflow populations. Stocking could also have resulted in largely inflated variance in reproductive success, thereby underestimating N_e as well as N_e/N ratios (Ryman and Laikre 1991). Overexploitation could also have led to the erosion of original genetic diversity and resulting maladaptation (Lacy 1995). Avoiding the potentially confounding effects of human activities in interpreting the ecology and

evolution of population structuring meant that we could be more confident about the processes governing population divergence within lake-migratory brook trout and in the plausible spatial scale of local adaptation in this species. This provided a lakewide scale perspective into what other systems may have been like before human activities became pronounced. Indeed, because the biology of Mistassini Lake trout shares a compelling number of similarities with what is known of the biology of coasters in Lake Superior (and other lakes), we believe that Mistassini Lake provides a useful case study that applies to lake-migratory trout elsewhere. We hope that our research on Mistassini Lake will stimulate managers and biologists working on similar systems to consider the interplay between ecology and evolution in future conservation and rehabilitation efforts.

Acknowledgments

We are grateful for the invitation to contribute this paper to the American Fisheries Society Symposium on the rehabilitation of coaster brook trout in Lake Superior. Comments from A. Calvert, M. Jennings, K. MacIntosh, and three anonymous reviewers improved the quality of the paper. Our research was supported primarily by a National Sciences and Engineering Research Council (NSERC) grant (Genomics) to L.B. D.J.F. was supported by NSERC Doctoral and Northern Research Scholarships.

References

- Behrmann-Godel, J., G. Gerlach, and R. Eckmann. 2004. Postglacial colonization shows evidence for sympatric population splitting of Eurasian perch (*Perca fluviatilis* L.) in Lake Constance. *Molecular Ecology* 13:491–497.
- Bernatchez, L. 2004. Ecological theory of adaptive radiation: an empirical assessment from coregonine fishes (Salmoniformes). Pages 175–207 in A. P. Hendry and S. C. Stearns, editors. *Evolution illuminated: salmonids and their relatives*. Oxford University Press, New York.
- Bouchard, A. 1981. Late quaternary geology, Temiscamie region, central Quebec. University of Montreal, Montreal.
- Burger, C. V., W. J. Spearman, and M. A. Cronin. 1997. Genetic differentiation of sockeye salmon subpopulations from a geologically young Alaskan lake system. *Transactions of the American Fisheries Society* 126:926–938.
- Caizergues, A., O. Ratti, P. Helle, L. Rotelli, L. Ellison, and J. Y. Rasplus. 2003. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Molecular Ecology* 12:2297–2305.
- Carmack, E. C., C. B. J. Gray, C. H. Pharo, and R. J. Daley. 1979. Importance of lake–river interaction on seasonal patterns in the general circulation of Kamloops Lake, British Columbia. *Limnology and Oceanography* 24:634–644.
- Castric, V., and L. Bernatchez. 2003. The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchell). *Genetics* 163:983–996.
- Curry, R. A., C. Brady, and G. E. Morgan. 2003. Effects of recreational fishing on the population dynamics of lake-dwelling brook trout. *North American Journal of Fisheries Management* 23:35–47.
- Danzmann, R. G., R. P. Morgan, M. W. Jones, L. Bernatchez, and P. E. Ishen. 1998. A major sextet of mitochondrial DNA phylogenetic assemblages in eastern North American brook trout (*Salvelinus fontinalis*): distribution and postglacial dispersal patterns. *Canadian Journal of Zoology* 76:1300–1318.
- DuBois, A. 1967. Age et croissance de la touladi (*Salvelinus namaycush*) du lac Mistassini. [Age and growth of the lake trout (*Salvelinus namaycush*) in Lake Mistassini.] Master's thesis. Université Laval, Quebec City, Quebec.
- Dutil, J. D., and G. Power. 1980. Coastal populations of brook trout (*Salvelinus fontinalis*) in Lac Guillaume-Delisle, Richmond Gulf, Quebec. *Canadian Journal of Zoology* 58:1828–1835.
- Endler, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton University Press, Princeton, New Jersey.
- Ferguson, A., and J. Taggart. 1991. Genetic differentiation among sympatric brown trout (*Salmo trutta*) populations of Lough Melvin, Ireland. *Biological Journal of the Linnean Society* 43:221–237.
- Flick, W. A. 1977. Some observations of age, growth, food habits and vulnerability of large brook trout (*Salvelinus fontinalis*) from four Canadian lakes. *Naturaliste Canadienne* 104:353–359.
- Fraser, D. J. 2005. Étude de la divergence populationnelle chez l'omble de fontaine: intérêt pour l'évolution et la bioconservation. [A study of population divergence in brook trout: implications for evolution and conservation.] Doctoral dissertation. Laval University, Quebec City, Quebec.
- Fraser, D. J., and L. Bernatchez. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology* 10:2741–2752.
- Fraser, D. J., and L. Bernatchez. 2005a. Adaptive migratory divergence among sympatric brook charr populations. *Evolution* 59:611–624.
- Fraser, D. J., and L. Bernatchez. 2005b. Allopatric origins of sympatric brook charr populations: colonization history and admixture. *Molecular Ecology* 14:1497–1509.
- Fraser, D. J., T. Coon, R. Dion, M. Prince, and L. Bernatchez. 2006. Integrating traditional and evolutionary knowledge in biodiversity conservation: a population level case study. *Ecology and Society* 11(2):4. [online].
- Fraser, D. J., P. Duchesne, and L. Bernatchez. 2005. Migratory charr schools exhibit population and kin associations beyond juvenile stages. *Molecular Ecology* 14:3133–3146.
- Fraser, D. J., M. M. Hansen, S. Ostergaard, N. Tessier, and L. Bernatchez. 2007a. Comparative estimation of effective population sizes and temporal gene flow in two

- contrasting population systems. *Molecular Ecology* 16:3866–3889.
- Fraser, D. J., M. W. Jones, T. L. McParland, and J. A. Hutchings. 2007b. Loss of historical immigration and the unsuccessful rehabilitation of extirpated salmon populations. *Conservation Genetics* 8:527–546.
- Fraser, D. J., C. Lippe, and L. Bernatchez. 2004. Consequences of unequal effective population size, asymmetric gene flow, and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* 13:67–80.
- Hansen, M. M. 2002. Estimating the long-term effects of stocking domesticated trout into wild brown trout (*Salmo trutta*) populations: an approach using microsatellite DNA analysis of historical and contemporary samples. *Molecular Ecology* 11:1003–1015.
- Heath, D. D., C. Busch, J. Kelly, and D. Y. Atagi. 2002. Temporal change in genetic structure and effective population size in steelhead trout (*Oncorhynchus mykiss*). *Molecular Ecology* 11:197–214.
- Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. *Genetica* 112–113:515–534.
- Lacy, R. C. 1995. Clarification of genetic terms and their use in the management of captive populations. *Zoo Biology* 14:565–577.
- Lu, G., and L. Bernatchez. 1998. Experimental evidence for reduced hybrid viability between dwarf and normal ecotypes of lake whitefish (*Coregonus clupeaformis* Mitchell). *Proceedings of the Royal Society of London B* 267:1025–1030.
- McPhail, J. D. 1993. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. *Canadian Journal of Zoology* 71:515–523.
- Meldgaard, T., E. E. Nielsen, and V. Loeschcke. 2003. Fragmentation by weirs in a riverine system: a study of genetic variation in time and space among populations of European grayling (*Thymallus thymallus*) in a Danish river system. *Conservation Genetics* 4:735–747.
- Moritz, C. 1999. Conservation units and translocations: strategies for conserving evolutionary processes. *Heredity* 130:217–228.
- Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology* 51:238–254.
- Mucha, J. M., and R. W. Mackereth. 2008. Habitat use and movement patterns of brook trout in Nipigon Bay, Lake Superior. *Transactions of the American Fisheries Society* 137:1203–1212.
- Newman, L. E., R. B. DuBois, and T. N. Halpern. 2003. A brook trout rehabilitation plan for Lake Superior. Great Lakes Fisheries Commission, Miscellaneous Publication 2003-03, Ann Arbor, Michigan.
- O'Connor, J. F., and G. Power. 1973. Homing of brook trout (*Salvelinus fontinalis*) in Matamek Lake, Quebec. *Journal of the Fisheries Research Board of Canada* 30:1012–1014.
- Perry, G. M. L., C. Audet, B. Laplatte, and L. Bernatchez. 2004a. Shifting patterns in genetic control at the embryonic boundary in brook charr. *Evolution* 58:2002–2012.
- Perry, G. M. L., P. Tarte, S. Croisetiere, P. Belhumeur, and L. Bernatchez. 2004b. Genetic variance and covariance for 0+ brook charr (*Salvelinus fontinalis*) weight and survival time of furunculosis (*Aeromonas salmonicida*) exposure. *Aquaculture* 235:262–271.
- Pigeon, D., A. Chouinard, and L. Bernatchez. 1997. Multiple modes of speciation involved in the parallel evolution of sympatric morphotypes of lake whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* 51:196–205.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141–203 in E. K. Balon, editor. *Charrs: salmonid fishes of the genus Salvelinus*. Dr W. Junk, The Hague, The Netherlands.
- Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. *Evolution* 54:1372–1385.
- Ricker, W. E. 1932. Studies of speckled trout (*Salvelinus fontinalis*) in Ontario. University of Toronto Studies Biological Series 36, Publications of Ontario Fisheries Research Laboratory 44:68–110.
- Ridgway, M. S. 2008. A roadmap for coasters: landscapes, life histories, and the conservation of brook trout. *Transactions of the American Fisheries Society* 137:1179–1191.
- Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology* 5:325–329.
- Shrimpton, J. M., and D. D. Heath. 2003. Census vs. effective population size in Chinook salmon: large- and small-scale environmental perturbation effects. *Molecular Ecology* 12:2571–2583.
- Skulason, S., S. S. Snorrason, D. Ota, and D. L. G. Noakes. 1993. Genetically based differences in foraging behaviour among sympatric morphs of Arctic charr (Pisces: Salmonidae). *Animal Behaviour* 45:1179–1192.
- Sloss, B. L., M. J. Jennings, R. Franckowiak, and D. M. Pratt. 2008. Genetic identity of brook trout in Lake Superior south shore streams: potential for genetic monitoring of stocking and rehabilitation efforts. *Transactions of the American Fisheries Society* 137:1244–1251.
- Smith, T. B., R. K. Wayne, D. J. Girman, and M. W. Bruford. 1997. A role for ecotones in generating biodiversity. *Science* 276:1855–1857.
- Taylor, E. B. 1999. Species pairs of north temperate freshwater fishes: taxonomy, evolution, and conservation. *Reviews in Fish Biology and Fisheries* 9:299–324.
- Taylor, E. B., and C. J. Foote. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* 38:407–419.
- Taylor, E. B., C. J. Foote, and C. C. Wood. 1996. Molecular genetic evidence for parallel life history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution* 50:401–416.
- Taylor, E. B., and J. D. McPhail. 1985. Variation in body morphology among British Columbia populations of

- coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2020–2028.
- Utter, F. M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Canadian Journal of Fisheries and Aquatic Sciences 38:1626–1635.
- Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of “species” under the Endangered Species Act. Marine Fisheries Reviews 53:11–22.
- Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution 58:386–403.
- White, H. C. 1942. Sea life of the brook trout (*Salvelinus fontinalis*). Journal of the Fisheries Research Board of Canada 5:471–473.
- Wilson, C. C., W. Stott, M. Jennings, L. Miller, S. D’Amelio, and A. Cooper. In press. Conservation genetics of Lake Superior brook trout: issues, questions, and directions. North American Journal of Fisheries Management.
- Wright, S. 1951. The genetic structure of populations. Annals of Eugenics 15:323–357.
- Yamamoto, S., K. Morita, I. Koizumi, and K. Maekawa. 2004. Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial–temporal changes in gene frequencies. Conservation Genetics 5:529–538.
- Youngson, A. F., W. C. Jordan, E. Verspoor, P. McGinnity, T. Cross, and A. Ferguson. 2003. Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics. Fisheries Research 62:193–209.