# A multidisciplinary approach to investigating population differentiation of lake trout in Québec's largest lake

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#### **ABSTRACT**

A multidisciplinary approach to investigating population differentiation of lake trout in Québec's largest lake

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Maintaining population diversity is important for species survival and fisheries productivity. Research on several large lakes has documented the presence of multiple genetically- and morphologically-distinct populations within harvested fish species but less is known of population structuring in pristine lakes. I characterized population structuring of lake trout throughout Mistassini Lake, Quebec (2,335km<sup>2</sup>), using data from nineteen microsatellite DNA loci, spatial habitat use, morphology and local Cree traditional knowledge. I found that the lake is home to a minimum of five populations. These exhibit low to modest levels of genetic differentiation, partial spatial segregation by depth and basin, indiscriminate body and head morphologies, but remarkable within-population variation in morphology. The relationship between genetic and ecological differentiation was inconsistent across ecological metrics assessed, and traditional knowledge recognized attributes of some, but not all of the demarcated populations. Adopting the conceptual framework of ecological speciation as a continuum, I contend that the higher apparent level of within-population phenotypic variation in lake trout relative to other previously studied fish species may explain their lower level of population differentiation, despite their use of numerous distinct habitat niches. I discuss how identifying and recognizing multiple forms in such a pristine boreal lake system, both with western and traditional knowledge, has implications for a better understanding of population diversity and conservation in lake trout and related species elsewhere.

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#### **Contributions of authors**

The principal author of this study, Kia Marin, performed the research, statistical analyses and writing for this project, with advice in regards to fieldwork, statistical tests and writing from Dylan J. Fraser. Mr. Andrew Coon coordinated the fieldwork, including logistical support for the collection of samples and coordination of compiling traditional ecological knowledge from local fishing experts. Mr. Robert Carson performed all of the molecular analyses completed in Chapter 1.

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#### **General Introduction**

The maintenance of biodiversity is currently one of the most important concerns that we face in light of climate change. As such, conservation has become a primary focus of many biologists. Genetic diversity, as the basis of evolutionary potential in the face of environmental change and phenotypic variation and differentiation, are two key aspects to the maintenance, growth, productivity and ultimately the persistence of a species (Bowen 1999; Frankham et al. 2002; Allendorf and Luikart 2007; Fraser 2013). Speciation, an evolutionary process by which new species arise from previously existing ones, which is driven by various geographic localities, usually involves genetic and/or morphological differentiation (Bergstrom and Dugatkin 2012). More recently, the term 'ecological speciation', has been given to the evolutionary process of divergence form a common ancestor through adaption to different environmental conditions (adaptive divergence), which in turn causes reproductive isolation and ultimately new species (Hendry et al. 2007). The rate and degree to which ecological speciation occurs fluctuates greatly and depends on multiple factors, that require further research. However, Hendry (2009) puts forth the idea of a 'speciation continuum' in which species range between adaptive variation between randomly mating populations all the way until completely isolated reproduction between two distinct species.

Understanding, managing and conserving such complex ecological interactions and processes often requires a multidisciplinary approach in order to represent a greater depth of knowledge. Such approaches often require a diverse group of stakeholders with familiarity and observations of a resource who collectively work together towards achieving a common goal. First Nations people of Canada have vast knowledge regarding their local natural environment given thousands of years of subsistence living. Traditional ecological knowledge (TEK) is detailed, cumulative, dynamic knowledge about living beings and their relationship with their environment, which is passed down from one generation to the next (Berkes et al. 2000; Menzies and Butler 2006). The James Bay Cree are a group of approximately 18,000 Cree (*Eeyouch*) located in northern Québec, Canada who have hunted, trapped and fished for thousands of years on 450,000 km² of traditional territory (Grand Council of the Crees 2011 and 2015). Fish (*namesh*) have been and continue to be part of the daily lives of the Cree as an important food source and economic resource (Grand Council of the Crees 1994). As such, the James Bay Cree

fishers possess a great wealth of knowledge regarding fish movement, distribution, phenotypic variation and seasonal cycles.

Salvelinus is a diverse genus that contains multiple species that are often harvested by local, commercial and sports fishers, in varying degrees, in many large lakes around the world. They are a diverse group of species that have been documented to have undergone evolutionarily-driven adaptive radiation in recently deglaciated systems (Taylor 1999; Muir et al. 2015). For example, research has found evidence for multiple sympatric morphological forms with different trophic ecologies, such as the Arctic charr (Salvelinus alpinus; Jonsson and Jonsson 2001) and different migratory life histories, such as brook trout (Salvelinus fontinalis; Fraser et al. 2004). Lake trout (Salvelinus namaycush and namekush in Cree) is a dominant freshwater predator that has been documented to have evolved a number of distinct forms within several large postglacial lakes (reviewed in Muir et al. 2015). The most famous forms are the 'leans', 'siscowets' and 'humpers' of the Laurentian Great Lakes, which are respectively middepth, deep-water and drop-off habitat specialists with trophic specializations for consuming different prey at these depths (Krueger and Ihssen 1995; Moore and Bronte 2001; Muir et al. 2015). These forms, and forms similar to these found in other large postglacial lakes (e.g., Great Bear Lake, Great Slave Lake, and Atlin Lake) demonstrate some apparent phenotypic differences; however, they often exhibit weak genetic differentiation (Page et al. 2004; Zimmerman et al. 2006; Northrup et al. 2010; Chavarie et al. 2014; Harris et al. 2014). This previous research has highlighted an array of morphological variation, plasticity and habitat niche exploitation without the presence of reproductive isolation. Given this, lake trout are a model species that can provide critical information with regards to the early stages of the ecological speciation continuum.

A major aspect of the ecological speciation process and lake trout diversity are habitat preference and availability. Recently deglaciated systems offer scientists a natural laboratory to study genetic and morphological variation of north temperate fishes. Situated within the traditional Cree territory is Mistassini Lake – Québec's largest natural lake (2335 km²) and one of its deepest (max. 180m; Statistics Canada 2005). The lake supports different habitat niches and therefore might harbour a variety of habitats favouring sympatric fish population diversity. Within species diversity has previously been documented in a number of species that hold both

historical and contemporary socio-economic and cultural importance for the Cree within the lake, including three distinct populations of brook trout (*Salvelinus fontinalis*) and four distinct populations of walleye (*Sander vitreus*) that contribute differentially to the lakes' annual fishery (Fraser et al. 2004; Fraser and Bernatchez 2005a; Dupont et al. 2007). Wilson and Hebert (1998) also suggested that multiple genetic groups of lake trout originally colonized the lake following deglaciations in eastern North America. Later research of Mistassini Lake found two forms of lake trout that occupy different depths, and differed in age, growth and maturity (Zimmerman et al. 2007; Hansen et al. 2012); however, due to small sample sizes, restricted geographical sampling and lack of examination of the genetic population structure, there is an incomplete picture of lake trout in Mistassini Lake. To date there has been no attempt to document what is known by the local Cree community about lake trout in Mistassini Lake. Over the last 10 years the region has seen an expanding human population and subsequent economic development, which has resulted in increasing fishing pressures (Fraser et al. 2006). Therefore, there is a growing need to expand upon the limited and preliminary scientific knowledge and compile TEK of the Mistassini lake trout to ensure its persistence and sustainability.

In the first chapter, I characterized the extent of population divergence of lake trout throughout Mistassini Lake using nineteen microsatellite loci and morphological analyses. I identified the spatial distribution of these populations relation to habitat and tested for positive relationships between genetic and phenotypic data. The second chapter aimed to compile and integrate TEK, via collaborative fieldwork and semi-directive interviews, of Mistassini lake trout over the last four decades with what is known scientifically (Chapter 1; Dubois and Lageaux 1968; Zimmerman et al. 2007; Hansen et al. 2012). Specifically, I wanted to expand upon existing knowledge, understand if our findings of Chapter 1 were commonly recognized, document potential temporal trends and identify conservation concerns. Based on previous research I hypothesized that Mistassini Lake would likely harbour multiple genetically- and morphologically-distinct populations and that local fishing experts would be able to provide a depth of knowledge regarding lake trout variation. Furthermore, I predicted that examination of habitat use through both quantitative data and TEK would help identify any factors that affect the early stages of ecological speciation in north temperate freshwater fishes. Finally, by understanding seasonal movements, potential temporal trends and management concerns indentified through TEK in combination with the quantitative findings of Chapter 1, I was able to provide both local and broad lake trout conservation and management implications. I hope that this research will contribute to a better understanding and identification of the natural population diversity of north temperate fish species that occupy a large, pristine north temperate lake ecosystem. Finally, this research demonstrates that human and ecological interactions are inevitably linked and the use of multidisciplinary approaches to research and conservation offer a greater depth of knowledge.

Chapter 1: Early stage	'lakescape'	ecological s	peciation s	haped by	depth,	basin,	and
plasticity in lake trout							

Kia Marin, Andrew Coon, Robert Carson, and Dylan J. Fraser

#### Abstract

Ecological speciation, the evolutionary process of divergence from a common ancestor via adaptive divergence, occurs on a 'speciation continuum'. Despite their common use as empirical models for the study of ecological speciation, little is still known among north temperate freshwater species regarding what influences the process (or lack thereof) in its earlier stages. I characterized the extent of population divergence of lake trout throughout Mistassini Lake, Québec (2,335km<sup>2</sup>), using nineteen microsatellite loci and morphological analyses. I also identified the spatial distribution of these populations in relation to habitat, and tested for positive relationships between extent of genetic and phenotypic differentiation. I found that the lake is home to a minimum of five genetically-differentiated populations, which are influenced primarily by depth and to a lesser extent basin. The extent of weak genetic population structure was somewhat associated with body size, colouration, and fish community structure but inconsistently associated with differences in body or head shape that is normally linked to trophic ecology. Intriguingly, all genetically distinguishable populations displayed striking phenotypic variation of lake trout occupying a large, pristine, postglacial lake. I suggest that these lake trout are at the early stages of ecological speciation. This research provides an excellent example for phenotypic plasticity within a north temperate species affecting the trajectory and progress towards ecological speciation. Sympatrically-occurring populations of lake trout appear rare, and their occupancy of large, deep lakes such as Mistassini Lake means that they act as reservoirs of genetic diversity and refuge habitat for the species in the face of future climate change.

#### Introduction

'Ecological speciation' is a term given to the evolutionary process of divergence from a common ancestor through adaptation to different environmental conditions (adaptive divergence), which in turn causes reproductive isolation and ultimately new species (Rundle and Nosil 2005; Hendry et al. 2007). Ecological speciation appears to best characterize the speciation process in a number of organisms, perhaps most famously in Darwin's finches, which underwent an adaptive evolutionary radiation from one ancestral species into a minimum of 13 different species differing in body size and beak morphology (Grant 1981). The rate and extent of ecological speciation likely fluctuates and differs greatly among taxa and depends on multiple factors meriting further research. It has been suggested that ecological speciation is best considered as a 'speciation continuum', in which species range from adaptive variation between randomly mating populations all the way to complete and irreversible reproductive isolation between two distinct species (Hendry 2009). A better understanding of the ecological speciation process in evolutionarily young, diverging populations of harvested species could also improve biodiversity conservation in many instances, given that evolving phenotypic and genetic differentiation can significantly influence population growth, productivity, and ultimately species persistence, as a source of adaptive potential in the face of environmental change (Taylor et al. 2011; Fraser 2013).

Many north temperate freshwater fish species occupying postglacial lakes contain phenotypically and genetically distinct populations that have primarily diverged in trophic niche use (reviewed in Taylor 1999; Hendry 2009; Klemetsen 2010). As these are often harvested locally (e.g., Taylor 1999; Taylor et al. 2011; Fraser et al. 2013) they provide excellent models for both the study of the ecological speciation continuum and its consequences for aquatic biodiversity conservation. In several cases, such as Icelandic Arctic charr (*Salvelinus alpinus*) and threespine stickleback (*Gasterosteus* spp.), populations exhibit varying degrees of genetic differentiation, moderate to relatively high gene flow, adaptive variation to limnetic and benthic feeding niches, and potentially reversible reproductive isolation (Gíslason et al. 1999; Jonsson and Jonsson 2001; Berner et al. 2009), placing them in the intermediary stages of ecological speciation (Hendry 2009). In more extreme cases along the continuum, such as dwarf and normal ecotypes of lake whitefish (*Coregonus clupeaformis*), divergent populations exhibit complete or

near complete reproductive isolation, and genetic incompatibilities might arise as a result of divergent selection, or for other reasons after gene flow was reduced due to divergent selection (Lu and Bernatchez 1999; Rogers and Bernatchez 2007; Hendry 2009).

Less attention has been paid to factors influencing the progress or lack of progress at earlier stages of ecological speciation in north temperate fishes wherein diversifying populations exhibit occasional adaptive variation with minor reproductive isolation (but see Hendry 2001; Berner et al. 2009). One possible species that might typify this situation, which is garnering more recent research attention is the lake trout (Salvelinus namaycush), a terminal predator fish found in many postglacial lakes of North America. Akin to other north temperate fishes, it has evolved a number of sympatric forms within several large postglacial lakes that are thought to be associated with the exploitation of different trophic niches at varying depths and specializations relating to buoyancy for occupying those depths (Blackie et al. 2003; Muir et al. 2015). The best known forms are the 'leans', 'siscowets' and 'humpers' of the Laurentian Great Lakes, which are respectively mid-depth, deep-water, and drop-off habitat specialists with trophic specializations for consuming different prey (Krueger and Ihssen 1995; Moore and Bronte 2001; Muir et al. 2015). These forms demonstrate clear phenotypic differences, yet exhibit weak genetic differentiation (Page et al. 2004). Forms documented in a few, other large lakes appear to have some similarities but also differences to Great Lakes forms. For example, Blackie et al. (2003) and Alfonso (2004) documented morphological variation between piscivorous and insect-eating forms unrelated to depth, within Great Bear Lake, Northwest Territories (NWT). Later works revealed that this lake contains up to four weakly genetically differentiated shallow-water morphs (Chavarie et al. 2014; Harris et al. 2014). In Atlin Lake, British Columbia, two morphotypes are not genetically-distinct but have clear depth and habitat preferences (Northrup et al. 2010). Finally, in Great Slave Lake, NWT, three morphologically-distinct forms exist and display partitioned trophic specialization (benthic and pelagic habitats) but their genetic differentiation has not been studied to date (Zimmerman et al. 2006; Muir et al. 2015). Collectively, previous research suggests that lake trout may be at the early stage end of the ecological speciation continuum (adaptive variation within randomly mating populations) in multiple, recently deglaciated north temperate systems.

Key features of ecological speciation and the array of lake trout diversity are habitat preference and availability. Postglacial systems provide a natural laboratory in which to study the driving factors affecting both phenotypic and genetic differentiation and how these fit onto the ecological speciation continuum. Mistassini Lake (18 U 592336 m E 5641397 m N; Fig. S1.1, Appendix 1) is Quebec's largest (2335 km<sup>2</sup>) natural lake and one of its deepest (180 m; Statistics Canada 2005), which supports different habitat niches and therefore might harbour a variety of habitats favouring sympatric fish population divergence. Within species diversity has previously been documented in a number of exploited species within the lake, including three distinct populations of brook trout (Salvelinus fontinalis) and four distinct populations of walleye that contribute differentially to the lake's annual fishery (Fraser et al. 2004; Fraser and Bernatchez 2005a; Dupont et al. 2007). Wilson and Hebert (1998) also suggested that multiple mitochondrial DNA haplotype lineages of lake trout originally colonized the lake following deglaciations in eastern North America. Two morphological forms of lake trout which differed in age, growth, maturity, and occupied different depths were also recently described in Mistassini Lake (Zimmerman et al. 2007; Hansen et al. 2012). While this initial research offered a glimpse into what such a large and pristine lake might harbour, the small sample sizes, lack of examination of population genetic divergence and complete spatial distribution left an incomplete picture of the geographical extent and distinctness of lake trout populations, as well as their ecology, evolution and origins in Mistassini Lake.

The primary research aim of this study was to: 1) characterize the extent of population divergence of lake trout throughout Mistassini Lake using morphological analyses and DNA surveys with nineteen microsatellite loci, including population relationships, effective population sizes, and the extent of contemporary gene flow; 2) identify the spatial distribution of populations in relation to habitat, specifically depth, basin, sector and fish community structure; and 3) test for positive relationships between the extent of genetic and phenotypic differentiation, chiefly body shape, head shape, body size, and colouration. Based on previous lake trout research described above, I hypothesized that Mistassini Lake would harbour multiple genetically- and morphologically- distinct populations, perhaps associated with spatial habitat and depth. Because our results supported this general hypothesis but only detected weak population genetic differentiation, I also considered factors within Mistassini Lake and other large postglacial lakes that affect the early stages of ecological speciation in north temperate

freshwater fishes, and its conservation implications. Our work signals a key role for phenotypic plasticity within some species in affecting the trajectory and progress towards ecological speciation.

# **Materials and Methods**

#### Fish sampling

A total of 636 lake trout were sampled throughout Mistassini Lake between June 12 and July 29, 2013 using gillnets and angling, in order to obtain genetic (n = 636) and morphological data (n =281). Gillnets were made of monofilament nylon; their design was based on previously conducted lake trout research in large lakes (Zimmerman et al. 2007). Gillnets were 183m long and 1.8m tall with six 30.5m gangs, one for each mesh size, ranging 51-114mm stretch mesh, which permitted targeting of all known sizes of Mistassini lake trout (Dubois and Lageaux 1968). Twenty-nine gillnets were set (Fig. S1.1) from depths of 3 to 178 m, soaked overnight and lifted after a 24-hour period. They were set intentionally throughout the lake and at varying depths to obtain a strong spatial representation within areas known to harbour lake trout according to local Cree fishers (Chapter 2). Gillnets were lifted slowly, bycatch were recorded and returned to the lake immediately, and trout were placed in fresh water baths with aerators. All living trout were anaesthetized with tricaine mesylate (MS-222) and then processed. Tissue samples (a small piece of adipose fin and data) collected from each trout included a standardized photograph, total and fork length (TL and FL, respectively), mass, depth, and location of capture (GPS). Tissue samples were also donated by local anglers. The location of donated samples was reported as a sector pre-determined on a map provided in a sampling kit. There were six sectors per basin (W1-6, E7-12; Fig. S1.1) to account for relative spatial location when GPS data were unavailable. Tissue samples were preserved in 95% ethanol until genotyping was performed.

## Genotyping

I analyzed DNA from the 636 trout by amplifying 19 microsatellite loci using multiplexed polymerase chain reactions (PCRs) (details of loci and PCR conditions are found in Appendix 2). Amplified products were electrophoretically migrated and allele sizes scored using an ABI 3500x Genetic Analyzer, associated size standards and software (Applied Biosystems Inc.). To ensure repeatability 16 samples (2.5%) were independently genotyped and scored 3 times.

#### Population genetic diversity

I firstly used MICROCHECKER (v.2.2.3; van Oosterhout et al. 2004) to test for the presence of null alleles, large allelic size dropout, or scoring errors associated with allelic stuttering issues in our dataset. Descriptive genetic statistics, including number of alleles (N<sub>A</sub>), expected (H<sub>E</sub>) and observed (H<sub>O</sub>) heterozygosities for each locus were computed using FSTAT (Goudet 2002). To also ensure that study loci fulfilled assumptions of selective neutrality in Hardy-Weinberg equilibrium (HWE) and clustering analyses below, tests of selection were performed using ARLEQUIN (v.3.5; Excoffier and Lischer 2010). I then tested for deviations from HWE and linkage disequilibrium (LD) using GENEPOP (v.4.2; Rousset 2008) by (i) assuming all 636 trout were one randomly mating population, under the null hypothesis of no population structuring within Mistassini Lake, but also (ii) at the level of individual population clusters defined below using the Bayesian model-based clustering software STRUCTURE (v.2.3.4; Pritchard et al. 2012), under the alternative hypothesis that more than one population inhabited the lake. If the null hypothesis was rejected, I expected many more HWE deviations to exist when assessing the lake as one population versus multiple populations. To adjust for any potential type I errors, I corrected HWE test p-values using the Bonferroni correction method (Rice 1989) when making multiple comparisons. As bottlenecks can be associated with post-glacial colonization, I also tested for these in each demarcated population using BOTTLENECK (v.1.2.02; Piry et al. 1999). This program compares heterzygosity excess (H<sub>E</sub>) to that expected (H<sub>EO</sub>) under mutation-drift equilibrium. During bottlenecks allelic diversity declines more rapidly than heterozygosity, therefore, populations that have undergone recent bottlenecks should reveal greater H<sub>E</sub> to H<sub>EO</sub> (Piry et al. 1999). This test was computed under the step-wise mutation (SMM) and two-phase mutation (TPM) models using 1000 iterations, and default settings (variance for the geometric distribution for TMP = 30 and proportion of SMM in TPM = 70% as recommended by Piry et al. 1999); significance was determined using Wilcoxon signed rank tests (p < 0.05).

#### Population genetic differentiation

Genetic population structure was assessed using STRUCTURE using no *a priori* information to quantify the most likely number of populations (clusters (K)) within the lake. It is an effective approach for demarcating populations in situations such as ours where low levels of genetic differentiation were anticipated within a sympatric lake environment (see Latch et al. 2006). I ran

STRUCTURE with our dataset under models of K = 1 - 20, a burn-in period of 500,000 followed by 2,000,000 iterations, and replicated 20 times each per K. I used an *ad hoc* statistic to select the appropriate  $\Delta K$  implemented in Structure Harvester (Evanno et al. 2005). This estimate was confirmed by determining the value of K with the highest log-likelihood value. The 20 iterations of the selected K value were then combined into a single output, providing an overall inferred ancestry coefficient (q) for each individual using the program CLUMPP (v.1.1.2; Jakobsson and Rosenberg 2007). Because q values were shared across multiple population clusters for many trout, I assigned individuals to a population cluster using three q values: a 'high' assignment threshold of q > 0.7, a 'low' threshold of q > 0.5, and the highest q value to any one cluster, regardless of the value. The extent of genetic differentiation between populations defined by STRUCTURE in all three q datasets was measured as global  $F_{ST}$  (Weir and Cockerham 1984) using GENEPOP.

To investigate whether genetic differentiation was also influenced by stepwise mutation ( $R_{ST}$ ), which in young postglacial lakes can reflect population divergence predating lake age (Fraser and Bernatchez 2005b), I used an allele size randomization procedure (10,000 permutations) in SPAGeDi (v.1.4; Hardy and Vekemans 2002) across all loci and populations (at all three q thresholds) If  $R_{ST}$  was significantly larger than permuted  $R_{ST}$  (p $R_{ST}$ ), it suggested that stepwise mutations had an important influence on current differentiation (Hardy et al. 2003). Previous research illustrated that  $F_{ST}$  typically has lower standard errors (Hardy et al. 2003), is more efficient when high gene flow is detected (Balloux and Goudet 2002) and performed better than  $R_{ST}$  for most typical sample sizes (Gaggiotti et al. 1999). As such, all subsequent analyses were based on  $F_{ST}$ 

#### Contemporary effective population sizes and gene flow

I estimated the contemporary effective population size ( $N_e$ ) for each demarcated population using the linkage disequilibrium method implemented in LDNe (v. 1.31; Waples and Do 2008) on all individuals (highest q). Lake trout were not aged as part of this research and thus our population samples consisted of overlapping generations, which is known to downwardly bias  $N_e$  estimates up to 25-30% (Waples et al. 2014). Therefore, reported  $N_e$  (and confidence intervals) represent a minimum per population.

I estimated contemporary gene flow using all individuals (highest q) with the program BayesAss (v.3.0; Wilson and Rannala 2003). BayesAss uses a Bayesian method to estimate recent (within the last few generations) gene flow (m) between population pairs. A total of five separate iterations were performed using  $10^7$  Markov chain Monte Carlo (MCMC) iterations with a burn-in period of  $10^6$  and sampled at a frequency of 100. Prior to each run, mixing parameters (allele frequencies, inbreeding and migration rates) were optimized until acceptance rates were between 20-35%, as recommended in the manual. To confirm assess MCMC had converged successfully on each run and overall, I used the program TRACER (v.1.6.0; Rambaut et al. 2014).

To further assess whether lake trout populations in Mistassini Lake have reached equilibrium conditions, I used Whitlock's (1992) equation for the time, in generations, required for  $F_{ST}$  to reach halfway to a new equilibrium:  $t_{1/2} = \ln(1/2) / \ln[(1-m)^2(1-2N_e)^{-1})]$ , where m = mean gene flow into each population, and  $N_e =$  mean effective population size.

#### Morphological analysis

#### i. Body and Head Morphology

To characterize gross body morphological variation, a full-bodied standardized photograph of each trout was taken immediately after capture using a digital Nikon D3100 with a UV filter mounted on a tripod. As our study was collaborative with the local Cree community and anglers, standardized photographs could only be obtained from a subset of the trout sampled (281of 636). Each fish was placed on its right side on a flat piece of plywood with the dorsal, caudal and anal fins in open positions. If fish were bent or distorted, photographs were not be used. Eighteen landmarks (Fig. S1.2A) were then digitized on each trout using tpsDig2 (v.2.17; Rohlf 2013).

A separate morphological analysis was performed on the head using 3 landmarks and 22 semi-landmarks, used to measure curvature, following Zimmerman et al. (2009) (Fig. S1.2B). Ten equally-spaced regions were produced by reference grid which was superimposed on each photograph between the snout and opercle using MakeFan (v.8; Sheets 2014). Semi-landmarks were then slid along both upper and lower curves using tpsDig2, aligning semi-landmarks perpendicularly to the curve by reducing the bending energy among individual points (Zelditch et al. 2004). The position of landmarks and semi-landmarks for both analyses were selected to

measure traits that are commonly associated with swimming and foraging performance; two traits that undergo rapid changes for local adaptation among salmonids (Gíslason et al. 1999; Kristjánssan et al. 2002; Rogers and Bernatchez 2007). In addition, the position of these landmarks and semi-landmarks are commonly used in previous lake trout (Zimmerman et al. 2009; Chavarie et al. 2014; Muir et al. 2014) and cogeneric species research (Fraser and Bernatchez 2005a).

Geometric morphometric analyses were conducted separately on body and head morphology datasets using tpsRelw (v.153; Rohlf 2013). This approach takes into account the spatial variation among assigned landmarks relative to all others (Rohlf 2013). Landmarks and semi-landmarks were assigned an x,y coordinate, centered, scaled and aligned in order to determine a consensus shape. TpsRelw uses a thin-spline analysis (Bookstein 1991) to compare the coordinates of each specimen to that of the consensus shape. The software produces partial warps, which are geometric constructs derived from the amount and direction of bending required to change the consensus shape (Zelditch et al. 2004). Principal components of these partial warps scores are termed relative warps (RWs), which quantify the majority of both body shape and head variation (Fraser et al. 2007). Only the first seven RWs for body shape (78% of variation) and first three RWs for head shape (70% of variation) were used for subsequent statistical analyses. I identified morphological clusters with MCLUST (v.4.4; Fraley et al. 2012) as implemented in RStudio (v.0.98.1102; R Core Team 2013). The first model assumed one morphological cluster best represented the data; subsequent models assumed two or more (up to 10) clusters existed. All models were analyzed using two (EII, VII) of the nine multivariate mixture options; the model with the highest Bayesian information criteria (BIC) was selected as best describing morphological clusters (Fraley et al. 2012).

#### ii. Body size and colouration

Body size and colouration were also compared among populations using all three datasets (q > 0.7, q > 0.5, and the highest q). I assessed population differences in mass with a basic linear model. To investigate population differences in the relationship between mass and length, I performed an analysis of covariance (ANCOVA) where the response variable was total length and the mass was transformed (natural log) and included as a continuous covariate with genetically-distinct population (factor) that was interacted with mass. I conducted a subsequent

pairwise comparison of the inferred slopes (length/weight curves) using 'lsmeans' in RStudio (v.2.17; Lenth and Herva 2015). Mass was recorded for 520 and TL for 472 (of 636) trout. Colour frequency distributions were compared using a chi-Square test in the 'vcd' package (v.1.3-2; Meyer et al. 2014). The colour of 422 (of 636) trout was classified and recorded at the time of capture based on being black, brown, dark silver, silver or light.

#### Associations between genetic, morphological and ecological differentiation

#### i. Genetic & morphological associations

To test for any association between genetically-demarcated populations (STRUCTURE) and morphological clusters (MCLUST), I performed a contingency test on all three datasets (q > 0.7, q > 0.5, and the highest q).

#### ii. Genetic & ecological associations

To determine whether the spatial distribution of genetically-demarcated populations was influenced by basin, sector and/or depth, I firstly performed a multinomial regression analysis on all three datasets (q > 0.7, q > 0.5, and the highest q) with individuals weighted based on their highest q value, using the package 'nnet' in RStudio (v.7.3-9; Venables and Ripley 2002). Model selection was based on Akaike's information criterion (AIC) and the most parsimonious model was chosen. Secondly, I carried out a redundancy analysis (RDA) using the 'vegan' package (v.2.2-1; Oksanen et al. 2015) which incorporated the raw q values for each individual. I used a both global permutation test of the RDA result to determine if there was a significant relationship between genetically-demarcated populations and ecological variables, as well as a permutation test on canonical axes with 1000 steps (Borcard et al. 2011); R-squared values were calculated for both the multinomial and RDA models as a measure of 'goodness-of-fit'. The relationship between basin and different populations was investigated using a generalized linear model (GLM) fitted with a binomial error distribution (count data).

#### iii. Genetic & fish community structure associations

Bycatch in gillnets was recorded throughout the field sampling period. I therefore tested whether different populations were associated with different fish community structure, using a contingency test. Namely, bycatch abundance and diversity captured within the same net and mesh panels as each individual trout provided a reasonable proxy for prey availability and the

extent of interspecific competitor species. The relationship between populations and fish community structure was then visualized with the aid of an RDA.

iv. Mantel tests: genetic differentiation vs. morphological or ecological differentiation. I further tested for associations between the extent of genetic and either morphological differentiation, depth, fish community structure (abundance), by using Mantel tests in the 'vegan' package in RStudio. These tests always compared two distance matrices: population pairwise  $F_{ST}$  values and either the (i) absolute difference in the mean scores for the first seven RWs for body morphology and first three RWs for head morphology, (ii) absolute difference in the median depth, or the (iii) absolute difference in prey abundance. All mantel tests were conducted on the three thresholds (q > 0.7, q > 0.5, and the highest q).

#### Results

# Population genetic diversity

Repeatability of genotyping was confirmed as the 16 samples that independently run 3 times were scored with 100% concordance. All loci screened were highly polymorphic, averaging 29.5 alleles per locus (range of 13 to 72) with an average observed heterozygosity of 0.813 (range of 0.526 to 0.939) (Table S1.1, Appendix 1). No locus showed evidence of being under selection, nor was there any evidence of scoring errors as reported from MICROCHECKER. Under the null hypothesis that all 636 trout were from one randomly-mating population, heterozygote deficiencies were detected at 15 of 19 loci (p < 0.05) (Table S1.2). At the level of individual population clusters defined by STRUCTURE using the three different thresholds of q for assigning individuals to those populations, these deficiencies were greatly reduced, providing a first indication of sympatric population structure (21 to 28 of 95 population-locus comparisons at uncorrected p < 0.05); the remaining 6-11 deviations from HWE after Bonferroni correction (p < 0.0005) were spread across all five identified populations and across 12 loci. I also detected significant LD in only 5 of 171 locus-population tests after Bonferroni correction (20 of 171 tests at p < 0.05), and found little evidence for significant LD when accounting for population structure (13 to 34 of 855 tests, depending on q threshold and after Bonferroni correction) (Table S1.3). Significant LD tests in the three q threshold datasets were spread across all identified populations and among 51 unique loci-pairs. Finally, there was also no evidence of recent bottlenecks in any demarcated populations under either mutation model employed (Table S1.4).

## Population genetic differentiation

Results from STRUCTURE and Structure Harvester supported the existence of five genetically-distinct lake trout populations in Mistassini Lake ( $\Delta K = 57.03$  mean LnP[D]= -58060.42) (Table S1.5). Global F<sub>ST</sub> values among populations derived from the three q threshold datasets were 0.017 (95% CI = 0.014-0.021), 0.021(95% CI = 0.017-0.026) and 0.028 (95% CI = 0.022-0.035) for the highest q, q > 0.5 and q > 0.7, respectively. Pairwise estimates of F<sub>ST</sub> ranged from 0.011 to 0.036 (highest q dataset), 0.015 to 0.042 (q > 0.5 dataset), and 0.021 to 0.048 (q > 0.7 dataset) (Table S1.6A). In all three datasets, population 2 vs. 3 and 4 vs. 5 showed the lowest and highest levels of differentiation, respectively.

Allele size permutation tests also suggested that stepwise mutation contributes to current population genetic differentiation: global  $R_{ST}$  was significantly greater than  $pR_{ST}$  across all populations in the three datasets (Fig. S1.3A) and also at 5 of 19 (highest q value), and 4 of 19 (q > 0.5 and 0.7) individual loci (Fig. S1.3B, C, D). This mutational influence was most evidenced among three population comparisons (population 1 vs. 4, 3 vs. 4, and 3 vs. 5) across all three q thresholds (after Bonferonni correction) (Table S1.7).

#### Contemporary effective population sizes and gene flow

Point estimates of  $N_e$  in general had fairly tight confidence intervals and ranged from 371 (population 5) to 4199 (population 2) (Table S1.8). Gene flow (m) estimates among populations were quite high, ranging from 0.0027 to 0.0905, with a global average of 0.0184 (Table S1.9). Some asymmetries in m also existed, namely more gene flow was exchanged from population 1 to populations 2, 4 and 5 than vise-versa (Fig. S1.4). Generation times (t) for  $F_{ST}$  to reach a new equilibrium between population-pairs range from 22 (pop. 2-5) to 177 (pop. 1-3) and approximately 37 generations across all populations (globally), suggesting that an equilibrium between genetic drift and m has been reached among populations.

## Morphological analysis

#### i. Body and Head Morphology

A high amount of variation for body and head morphology was observed within demarcated populations. With respect to body and head shape, respectively, the first three RWs (of 34 and 28) accounted for 55% and 61% of the total variation. Major shape differences included differences in the slope of the snout and lower jaw, dorsal and belly curvature (body RW1; 36%), slope of top of cranium and dorsal side, length and depth of caudal peduncle (body RW2; 17%), body depth, eye size (body RW3; 12%), length of head and snout, eye position, length of upper jaw (head RW1; 36%), head depth and bluntness of snout (head RW2; 23%) and slope of lower and upper jaw (head RW3; 12%). Visualizations of these morphological shifts can be seen in Fig. S1.5. Clustering analysis defined three separate body shape clusters (B1-3) with a ΔBIC value of 4, and five head shape clusters (H1-5) with a ΔBIC value of 6 (Table S1.10; Fig. S1.5A, B). This analysis also revealed that the first 7 body RWs body and 3 head RWs were to be carried forward for all further analyses. Consensus body shapes of the three clusters did not

differ greatly, however, B1 (n = 144) had a long and steep lower jaw and long and narrow caudal peduncle, B2 (n = 111) had a shorter head with a steep cranium top and a long and narrow caudal peduncle, whereas B3 (n = 26) had the greatest body depth, smallest eyes and a thicker and shorter caudal peduncle (Fig. S1.6A). Morphological variation was greater among head shape clusters: H1 (n = 19) had the most blunt snout and shortest upper jaw, H2 (n = 45) had the longest head and a snout that was in between blunt and streamlined, H3 (n = 22) was the most streamlined with the longest upper jaw, H4 (n = 177) was very similar to H2 but with a slightly greater depth and longer upper jaw, and H5 (n = 18) had the shortest and deepest head with eyes located most dorsally (Fig. S1.6B).

# ii. Body size and colouration

The mean mass of population 4 was significantly greater compared to all populations and across all thresholds (all p < 0.0001) (Fig. S1.7A); population 3 was also significantly larger in size than population 1, 2, and 5 (all p < 0.003). Results from the ANCOVA revealed that the interaction between mass and population had a significant effect on TL across all thresholds (all p < 0.02). A pairwise comparison revealed that the length/weight curves (slopes) of populations 1 vs. 3 and 1 vs. 4 were significantly different across all three thresholds (all p < 0.005) (Fig. S1.7B). Specifically, population 1 exhibited a much shallower curve (slope) compared to the other two populations: at greater lengths populations 3 and 4 are much heavier compared to population 1. Furthermore, populations 2 vs. 3 were also significantly different at the highest q and q > 0.5 threshold (p = 0.001 and 0.004 respectively). Populations varied in the proportions of individuals with different colouration across all q thresholds ( $X^2 = 130.92 - 139.3$ , df = 16, all p < 0.0001). Populations 2, 3, and 5 were comprised predominately (between 73 – 80%) of black coloured lake trout (Figure 1.1A) whereas populations 1 and 4 contained between 69 and 72% of lighter (dark silver, silver or light) coloured lake trout.

#### Associations between genetic, morphological and ecological differentiation

# i. Genetic & morphological associations

Genetically-demarcated populations and both body and head clusters to some extent were associated with each other at all q thresholds (genetic-body:  $X^2 = 30.5$ -38.1, all df = 8, all p < 0.001 and genetic-head:  $X^2 = 38.2$ -39.5, all df = 16, all p < 0.002) but the strength of these relationships was best described as weak (genetic-body: Cramer's V = 0.26-0.31; genetic-head:

Cramer's V = 0.18-0.25). This can be seen in Figure 1.2, where each morphological cluster contains individuals in varying frequencies from all demarcated populations.

#### ii. Genetic & ecological associations

Depth was the most important ecological variable influencing population genetic clustering, followed by basin and sector to a lesser extent. Using a multinomial regression, the best fit model included both depth and sector (Table S1.11A) with McFadden's pseudo-R<sup>2</sup> value ranging from 0.45 to 0.49 across the three *q* thresholds. Individuals from population 1 were captured disproportionately in deeper water, followed by population 4 which were typically mid-depth, while populations 2, 3 and 5 typically occupied shallow water (Figure 1.1B, Table S1.11B). This analysis also revealed population spatial differences with respect to sector: population 1 was captured predominantly in sectors E9, W3 and W4, population 2 and 3 in sector W3 and W4, population 4 in sector W3, and population 5 in sector E11. However, individuals from each population were captured in almost every sector except E12 and E7 wherein only one individual was captured.

The RDA model selected included all three ecological variables (depth, basin and sector) and had essentially congruent results as the multinomial regression analysis ( $R^2_{adj} = 0.12$ ). A global permutation test of the model revealed significant relationships between ecological variables and population genetic clustering (p = 0.001). A subsequent canonical axes permutation test revealed that only the first three RDA axes were significant in explaining this relationship (all p = 0.001). RDA1 (50% of the variation) was driven primarily by depth and was especially important for distinguishing population 1 as occupying deeper water than all other populations (Fig. S1.8). RDA2 (37%) was primarily driven by individuals located in the eastern basin and sectors, and distinguished primarily population 5. RDA3 (12%) was primarily driven by individuals located in the western basin and sectors and was most important for distinguishing populations 2 and 4. A supplementary, pairwise comparison of the least square mean depth showed that population 1 was captured at greater depths than all other populations across all q-thresholds (Figure 1.1B).

Results of a GLM on fishing-effort-corrected proportions also exemplified that populations 1 and 5 were captured disproportionately more in the eastern than western basin (p < 0.01 and p < 0.001 respectively), whereas populations 3 and 4 showed the converse pattern (p <

0.01 and p < 0.05 respectively), while population 2 was captured in roughly equal numbers in both basins (p = 1.000) (Figure 1.1C).

Given the influence of depth on population genetic clustering, I also examined the relationship between morphological clusters and depth. I used a linear model and then extracted the least square means in order to conduct a pairwise comparison to determine if depth could predict morphological cluster. Depth was only a weak predictor of body shape cluster (p = 0.03) and there were no significant population pairwise comparisons (Fig. S1.9A). Conversely, depth was a good predictor of head shape cluster (p < 0.001), with head cluster 5 being captured in deeper water and statistically significant from populations 2, 3 and 4 (Fig. S1.9B).

## iii. Genetic & fish community structure associations

Different populations were associated with different quantities of bycatch of other fish species (all p < 0.001) across all three q-threshold datasets, though the associations were weak (Cramer's V = 0.168-0.174). Population 1 was rarely captured with other fish species, whereas populations 2 and 3 were closely associated with burbot and whitefish, population 5 with walleye, and population 4 with all bycatch species (Fig. S1.10).

iv. Mantel tests: genetic differentiation vs. morphological or ecological differentiation There was little evidence for a significant relationship between  $F_{ST}$  and the extent of morphological, depth and prey differences across all thresholds (Table S1.12), as the only significant relationship existed between  $F_{ST}$  and the difference in RW6 for body morphology (p < 0.02). There were, however, some evident positive trends between increasing  $F_{ST}$  and increasing morphological differences (body: RW1, RW2, RW4, RW5; head: RW1, RW2) (Figure 1.3; Fig. S1.11).

#### **Discussion**

I found weak but biologically relevant population genetic differentiation and striking phenotypic variation in lake trout occupying a large, pristine, postglacial lake. Population divergence was (i) influenced primarily by depth and to a lesser extent, basin and geographic distance (sector); (ii) associated with some variation in body size, colouration, and fish community structure, but (iii) was inconsistently associated with differences in body or head shape normally linked to trophic ecology and locomotory mode. Rather, genetically distinguishable populations displayed a high amount of morphological variation, with all populations containing individuals from each one of the three body shape or five head shape clusters.

## Factors influencing the weak extent of population divergence

Where clear examples of multiple, sympatrically-occurring morphotypes of lake trout have been described, they are almost universally found in very large postglacial lakes (Wilson and Mandrak 2003), and their genetic differentiation is always weak or relatively weak (range global  $F_{ST}$  of 0.008 – 0.022; Northrup et al. 2010; Page et al. 2004; Harris et al. 2014; Mistassini, this study: 0.017). I suggest that this large lake specificity and consistently weak genetic differentiation, along with high morphological variation and a combination of factors influencing these attributes, place lake trout at the early stages of ecological speciation described by Hendry (2009), with specific factors including (i) the large effective sizes ( $N_e$ ) that a large lake size confers towards sustaining multiple evolving populations of a large-bodied fish; (ii) the preponderance for large postglacial lakes in North America to have been colonized by multiple, previously isolated lineages of lake trout from geographically disparate glacial margins, (iii) the variety of different habitat niches available in larger lakes that lake trout can exploit; and (iv) the high morphological plasticity of lake trout.

The carrying capacity, genetic diversity and  $N_e$  of lake trout populations appears proportional to the lake area (Shuter et al. 1998; McCracken et al. 2013; Valiquette et al. 2014). So in spanning 2,335 km<sup>2</sup> and in being pristine, I unsurprisingly detected high levels of genetic diversity (mean  $A_R = 29.51$ ) and  $N_e$  (range: 371-4199) among different Mistassini lake trout populations (Table S1.1A, Table S1.8), compared to forty populations inhabiting smaller, unstocked lakes throughout Québec (mean  $A_R = 6.160$ ) (Valiquette et al. 2014), and smaller

Mistassini brook trout populations (mean  $A_R = 4.03$ ,  $N_e = 89-224$ ; Fraser et al. 2013). Phylogeographically, Mistassini was also postglacially colonized by multiple (up to four) mitochondrial DNA lineages from wide-ranging regions (Wilson and Hebert 1998). Our study affirms this finding – population differentiation accounting for the mutational properties of microsatellites ( $R_{ST}$ ) exceeded global  $F_{ST}$  and at several individual loci; the age of the lake is too young (8,000 years) and the number of generations passed is too few (667, based on a 12 year generation time; Dubois and Lageaux 1968; Hansen et al. 2012) to have generated this mutationally-driven differentiation entirely within sympatry. Populations exhibited no evidence of bottlenecks and the pristine nature of the lake probably means that population sizes have not been significantly reduced since it was colonized. I did find, however, that an equilibrium between drift and gene flow has likely been reached among populations since lake colonization, through simulations based on observed  $F_{ST}$  and  $N_e$  values, due to relatively high contemporary gene flow compared to  $N_e$  (Fig. S1.4; Table S1.9).

Aspects of the ecology and behaviour of lake trout might also explain the weaker extent of population divergence relative to previously studied fishes in Mistassini Lake (e.g. brook trout,  $F_{ST} = 0.02 - 0.10$ ; walleye,  $F_{ST} = 0.017 - 0.079$ ; Fraser et al. 2004; Dupont et al. 2007). First, the tributary spawning nature of these other species generates considerable spatial isolation (10s to 100s of kilometres) and a more complex lifecycle, whereas lake trout spawn along lake shorelines, and local fishing experts have described the spawning sites of various morphs in close geographic proximity (see Chapter 2). Although natal fidelity is well documented among postglacial lake-dwelling salmonids (Stewart et al. 2003), there is weak and even contradictory evidence for this among lake trout populations (Scott and Crossman 1973; MacLean et al. 1981). The close proximity of these locations in Mistassini Lake could facilitate gene flow and reduce reproductive isolation in the long-term. Second, while Mistassini populations exhibited summer depth preferences, individuals from different populations were captured throughout the water column, and the striking morphological variation was more continuous within populations and less discrete among populations, suggesting a highly plastic propensity for occupying multiple habitat niches (see below). Habitat use among individual lake trout has indeed been found to be highly variable but consistent between years in previous research (Snucins and Gunn 1995; Sellers et al. 1998; Morbey et al. 2006). Third, different habitat niches associated with depth that promote population diversification might not be well-defined within Mistassini Lake, and are

probably influenced by lake basins. For example, the deepest areas of Mistassini Lake are comparatively closer to shallow habitat, and the western and eastern basins differ in deep water habitat area, documented spawning sites (see Chapter 2) and geomorphology, perhaps explaining why certain populations correspond to one or the other basin (with the exception of population 2 that was equally represented in both basins).

# Phenotypic differentiation, associations with genetic differentiation, and comparisons with lake trout morphs in other large, postglacial lakes

Mistassini Lake differs from other large postglacial lakes having lake trout morphs in being teacoloured and in having a relatively shallow secchi depth ( $\sim 9$  m) for such a deep lake (Legendre & Beauvais 1978; Muir et al. 2015). Correspondingly, populations (#2, 3, 5) living at shallower depths (median = 5-10 m) were predominately black and brown in colouration, the population (#1) inhabiting the deepest waters (median = 30 m) was more frequently silver or white, while the population (#4) occupying mid-depths (median = 27 m) was intermediate in colouration between these extremes. Furthermore, the population with the largest body size (#4) was most frequently captured at mid-depths associated with steep slopes (see also Chapter 2) that consistently harboured all prey. Conversely, the population with the smallest body size (#1), was consistently captured with less abundant prey species.

I also detected three body shape and five head shape clusters that appear broadly associated with distinct trophic niches at varying depths – from multiple deep (~ 600') benthic depressions to ample littoral waters with different geomorphologies and the steep cliffs in between. These morphs have general similarities and differences with those documented in other lakes (reviewed in Muir et al. 2015). For example, a shallow-water, streamlined, long and narrow caudal peduncled 'lean' morphotype in other lakes (Muir et al. 2015) is most similar to the black morphs (populations 2, 3 and 5) of Mistassini, and likely derived for pelagic swimming. Two deep-water morphotypes have also been identified in other lakes, including the 'humper', which is small-bodied with large dorsally positioned eyes and typically found on banks within Lake Superior and the 'siscowet', which is deeper-bodied with a sloping snout and thick and short caudal peduncles and most similar to population 4 (giants) (Muir et al. 2015). These morphological features are likely related to aspects of swimming performance needed in complex habitat such as manoeuvrability (Kristjánssan et al. 2002), burst swimming and

acceleration (Webb 1984). Although subtle, head shape differences in Mistassini also related most to eye position, head depth and bluntness of the snout that commonly distinguish benthic, piscivorous or a mix of feeding preferences (Jonsson and Jonsson 2001). However, Mistassini's genetically indistinguishable deepwater and silver lake trout (population 1) have characteristics most similar to the humper and smaller siscowet, whereas, Mistassini's giant morph (population 4) occupies humper-like habitat (steep drop-offs) but has morphological characteristics between siscowets and leans (Table 1.1).

Despite evidence for drift-migration equilibrium conditions and phenotypic-environmental associations described above, I found only weak support for a positive relationship between genetic and ecological or morphological differentiation and hence a putatively adaptive basis for occupying distinct habitat niches. For example, although some populations contained slightly higher or lower frequencies of individuals with one of the three or five distinct body/head shapes, all populations contained individuals exhibiting all three body or all five head shape types. Furthermore, despite evident colouration patterns and availability prey (fish community structure), all five populations contained individuals from each one of the colours previously identified and available prey. When compared with collated data from other large, postglacial lakes harbouring lake trout morphs, such relatively weak or little association between morphological and genetic differentiation appears common (Table 1.1).

Mistassini lake trout display a high amount of genetic diversity (mean  $A_R = 29.51$ ) when compared to other large, postglacial lakes (mean  $A_R = 3.01 - 11.80$ ) (Table 1.1). A previous, independent study on Mistassini lake trout, which used the same 19 loci, found similarly high genetic diversity (mean  $N_A = 17.26$ ) based on 46 samples from unknown localities (Valiquette et al. 2014). The reported genetic diversity in these other lakes were based on fewer (with the exception of Great Bear Lake) and different microsatellite loci. Furthermore, factors, such as incomplete spatial distribution of samples, different number of colonizing mtDNA lineages and potential bottlenecks from overfishing and invasive species help explain why the genetic diversity of Mistassini lake trout is much higher when compared to other lakes, despite their physical similarities.

# Population divergence and ecological speciation relative to other post-glacial fishes

Similar to other large, postglacial lakes, Mistassini Lake harbours a complex of weakly diversifying populations of lake trout with often striking phenotypic variation in body shape, size and colouration that can be associated with depth, spatial distribution and resource exploitation (Figure 1.4; Table 1.1). These lakes have many physical similarities including large surface area, shallow and deep water habitat, extensive shoreline distance, multiple basins and multiple fish species (Table 1.1). An allopatric phase does not appear to be a prerequisite for intra-lake population divergence in lake trout as has been observed in some cases of ecological speciation in north temperate freshwater fishes (e.g., Bernatchez and Dodson 1990; Taylor and McPhail 2000): at least one lake (Great Bear) was postglacially colonized by only a single mtDNA lineage (Wilson and Hebert 1998; Harris et al. 2014). Nonetheless, our study reinforces that different lake trout lineages have a propensity to occupy and exploit multiple habitat niches available to them within a lake. Each Mistassini population appears to harbour considerable phenotypic plasticity, implying that individuals within populations patchily occupy different habitat niches within the lake. Population habitat use distinctions were not clearly defined, reproductive habitats of different morphs are in close spatial proximity, and as previously discussed, any adaptive divergence generated from differential habitat use appears to only generate weak reproductive isolation.

Phenotypic plasticity is thought to act both as a facilitator and as a constraint to adaptive divergence and reproductive isolation during the process of ecological speciation (Hendry 2009). Our study suggests that sympatric population divergence in lake trout might be quite unique in commonly exemplifying how plasticity might constrain further steps towards ecological speciation. In Mistassini Lake, weak genetic differentiation was unrelated to a potential downward bias in  $F_{ST}$  and a lack of migration-drift equilibrium, but instead to high contemporary gene flow despite large  $N_e$ . And, in contrast to other cases in north temperate fishes, including co-generic Arctic charr (Gíslason et al. 1999; Taylor and Bentzen 1993; Hendry et al. 2009), remarkable phenotypic variation in Mistassini lake trout and in other lakes does not result in appreciable genetic segregation nor a clear correspondence between different phenotypes and different habitat niches, despite evidence for the availability of the latter. Such discontinuous adaptive variation with minor reproductive isolation implies that selection against migrants or

hybrids between diversifying lake trout populations is not very strong, that morphological plasticity is not very costly in this species, and/or that the extent of adaptive divergence might be constrained by adaptive plasticity (Hendry 2009).

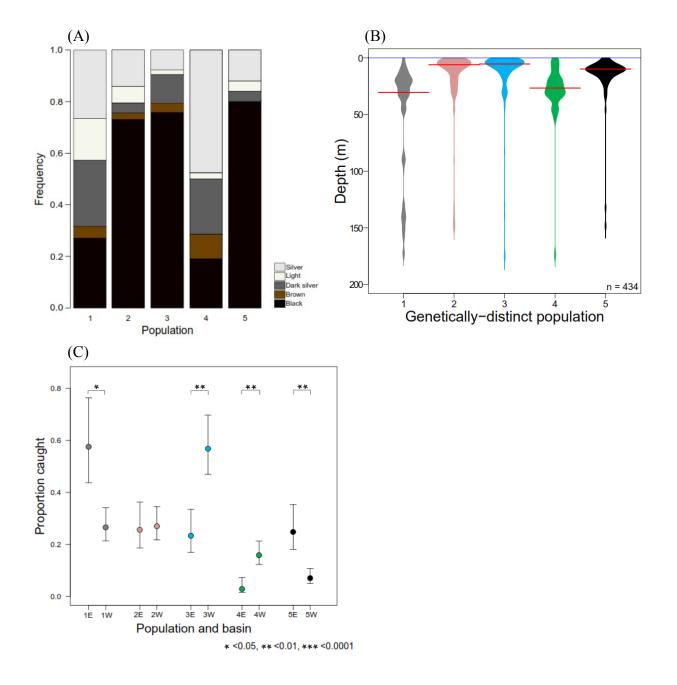
If this is true, then a key question is why plasticity might more readily constrain later steps of ecological speciation in lake trout relative to co-generic Arctic charr. One possibility might be that the evolution of lake trout was initially born out of specialization for terminal piscivory in coldwater lakes (Wilson and Mandrak 2003), whereas Arctic charr do not exhibit such near ubiquity in trophic specialization (Klemetsen 2010). Such specialization might act as a developmental limitation to further diversification through phylogenetic niche conservatism, and may in part explain the rarity of genetically-distinguishable morphotypes in lake trout. Another possibility might be due to life history differences that have evolved in response to previous glacial events. The evolution of lake trout, unlike Arctic charr, was purely in a freshwater environment, as they lack the ability to live in salt water (Wilson and Mandrak 2003). The evolution of the anadromous life history stage of Arctic charr may have therefore played a critical role in natal homing of the species, and hence adaptive plasticity and adaptive divergence might be more coupled to increase the likelihood of greater genetic segregation to occur where different habitat niches exist. Unlike lake trout, recent research has documented high precision of natal homing of sympatric populations of Arctic charr in Norway (Nordeng 2009). These two possibilities suggest that the unique evolutionary history of two co-generic species allow plasticity to act as a constraint for early stages of ecological speciation in one species (lake trout) and help facilitate it at later stages in another (Arctic charr).

## Conservation and management implications

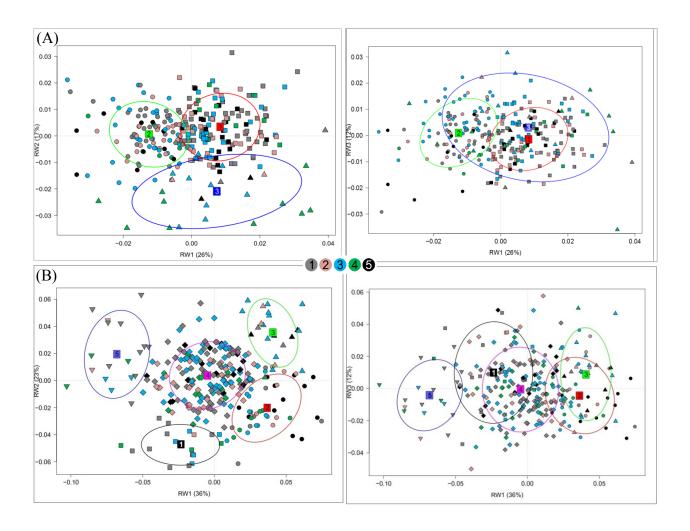
Whether diversifying lake trout populations have 'plateaued' in their steps towards ecological speciation, or whether further adaptive divergence and strengthening of reproductive isolation is still to come in a future context, the maintenance of such subpopulation genetic structure may be important for species persistence in the face of changing environments (Frankham et al. 2002). As a top predator in Mistassini Lake, this conservation should include a consideration of the role and survival of both prey and conspecifics (e.g., brook trout, walleye, pike, whitefish, etc.) that thrive across a diversity of habitats, so that the interactions and balance among these species is maintained.

Sympatrically-occurring populations of lake trout appear rare, and their occupancy of large, deep lakes such as Mistassini Lake means that they act as reservoirs of genetic diversity and refuge habitat for the species in the face of future climate change. Although our results suggest a great propensity for different lake trout lineages to occupy different habitat niches, I cannot exclude the possibility that phylogenetic constraints exist among lineages. Hence, because sympatrically-occurring populations of lake trout often originate from different ancestral lineages, it should not be assumed that if one population is removed or extirpated that another population will simply fill that niche. As different methods of capture (gillnetting vs. angling) also appear to target populations differently (Chapter 2), it is important to take into consideration unequal harvesting rates during different fishing seasons.

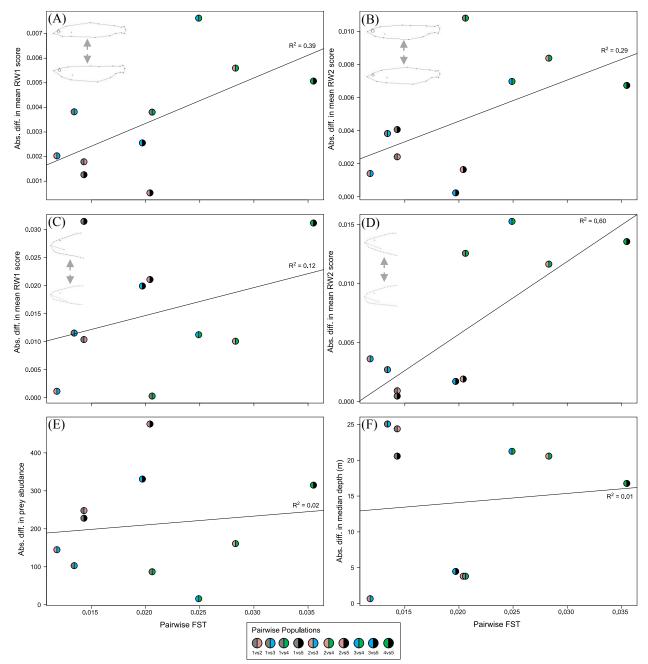
As a natural laboratory, Mistassini Lake provides an excellent example of the evolution and current state of lake trout populations in the wild. The information and results of this study could be useful for future rehabilitation, management and ultimately the conservation of the species where extirpated forms exist (e.g. Laurentian Great Lakes). For example, previous research has articulated that the classical lake trout morphotypes should be treated as distinct units for future management plans (Page et al. 2004); however, our study has shown that weakly distinguishable genetic populations, in part differentiated due to phylogeographic origins (similar to the Great Lakes), contain a high amount of morphological variation that do not necessarily fill the classical benthic-limnetic morphotypes found in other postglacial systems. This suggests that rehabilitation, management and conservation plans should focus on both historical and contemporary genetic diversity, the factors affecting this diversity (e.g. available habitat niches, prey community structure, migration, etc.), the inherently phenotypically plastic ability of lake trout and less so on discrete morphological differences.



**Figure 1.1**: **(A)** Frequency of colours observed in each genetically-distinct lake trout population in Mistassini Lake. **(B)** Beanplot, which shows accurate densities, illustrates the depth distribution of genetically identified populations. The red line indicates the medium. **(C)** Results of a generalized linear model (GLM) show populations 1 and 5 were statistically caught in higher numbers in the eastern basin after taking into account the fishing effort. Population 3 and 4 were statistically caught in higher numbers in the western basin after taking into account the fishing effort.



**Figure 1.2:** Association between morphological clusters and genetically-differentiated populations of lake trout present in Mistassini Lake. Morphological clusters are identified by symbol shape and ellipses which represent 67% of that cluster's variation and genetically-differentiated populations are identified by symbol colour. **(A)** RW1 vs. 2 and 1 vs. 3 (55%) of body shape variation. Morphological shifts for RW1 (26%) correspond to the slope of the snout, lower jaw and dorsal and belly curvature; RW2 (17%) correspond to slope of top of cranium and dorsal side, length and depth of caudal peduncle; RW3 (12%) correspond to body depth, eye position and size. **(B)** RW 1 vs. 2 and 1 vs. 3 (71%) of head shape variation. Morphological shifts for RW1 (36%) correspond to length of head and snout, eye position ad length of upper jaw; RW2 (23%) correspond to head depth and bluntness of snout; RW3 (12%) correspond to slope of lower and upper jaw. Visualizations of these morphological shifts can be seen in Fig. S1.5.



**Figure 1.3**: Visualization of Mantel tests, which shows comparisons of genetic distance (pairwise  $F_{ST}$ ) versus (i) the absolute difference in mean relative warp (RW) score for the first two RWs for body ( $\bf A$ ,  $\bf B$ ) and head morphology ( $\bf C$ ,  $\bf D$ ); (ii) absolute difference in prey abundance ( $\bf E$ ); and (iii) the absolute difference in median depth (in metres) ( $\bf F$ ). Inset for  $\bf A$ - $\bf D$  are visualizations of the extreme shape differences corresponding to that relative warp. Body RW1 and 2 represent 26% and 17% of the total variation; whereas head RW1 and 2 represent 36% and 23% of the total variation. The remaining visualizations of Mantel tests can be seen in Fig. S1.11.



**Figure 1.4:** Morphological variation among individual lake trout and across all genetically-distinct populations (coloured circles and numbers) within Mistassini Lake, Québec, Canada.

**Table 1.1:** A comparison of lake physical attributes and sympatric population differentiation of lake trout as currently described in the literature: Mistassini Lake (ML), Great Bear Lake (GBL), Great Slave Lake (GSL), Lake Superior (LS) and Atlin Lake (AL).

	ML (this study)	GBL	GSL	LS	$\mathbf{AL}$	
Surface area (km <sup>2</sup> )	2,335 <sup>a</sup>	31,328 <sup>e</sup>	28,568 <sup>k</sup>	82,100 <sup>l</sup>	792 <sup>p</sup>	
Depth (mean, max m)	75, 183 <sup>b</sup>	90, 450 <sup>e</sup>	73, 614 <sup>g</sup>	147, 406 <sup>1</sup>	86, 283 <sup>q</sup>	
Secchi depth (m)	9°	$20 - 30^{\mathrm{f,g}}$	$\sim 9^{\rm g}$	15-20 <sup>m</sup>	10 <sup>r</sup>	
Number of basins	2	5 <sup>e</sup>	$2^k$	2	4 <sup>p</sup>	
# Fish species	12	15 <sup>e</sup>	211	87 <sup>1</sup>	10 <sup>r</sup>	
Shoreline distance (km)	1,509 (+ 967 islands)	2,719 (+ 824 islands) <sup>f,h</sup>	3,057 <sup>1</sup>	2,938 <sup>1</sup>	391 (+ 214 islands)	
# of mtDNA lineages	4 <sup>d</sup>	1 <sup>i</sup>	3 <sup>d</sup>	4 <sup>d</sup>	2 <sup>p</sup>	
# genetically diff. pops	5	$2^{j}$	Not tested to date	3 <sup>n</sup>	3 <sup># p</sup>	
# of morph clusters	3 body, 5 head	$3 - 4^{e,i}$	31	4 <sup>1</sup>	2 <sup>p</sup>	
Ass. btw morph and genetic?	Weak	None <sup>e</sup> – some <sup>j</sup>	Not tested to date	Some <sup>n</sup>	None <sup>p</sup>	
Genetic diff. (global F <sub>ST</sub> )	0.017 - 0.028	0.008 <sup>j</sup>	Not tested to date	$0.024 - 0.033^{\rm n}$	0.022 <sup>p</sup>	
AR (# loci)	29.51 (19)	8.30 (22) <sup>j</sup>	Not tested to date	3.01 (9) <sup>l</sup>	11.8 (8) <sup>p</sup>	
'Shallow' body morphology (0-30m)	1.Lean, streamlined, dark (black, brown)	1.Stream-lined, small, dark/silvery 2.'Lean-like', large, silvery 3.Stream-lined, dark, red fins 4.'Redfin-like', darker, red fins	1. 'Lean-like', streamlined, large, light*,k	1. 'Lean': large-bodied, silvery or light <sup>l,o</sup>	1. 'lean-like' morphs (streamlined, silvery)*,p	
'Mid-depth' body morphology (30-100m)	Large, deep-bodied, various colouration	No data to date	1. 'Siscowet-like', deep-body, large, dark^ 2. Deep body ^,k,l	1. 'Humper': small, narrow- bodied, silvery or light colour 2. 'Redfin': robust, large/deep- bodied, dark, red/yellow fins <sup>l,o</sup>	1. 'Siscowet-like', deeper body <sup>% p</sup>	
'Deepwater' body morphology (>100m)	1.Small, deep-bodied, light or silvery	No data to date	No LT captured	1. 'Siscowet': large, deep-bodied, dark colour <sup>l,o</sup>		

<sup>a</sup>Statistics Canada 2005; <sup>b</sup>ILEC 1999; <sup>c</sup>Legendre and Beauvais 1978; <sup>d</sup>Wilson and Hebert 1998; <sup>e</sup>Chavarie et al. 2014; <sup>f</sup>Johnson 1975; <sup>g</sup>Evans 2000; <sup>h</sup>Alfonso 2004; <sup>i</sup>Chavarie et al. 2013; <sup>j</sup>Harris et al. 2014; <sup>k</sup>Zimmerman et al. 2006; <sup>h</sup>Muir et al. 2015; <sup>m</sup>Axler 2004; <sup>n</sup>Page et al. 2004; <sup>o</sup>Muir et al. 2014; <sup>p</sup>Northrup et al. 2010; <sup>q</sup>Downie 2005; <sup>r</sup>Lindsey et al. 1981; \*Captured between 0-50 m; <sup>c</sup>Captured between > 50-100m.; <sup>o</sup>Captured between 70-150 m; <sup>#</sup>Three genetically-differentiated populations and their descriptive statistics were described in Northrup et al. 2010 for the Atlin-Tagish Lake system (two lakes interconnected by river in which lake trout are also found).

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# Chapter 2: Lake trout diversity and ecological preferences as revealed by Cree Traditional Ecological Knowledge

Kia Marin, Andrew Coon, and Dylan J. Fraser

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#### Abstract

Multidisciplinary approaches to conservation have become increasingly successful in recent years, especially within fisheries management. Many First Nations communities have relied upon a variety of north temperate fish populations as an essential food source and economic resource for thousands of years. As such, members of these communities often possess traditional ecological knowledge (TEK). I consulted fishing experts from the Cree Nation of Mistissini via collaborative fieldwork and semi-directive interviews to expand upon lake trout knowledge in Québec's largest natural lake (2,335km<sup>2</sup>). Specifically, I compiled and integrated TEK with what is known scientifically in order to expand upon the knowledge of lake trout, document potential changes, and to identify any conservation and management concerns to ensure the long-term sustainability of lake trout for the local fisheries. Informants with an average of 31 years fishing experience on the lake described diverse lake trout forms, with colour and body size differences, that exhibit both depth and spatial preferences. Overall, the high morphological variation and habitat preferences were congruent with the quantitative findings of Chapter 1. Fishing experts also provided descriptions of seasonal movements and spawning locations and timing. TEK highlighted a number of management and conservation concerns, such as potential temporal changes to lake trout populations, harvesting practices, and environmental changes over the last four decades. With this insight and Chapter 1 findings, I recommend that collaborative long-term population monitoring of Mistassini lake trout be initiated to ensure the sustainability of the species. I hope that this research shows that human and ecological interactions are inevitably linked and that the use of multidisciplinary approaches offer a greater depth of knowledge for both research and conservation initiatives.

#### Introduction

Under a changing globe, conservation has become a primary focus of many biologists. In an attempt to understand, manage and conserve complex patterns of ecological interactions, multidisciplinary approaches have become necessary. Such approaches often require a diverse group of people working collectively together towards achieving a common goal. Increasingly, this approach to conservation and/or management of ecological resources has seen much success (Drew and Henne 2006). For example, successful multiparty management has led to sustainable mussel beds in South Africa's Maplane Nature Reserve (Harris 2003) and to twenty years of sustainable land-use planning and resource management of Clayoquot Sound forest stands in British Columbia, Canada (Braun 2002). By using multidisciplinary approaches, researchers can gain and represent a greater depth of knowledge, especially when attempting to understand, manage and conserve entangled ecological resources.

People who live or work closely with the natural environment (e.g. traditional hunters and trappers, fishers, farmers, etc.) often develop extensive knowledge (Berkes et al. 2000). It has been increasingly popular to consult people with this kind of knowledge when wanting to expand upon existing information, to explore complex interactions or to implement management strategies about a resource. For example, many First Nations people of Canada have vast knowledge regarding their local natural environment given thousands of years of subsistence living. This detailed, cumulative, and often dynamic knowledge of both past and present ecological systems has been termed 'traditional ecological knowledge' (TEK; Menzies and Butler 2006). It is defined as the "cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment." (Berkes et al. 2000: 1287). There are now examples from around the world and in a variety of biodiversity facets which have integrated TEK with traditional 'western' science. For instance, since the 1970s, the integration of local fisher knowledge into fisheries management has become increasingly favoured (McGoodwin 2006). TEK provided key information regarding historical trends and habitat knowledge for bonefish (Albula glossodonta) populations of Kiribati, which ultimately lead to protection of the species (Johannes and Yeeting 2001). In the Western Solomon Islands, the protection of critical bumphead parrotfish (*Bolbometopon muricatum*)

habitat was a result of fundamental TEK regarding life history characteristics (Aswani and Hamilton 2004). TEK can therefore often supplement, complement and help guide biological science and structure the management and conservation of natural resources (Menzies and Butler 2006).

The James Bay Cree are a group of approximately 18,000 Cree (*Eeyouch*) people located along eastern James Bay and southern Hudson's Bay in Northern Québec, Canada (Grand Council of the Crees 2015). There are a total of nine communities situated on 450,000 km<sup>2</sup> of traditional Cree territory (*Eeyou Istchee*, 'The People's Land'; Grand Council of the Crees 2011). Respect and gratitude are two fundamental aspects that shape the Cree's relationship with their natural environment (Cree Culture Institute 2015). Water (neebee), imperative for the health, productivity and integrity of the sub-Arctic environment as a whole, and fish (namesh) are part of daily lives of the Cree (Grand Council of the Crees 1999). During times of starvation or when large game was scarce, fish were the only natural resource the Cree could rely on (Grand Council of the Crees 1994; Berkes 1999). For thousands of years, and continuing on today, the Cree have lived off the land by hunting, trapping and fishing for subsistence, economic and cultural reasons. As such, they possess a vast amount of knowledge that has been passed down from one generation to the next about their traditional territory, and specifically with regards to fish. As Berkes (1999) observed while starting his career in fisheries research and human ecology in the 1970s, the James Bay Cree fishers possess a great wealth of knowledge regarding fish movement, distribution and seasonal cycles.

Mistissini (Cree for 'big rock') is one of the nine James Bay Cree communities, which is situated on the southeastern tip of Mistassini Lake, Québec's largest natural lake (2,335km²) and one of its deepest (180 m; Statistics Canada 2005; Figure 2.1). The lake and its tributaries have been a fundamental aspect of Mistissini and its people's history. Mistassini Lake has been largely un-impacted by human activity and is home to diverse populations of brook trout (*Salvelinus fontinalis*), walleye (*Sander vitreus*) and lake trout (*Salvelinus namaycush*). These species hold both historical and contemporary socio-economic and cultural importance as they are targeted by Cree subsistence fishers and by sport fishers that fish from local Cree operated outfitting camps, the community of Mistissini, and the Réserve Faunique des Lacs Albanel Mistassini-et-Waconichi. Previous brook trout (*maasimekw*) studies successfully integrated TEK

from local fishing experts to provide additional information regarding the persistence of populations, breeding areas, behavioural ecology and critical temporal knowledge of fishing efficacy and population and life history trends over the last four decades (Fraser et al. 2006). This lead to the identification of conservation and management concerns while developing a collaborative relationship necessary for long term population monitoring (Fraser et al. 2006).

Lake trout (namekush) is another species that is targeted by both local subsistence and sport fishers who utilize Mistassini Lake. To date, however, there has been no attempt to document what is known by the local Cree community about lake trout in Mistassini Lake. As the Mistassini Lake region has seen an expanding human population, economic development and increasing fishing pressures over the last 10 years (Fraser et al. 2006), there is a growing need to expand upon the limited and preliminary scientific knowledge and to compile TEK of the Mistassini lake trout towards ensuring its persistence and sustainability. Indeed, until recently, little was known scientifically about lake trout in Mistassini Lake. Dubois and Lageaux (1968) documented the age and size of lake trout from unknown localities. Zimmerman et al. (2007) identified two morphotypes, which differed in age, growth and maturity (Hansen et al. 2012). This initial research offered a glimpse into what such a large and pristine lake might harbour; however, with small samples size, lack of examination of population genetic divergence and complete spatial distribution, we are left an incomplete picture regarding lake trout diversity in Mistassini Lake. The research objectives of Chapter 1 filled this gap and provided evidence for five weakly genetically-distinct populations with striking phenotypic variation, including differences in body size, colouration and overlapping morphological features, including body depth, caudal peduncle size, eye position, and head shape. These populations were situated at different localities, and exhibited depth, spatial (basin) and prey preferences, and were noted to travel a great distance (i.e., populations with a western basin preference and a median depth of 5-10m were also found in the eastern basin at depths of 140m). However, as samples for this research were collected over a 2 month period in 2013, this study was merely a snapshot of time. I did not know whether these genetically-distinct populations/forms were recognized similarly by the Cree, how they were harvested, if the spatial distribution of these forms were recognized and if there were any potential temporal trends concerns regarding lake trout population trends in Mistassini Lake.

The objectives of this chapter were to compile and integrate TEK of Mistassini lake trout over the last four decades with what is known scientifically (Chapter 1; Dubois and Lageaux 1968; Zimmerman et al. 2007; Hansen et al. 2012). Specifically, I intended to expand upon the knowledge of Mistassini lake trout, document potential changes to overall lake trout population abundance and potential ecological changes and to identify any conservation and management concerns to ensure the long-term sustainability of lake trout for the local fisheries. I participated in collaborative fieldwork and conducted semi-directive interviews from a number of local fishing experts over a two month period in 2013. Based on previous literature and studies (e.g., Fraser et al. 2006), I predicted that local fishing experts would be able to provide details regarding lake trout variation, habitat use/seasonal movements, temporal trends and identify any potential concerns.

#### **Materials and Methods**

## Collaborative fieldwork

Collaborative fieldwork allows TEK to be gathered over extended period of time (Huntington 2000). TEK of Mistassini lake trout was collected through continued frequent interaction with local fishing guides and community members throughout duration of two month fieldwork in 2013. As our quantitative data for Chapter 1 included collecting tissue samples from local fishing guides, clients and community members at the local outfitting camp, I was able to interact with such people on a regular basis – approximately once every two days over two months. These interactions lasted anywhere from 5 (e.g. collection of a sample) to 60 minutes (e.g., discussion over a meal) and recorded by hand in a notebook. Knowledge compiled during this time was not gathered from structured questions, however, from observations and knowledge possessed by individuals.

#### Semi-directive interviews

I also collected TEK on lake trout from 15 local fishing experts through semi-directive interviews. I considered experts as individuals from the local community of Mistissini with greater than 20 years fishing experience on Mistassini Lake. To help identify these experts and to ensure that they represented those with the most knowledge regarding this species in the community, I asked the Cree Trapper's Association, fishers and community members to identify who they believed to be experts – a process known as peer-referencing (Davis and Wagner 2003). A total of 18 lake trout experts were identified from the community of Mistissini via peer-referencing methods. I recorded information, both through collaborative fieldwork and/or semi-directive interviews, from 15 of those identified. Great efforts (e.g., multiple attempts during the 2013 sampling period and again in the summer of 2014) were made to screen all 18; however, due to logistical or seasonal reasons and in one instance resistance, I was still able to compile knowledge from over 80% of all identified experts.

Typically, these individuals were Cree elders, fishermen and/or tallymen that possessed a wealth of knowledge about lake trout in Mistassini Lake. The interviews took place at the local outfitting camp, the informant's home or in the Tourism Office in Mistissini. Interviews, which lasted between 30 and 90 minutes, were guided by the interviewer with a series of questions

(Table 2.1); however, the interview was free to flow with the informant's observations and stream of consciousness (Huntington 2000). Semi-directive interviews guide the informant through a semi-constrained discussion. Major advantages of this method include flexibility based on each informant's observations, supplementary information not expected by the interviewer and the freedom of influence of other individuals (Ferguson and Messier 1997; Huntington 2000).

Each interview began with outlining the objectives and procedures of the interview. Each informant was told that the information they provided would be compiled into a report for future management and conservation of the species. Informants were also informed that the information provided during the interview process was confidential and that their names would not be included in the report or potential publications. Informants were assigned a random number (1-15). Oral consent was obtained from the informants. This method is appropriate for our research as some of the participants may not be able to read or write in English, French or Cree. Visual aids, such as maps of Mistassini Lake and photos of lake trout taken throughout the fieldwork, were used in conjunction with specific questions. The information provided by the informant was recorded by hand, in a notebook by the interviewer and not audio-recorded. Finally, the participant was free to any the questions in Cree, English or French and local expressions were clarified with a third-party translator. Collection of TEK from 15 experts, both via collaborative fieldwork and semi-directive interviews, was approved Concordia University's Human Research Ethics Committee (protocol # 30003281).

### Results

## Summary of traditional ecological knowledge (TEK)

The 15 informants offered lake trout knowledge based on an average of 31 years fishing experience (range 20 – 49 years) in Mistassini Lake. All informants described a number of locations, depths and methods for capturing lake trout during specific times of the year and provided considerable details regarding the species' morphological diversity. Additionally, most informants provided descriptions of both the locations and timing of lake trout reproduction. Finally, all informants supplied details regarding potential temporal changes and articulated a number of concerns regarding lake trout management and conservation for the future.

Lake trout can be captured throughout Mistassini Lake in a number of known locations based on seasonal changes (Table 2.2). During the winter, a few informants typically use gillnets to capture lake trout in the shallow waters in the southern end of the lake. As the water warms and the ice melts, lake trout can be found throughout the lake, again in shallow waters. The most common time of year to capture lake trout described by informants was from mid-June and throughout July in deeper water. Most informants (14 of 15) described various locations in the western basin in which lake trout are abundant and easy to capture via gillnet, nightlines or angling methods (Figure 2.2). Commonly, the western basin was regarded by multiple informants as harbouring more productive lake trout fishing in terms of numbers and size, perhaps due to prey abundance, water temperature, and/or available habitat. Concurrent with our findings in Chapter 1, populations 3 and 4, which are incidentally bigger in body size and average mass (Fig. S1.7A, B), were captured predominately in the western basin (Figure 1.1C). Lake trout are also found throughout the eastern basin; however, fewer informants reported fishing there for this species (6 of 15), and of those, 3 of 6 informants found lake trout harder to catch in the eastern than western basin.

All informants described a number of different lake trout phenotypic variations (Table 2.2). Almost all informants (14 of 15) were familiar with small (3 - 5 lbs), black forms, and giant (> 8 lbs) forms with various colours, and fewer informants described lake trout that were silver or grey in colour. Additionally, informants described other forms, such as, lake trout with pointed snouts (that eat other fish), "with big spots - they are the ones that get big" (informant 2).

Even descriptions of the black forms varied (e.g., very black with spots hard to see, black with identifiable spots and yellow-tipped fins, and *maasimekw-namekush* (brook trout-like) – caudal fin not as deeply forked, texture of the scales different from typical lake trout and pink meat). In addition to specific morphological differences, colour was also described as a major source of variation. Informants used colours such as black, black-black, green, brown, light, pale, silver and greyish to describe lake trout in Mistassini Lake. Overall, there were roughly 11 different lake trout variations described by the informants, some of which were consistently described and others just mentioned by one informant. In contrast, previous scientific research based on geometric morphometric analyses, detailed a minimum of 3 distinct clusters based on body and 5 clusters based on head shape alone (Chapter 1).

When informants were shown a collage of various lake trout caught throughout Mistassini, only 3 (of 15) were recognized lake trout caught most closely related to population 1 (deepwater; Figure 1.4). While this population of lake trout is found throughout the water column, its individuals are typically associated with deeper water (Figure 1.1B) and informants only set gillnets to a maximum of 200 feet. Moreover, these informants expressed that these lake trout are rarely captured using gillnet methods and not targeted as they are small in body size and extremely lean. Based on the descriptions provided through TEK and geometric morphometric analysis in Chapter 1, it is highly likely that there is even more morphological variation among lake trout populations than described and documented within this thesis.

Informants also described various summer habitats and depths at which they typically captured the lake trout forms described above (Figure 2.1). Specifically, lake trout black in colour (with various spot patterns) are typically captured in open water between 0 and 20 feet within the western basin. Some informants described capturing giants at greater depths (between 40 and 100 feet) and commonly on steep drop-offs in specific areas within the western basin. The Rupert River, Mistassini Lake's outflow, is located just above the 51<sup>st</sup> parallel on the western shoreline of the lake. Lake trout captured at the mouth of this river and within the river itself were described as bigger/fatter (6-8 lbs) with a different appearance (e.g. grey in colour, with big white spots, scratch marks from bumping into rocks) by some informants (4 of 15). Finally, lake trout that were grey/silver in colour (with varying head shape/size, spot pattern and fin accent colours) were associated with medium depths (20-50 feet) and the centre chain of

islands that runs down the length of the lake (Figure 2.1) by just over half of the informants (8 of 15). Additionally, small-medium sized brown lake trout were most closely associated with the northern end of the lake, while medium-sized paler individuals were associated with the southern end (closer to Mistissini).

For the most part, these descriptions of habitat and depth preferences gathered through TEK were congruent with our findings in Chapter 1. Specifically, I typically found lake trout that were dark in colour (populations 2, 3 and 5) in shallow water, giants on steep drop-offs typically in the western basin. However, I did not capture many individuals in the northern in the end of the lake that were greater than 3 lbs and brown in colour and even fewer individuals in the southern end that were pale. In addition to these descriptions, informants also depicted the seasonal changes and movements of these lake trout variations. In the winter, multiple informants (6 of 15) described capturing black, brown, silver and even giants in areas closer to Mistissini and the southern ends of the lake. As the ice melts, lake trout (usually silver or black forms) are typically found in the shallow water, specifically shorelines in the north, centre chain of islands and western side of the lake (8 of 15 informants). In the summer months, and as the water warms, multiple lake trout forms were are depicted as being located in the deeper water, specifically in the centre of the basins by the majority of informants (10 of 15).

Lake trout spawning locations and timing appeared to be fairly consistently detailed by the informants; however, specific details were kept to a minimum. These locations may be well known among local fishing experts, but most informants were keen to keep the specific locations to themselves. All of the informants (13 of 13) willing to share this information depicted lake trout spawning in shallow water (0-20 feet) any time between late August and the 3<sup>rd</sup> week of September (Table 2.2); however, 8 out of 13 informants only described locations on the western shoreline of the lake and fewer informants (5 out of 13) described areas in addition to these (e.g. both west and east shorelines of the chain of islands, eastern shoreline of the lake, etc.).

## Cree concerns regarding the status of lake trout populations in Mistassini Lake

Over the course of two months of collaborative fieldwork and through semi-directive interviews, informants revealed a number of concerns regarding lake trout population conservation and management in Mistassini Lake (Table 2.3). Just over half of the informants (8 of 15) felt that

Mistassini's lake trout population has been stable over the last 30 years. However, just under half (7 of 15) informants also showed concern regarding a decrease in overall abundance over the last 40 years. In addition, other concerns included changes to spawning timing and location, morphological and size changes, as well as behavioural changes. While there were mixed concerns regarding temporal population trends, the majority of informants articulated trepidation regarding the decrease in fishing efficiency, increase in overfishing, increase in the number and size of boats, and people on the lake over the past 10 to 40 years.

Additionally, multiple informants described how different fishing methods have changed over the past 40 years. For example, every generation of Cree fishermen have used gillnets. In the past fishermen would remove a gillnet, consume the fish and then reset the net once they required more fish for subsistence. Today, as one informant expressed, the mentality has changed - a gillnet is hauled, fish are removed and the net is set back immediately. This results in overfishing, especially in one location or habitat. Over the last 10 years, Mistassini Lake region has seen expanding human population which has brought with it economic development. As such, mining exploration and exploitation, logging, and hydro projects have been present within Mistissini's traditional Cree territory, as well as, increased tourism and sport fishers on the lake itself. As such, many informants (7 of 15) conveyed concerns regarding the potential changes to Mistassini Lake, including potential pollution or contamination from human activities and the threat of invasive species. Multiple seasonal changes have been observed over the last 40 years, including fluctuations in Mistassini's water level due to varying amounts of winter precipitation, movement of lake trout, and prey abundance. While descriptions of seasonal lake trout movements described above were typical, it should be noted that multiple (3 of 15) informants commented that some years lake trout (and even their conspecifics and/or prey) are not easily captured in places previously known to have been plentiful. And these changes, as described by one informant, are not due to changes in overall lake trout abundance, but merely because "sometimes you catch a lot and sometimes not as much – it changes year to year" (informant 9). Finally, a temporal change that was of concern to some (4 of 14) informants, was an increase in water temperature over the last 15 years.

With a variety of concerns expressed, some informants articulated the need for increased protection or changes to current fishing practices. In response to the idea that overfishing and the

number of people fishing on the lake has increased over the last four decades, multiple informants expressed their desire to have this controlled, specifically among local fishers. Specific examples included limiting the number of lake trout harvested and gillnets used during spawning season and quotas/limits to the number harvested per fisher per season. With respect to sport fishers (non-Cree fishers), few informants expressed the need to limit the number of permits issued through the provincial government. Finally, with respect to the health of the lake, the majority of informants expressed the need to limit human activity within the Mistassini Lake watershed that could cause contamination or pollution, to safeguard Mistassini's tributaries and to reduce pollution from boats and increase the number of clean boats.

#### **Discussion**

The main objectives of this chapter were to integrate TEK to expand upon the existing knowledge of lake trout population diversity, document existing temporal changes and to assist in identifying any potential concerns that will aid in the management or conservation of lake trout in Mistassini Lake. With increasing recognition and success of the integration of TEK and fisheries research and management (reviewed in McGoodwin 2006), I hope that this study will shed light on the importance and benefit of such integration.

First and foremost, the information gained through TEK allowed for successful collection of quantitative data utilized in Chapter 1. Expert's knowledge of seasonal lake trout distribution and morphotypes in Mistassini Lake allowed us to capture lake trout throughout the lake in a timely fashion. I targeted all areas of the lake in which lake trout were known to utilize. As such, gillnets were set in particular locations based on the knowledge provided by local fishing guides and all 29 24-hour gillnet sets contained lake trout. To target specific morphological forms described by the local experts, (detailed in Table 2.2), informants were able to detail exact locations, depths and the type fishing equipment required. Such details and the large amount of knowledge regarding lake trout in Mistassini Lake were similar to that described in earlier research with the James Bay Cree (Berkes 1999). Based on the success of our collaborative fieldwork, it is highly likely the subsequent information gathered in semi-directive interviews was deemed reliable.

## Similarities and differences between TEK and Chapter 1 findings

Broadly speaking, there was a congruence of TEK observations and quantitative findings of Chapter 1, with respect to the high amount of morphological variation, habitat use and depth preferences of different lake trout forms within Mistassini Lake. While multiple forms were described, informants revealed that despite clear differences in colour and body size for example, there are no specific Cree words to describe these forms. Lake trout were always described as *namekush* with the exception of a few lake trout captured over the course of field season which one informant called *maasimekw-namekush* (brook trout-like lake trout). This finding is similar to Fraser et al. (2006), who documented that Mistassini experts described differences in brook trout appearance, movements and spawning locations but only used the word *massimekw* and not

multiple variants to describe these forms. Often, if forms are clearly visible, the same taxonomic species can be named in multiple ways (e.g., Lobel 1978). Intriguingly, informants described capturing black forms in open water in at depths of 0-20 feet; however, Chapter 1 findings revealed that population that were predominately black (#2, 3, and 5) could be captured by angling in similar depths but also at even greater depths by gillnetting (Figure 2.2). With some black populations more susceptible to different kinds of fishing, this suggests that there is cryptic diversity (e.g., biomechanical or physiological), not detected by colouration alone. Despite these striking phenotypic differences, as described through TEK and our findings in Chapter 1, perhaps because of weak genetic population structure (i.e., contemporary gene flow), lake trout in one population can adapt to take on phenotypic characteristics of lake trout in another population and any form or combination of forms in between. It is possible that the differences between such forms are not clear enough, and the vast amount of variation even within one location or genetic population is so great, that over generations, the lake trout have not been identified as multiple variants corresponding to each form. Finally, it should be noted that multiple phenotypic traits (i.e., dorsal and lateral vermiculation patterns, spot pattern or intensity, and fin accent colouration) were detailed by local fishing experts but were not quantified in Chapter 1. Despite an overall congruence of TEK and Chapter 1, these subtle phenotypic characteristics not quantified likely provide an underestimate the array of Mistassini lake trout morphological variation and should therefore should be regarded together (TEK descriptions and quantitative findings of Chapter 1 morphological variation).

At finer geographic scales, previous research has noted that TEK can provide additional and sometimes more detailed information (Huntington 1998; Neis et al. 1999; Moller et al. 2004). Similarly, Fraser et al. (2006) also documented that Mistissini Cree experts provided precise details at a finer geographic scale because brook trout spawn in tributaries that lie within traditional family traplines. Unlike brook trout, lake trout spawn within the lake, which spans just over 2,335km² in surface area and can be accessed by any local Cree fisher with access to a boat. While lake trout have been known to enter these tributaries for periods of time, they are typically found at a much larger geographic scale, when compared to their conspecifics (i.e., brook trout and walleye). Frequently, lake trout informants described capturing lake trout in many of the same general locations; however, in a few circumstances informants provided detailed information regarding specific locations, fishing methods, gear and timing based on a

knowledge passed down from one generation to the next within a family. Given that the Cree are gregarious people, knowledge sharing is common (Berkes 1999; Fraser et al. 2006) and Mistassini Lake is immense, it is likely that lake trout knowledge, specifically where and when to capture numerous forms, is shared among fishers.

# Factors affecting the acquisition of TEK

Previous research has highlighted that acquiring available TEK may be difficult for a number of reasons, including communication, language, or cultural issues (Huntington 2000; Usher 2000; Drew and Henne 2006). First and foremost, I continually consulted a variety of community members from Mistissini to help identify potential fishing experts and key informants for the acquisition of knowledge, a process known as peer-reference (Davis and Wagner 2003). Furthermore, Ferguson and Messier (1997) demonstrated that different types of local experts differ in the extent and type of the knowledge they possess. Therefore, I also ensured that our informants represented not just one type of fisher (e.g. current/former fishing guide at the local outfitting camp and a fisher who fishes for subsistence or economic reasons). I found that most individuals were willing to share their knowledge once trust had been established, their confidentiality was ensured and when they understood the goals of the project (Ferguson and Messier 1997; Fraser et al. 2006). This allowed informants to understand why this project would be beneficial to the all members of the Mistissini community, which resulted in informants more likely to share their knowledge.

Within the local community, TEK was scattered amongst many individuals and the extent of lake trout knowledge varied. In accordance with the working definition of TEK (Berkes et al. 2000), fishing knowledge within the local community is passed down from one generation to the next through cultural transmission, such as through stories or actively fishing with elders. Certain fishing experts therefore possessed more knowledge about lake trout habitat and use of the lake in one particular area or season, for example. Fish are an important food source for Cree of Mistissini (Fraser et al. 2006); however, individuals did express interest in some species over others. For instance, brook trout and walleye are sometimes more popular to eat among certain fishers and their families, thus the extent of TEK for lake trout may be more restricted. Considering these factors, our study demonstrates that the incorporation of TEK from the

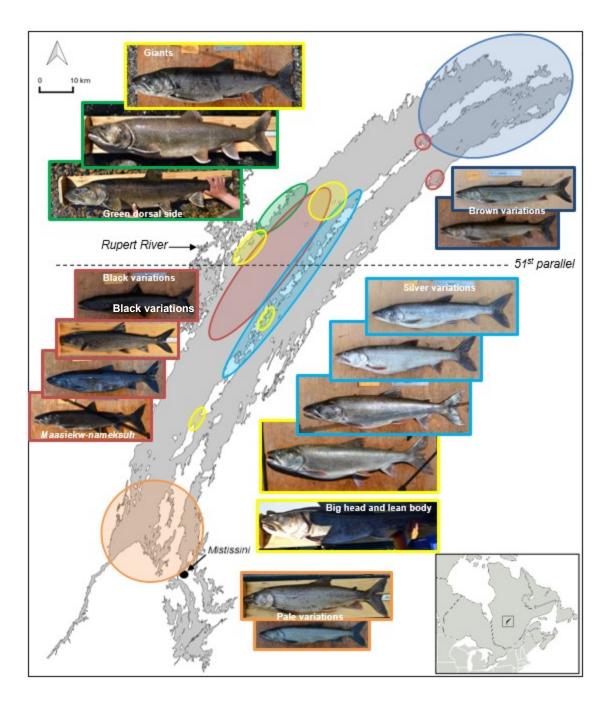
commencement of such a project requires both time and careful planning and consideration to be integrated successfully (similarly to Fraser et al. 2006).

## Access to temporal trends of lake trout through TEK

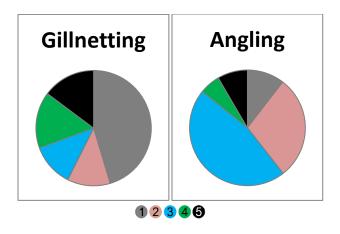
Because of hundreds of generations of subsistence living, which is still prevalent to a lesser extent today, the Cree fishing experts of Mistissini provided a wealth of lake trout knowledge. Specifically, observations over the last four decades offered this research a sense of existing temporal changes that lake trout populations may have undergone. While the majority (9 of 15) of experts felt that lake trout populations in Mistassini Lake have been stable over the last thirty years, fewer (6 of 15) believed that over the past forty years populations have been declining. Furthermore, other temporal changes, such as an increase in overfishing, number and size of boats on Mistassini Lake, different capturing techniques, etc., over the last fifteen to forty years were also noted, which may negatively affect lake trout populations in the future. Based on these observations and the expanding human population in the Mistassini Lake region, I recommend that the information collected and compiled above and in Chapter 1 be used as baseline information regarding lake trout population diversity and that long-term, collaborative monitoring of the species is undertaken every lake trout generation (a decade or so). Previously, TEK has made an undeniable difference in various research studies and management plans across various ecological scales (Huntington 2000). Similarly, this research has successfully complemented TEK and scientific findings together and as such, it is recommended that additional monitoring and/or any changes to management of the species include consultation with peer-referenced fishing experts.

In conclusion, this chapter documented and integrated TEK of Mistassini lake trout over the last four decades with what is known scientifically. Specifically, Mistassini Lake is home to diverse lake trout forms, with colour and body size differences, that exhibit both depth and spatial preferences. As such, these preferences have direct implications for both local and sport fishers that utilize the lake. In particular, future lake trout management strategies should take into consideration that different fishing techniques target different genetically-distinct populations. More broadly, conservation and management strategies within the watershed should consider lake trout spatial preferences (i.e., basin), which have also been highlighted in recent Mistassini brook trout population monitoring. This research provides insight into the importance of

collaboration and integration of TEK for fisheries research and benefits for management and conservation of species at large geographic scales. More broadly speaking, I hope that this research shows that human and ecological interactions are inevitably linked and that the use of multidisciplinary approaches to research and conservation offer a greater depth of knowledge.



**Figure 2.1:** Geographic location of Mistassini Lake, Québec showing examples (inset photos) of the lake trout variations and their geographical summer distribution (coloured ellipses) as described by multiple informants.



**Figure 2.2**: Different methods of capture target different genetically-differentiated populations (1 -5; coloured circles) of lake trout in Mistassini Lake.

 Table 2.1: Series of questions used for semi-directive interviews with peer-reference experts.

Subject	General Questions
General informant information	How many years have you been fishing on Mistassini Lake? When do you typically fish for lake trout?
Ecology	Where do you typically fish for lake trout? What do you use to capture lake trout? At what depth do you capture lake trout? Are there differences between lake trout in the west and east basins, shallow and deep water and north and south tributaries?
Morphology	Can you describe what lake trout look like that you capture? Have you seen lake trout that look like this?* If yes, can you please describe/show me where and when do you capture them? Can you describe any other colours, shapes or kinds of lake trout not seen in this picture?
Spawning	Do you know when and where lake trout spawn? If yes, can you describe/show their location? If yes, do all lake trout that you described earlier spawn in the same location?
Conservation	Have you noticed any changes to lake trout on the lake since you've been fishing?  If yes, do you know what might be causing these changes?  If yes, when did you notice these changes?  Have the number of lake trout decreased, increased or remained the same over the years you have been fishing?  Do you have any overall concerns about the health of lake trout in Mistassini Lake?  What factors might contribute to:  1) Short term changes to the number of lake trout there are?  2) Where lake trout move/inhabit the lake?  What do you think can be done to protect lake trout population for future generations?

<sup>\*</sup>Collage of photos showing a wide variety of lake trout sampled throughout the fieldwork.

**Table 2.2:** Overall ecological and morphological diversity of lake trout in Mistassini Lake as described by local experts.

Informant	Observation / Description
Ecology – where lal	ke trout are primarily captured
May – early June	
1-4, 7, 9, 10, 13, 14	Shallow shorelines throughout the lake
Mid June - July	
1-3, 5-15	Western basin (from island chain to western shoreline) but not in the shallows
5, 7, 9, 13, 15	Eastern basin
1-6, 10, 13-15	North passage
6, 10	North end
Aug – Sept	
4- 8, 10, 11, 13, 14	Western shoreline shallows
Winter	
4, 10, 13	South end shallows
Morphology – varie	ety of morphs described
3, 13	Big head and lean body
1-14	Black, small (3-5 lbs)
2, 4, 8, 9	Black with faded spots, small (3-5 lbs)
7, 13	Brown
7, 13	Dark brown with light belly
1-14	Giant (> 8 lbs) of various colours
1, 7	Green dorsal side
1, 4	Light coloured and deep bodied

Maasimekw-namekush (brook trout-like lake trout)
Silver / grey
Silver / grey with big spots, big head and red/yellow tipped fins
and timing
Western shoreline in shallow water (0-20')
Shallow areas but not exclusively the western shoreline
Late August - September
Different morphs spawn in different areas

**Table 2.3:** Local Cree concerns relating to lake trout conservation and management according to local experts.

Informant	Observation		
2, 3, 6-8, 13	Population	Decreasing	Past 40 years
1, 4, 5, 9-12, 14-15	Population	Stable	Past 30 years
4, 5	Spawning timing	Later	Past 10 years
2	Spawning in deeper water	Increasing	Past 10 years
2, 7	Feeding at the surface	Decreasing	Past 40 years
4	Size captured	Increasing	Past 10 years
2, 14	Size captured	Decreasing	Past 40 years
2, 14	Morphological changes (e.g. body depth)	Increasing	Past 40 years
2, 7, 10, 12-15	Fishing efficiency	Decreasing	Past 10 years
2, 3, 4, 7, 9, 10	Overfishing	Increasing	Past 10 years
2, 4, 7	Different capture techniques/methods	Increasing	Past 40 years
3-5, 10, 13, 15	Numbers and/or size of boats on ML	Increasing	Past 15 years
2	Numbers and/or size of boats on ML	Decreasing	Past 40 years
4, 13	Number of people fishing (both local and sport fishermen)	Increasing	Past 30 years
5	Number of people fishing	Decreasing	Past 5 years
1, 4, 5, 8, 13-14	Pollution / contamination from potential mining and human activities	Increasing	Past 40 years
2, 7, 12, 14	Water temperature	Increasing	Past 15 years
7	Threat of invasive species	Increasing	Past 20 years

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### **General Conclusions**

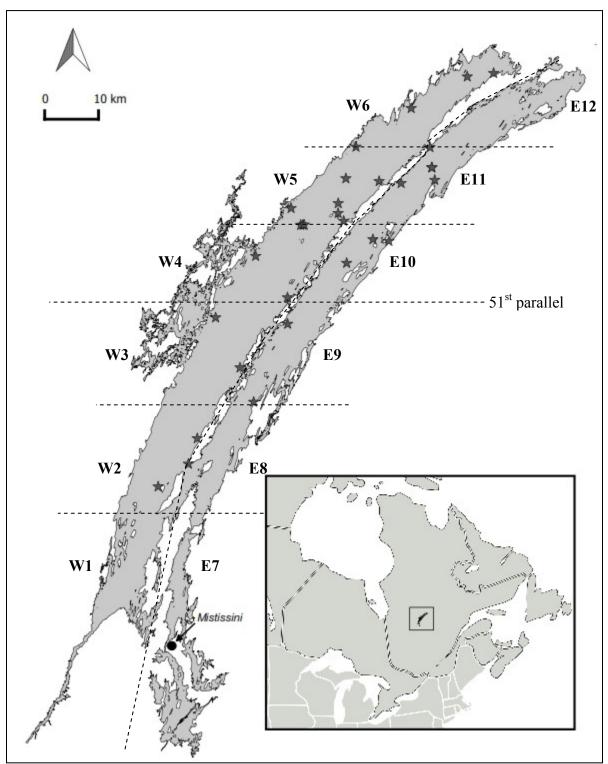
Quebec's largest natural lake, Mistassini Lake, is home to a minimum of 5 genetically-distinct lake trout populations. This differentiation, although weak yet biologically relevant, was primarily influenced by depth and to a lesser extent basin and geographic distance (sector). This divergence was also associated with some variation in body size, colouration and fish community structure but was inconsistently associated with difference in body or head shape. Moreover, each genetically distinguishable population displayed a high amount of morphological variation, with all populations contained individuals from each one of the three body shape or five head shape clusters. I suggest that this weak divergence and high morphological variation is likely due to a combination of factors including (i) large effective sizes ( $N_e$ ); (ii) relatively high (to  $N_e$ ) contemporary gene flow (iii) previously isolated lineages of lake trout from geographically disparate glacial margins colonizing Mistassini Lake; (iv) variety of habitat niches; and (v) phenotypic plasticity of lake trout. I propose that these factors place lake trout at the early stages of ecological speciation described by Hendry (2009). Our study suggests that sympatric population divergence in Mistassini lake trout might be quite unique in commonly exemplifying how plasticity might constrain further steps towards ecological speciation.

Broadly speaking, there was a congruence of traditional ecological knowledge (TEK) observations and quantitative findings of Chapter 1, with respect to the high amount of morphological variation, habitat use and depth preferences of different lake trout forms within Mistassini Lake. Furthermore, TEK shed light on potential temporal trends among existing populations of lake trout and highlighted a number of concerns, including possible overfishing, potential pollution from expanding human population and subsequent economic development and rising water temperatures.

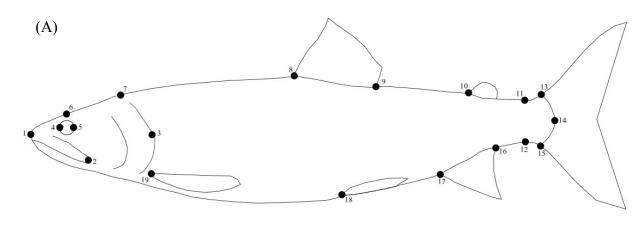
As a natural laboratory, Mistassini Lake provides an excellent example of the evolution and current state of lake trout populations in the wild. On a local scale, I recommend that the research within this thesis is used as baseline study and that long-term population monitoring of lake trout in Mistassini Lake be undertaken every 1-2 generations. More broadly speaking, this research sheds let on the importance of both historical and contemporary genetic diversity, the factors affecting this diversity, the inherently phenotypically plastic ability of lake trout that is essential for future rehabilitation, management and ultimately the conservation of the species

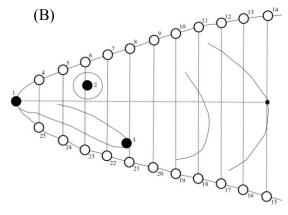
where extirpated forms exist. Finally, sympatrically-occurring populations of lake trout appear rare, and their occupancy of large, deep lakes such as Mistassini Lake means that they act as reservoirs of genetic diversity and refuge habitat for the species in the face of future climate warming.

# **Appendix 1: Supplemental Figures & Tables**

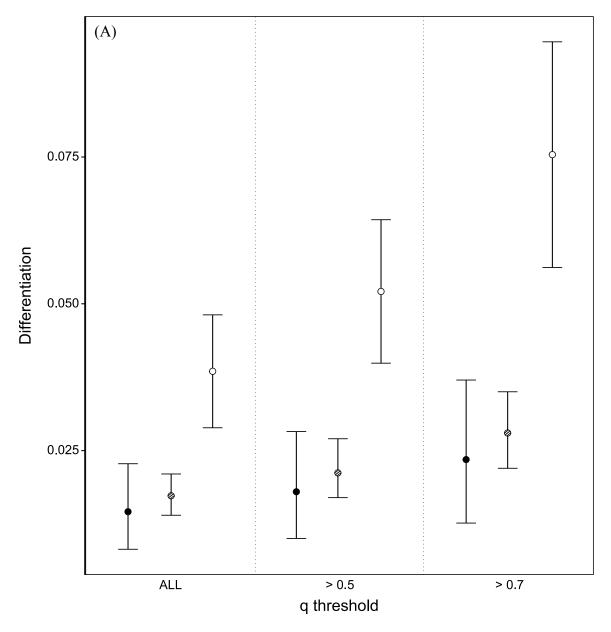


**Fig. S1.1:** Geographic location of Mistassini Lake, Québec, Canada showing sampling locations of gillnet sets (star) and lake sector (W1 - 6 and E7 - 12).

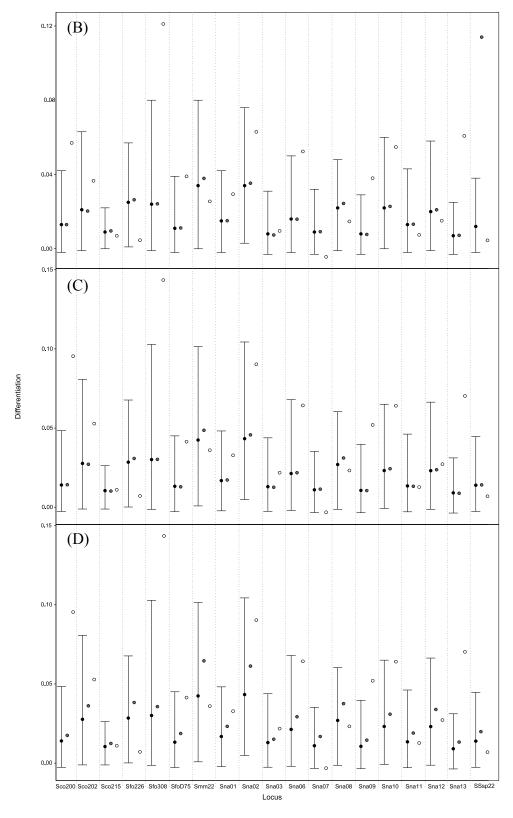




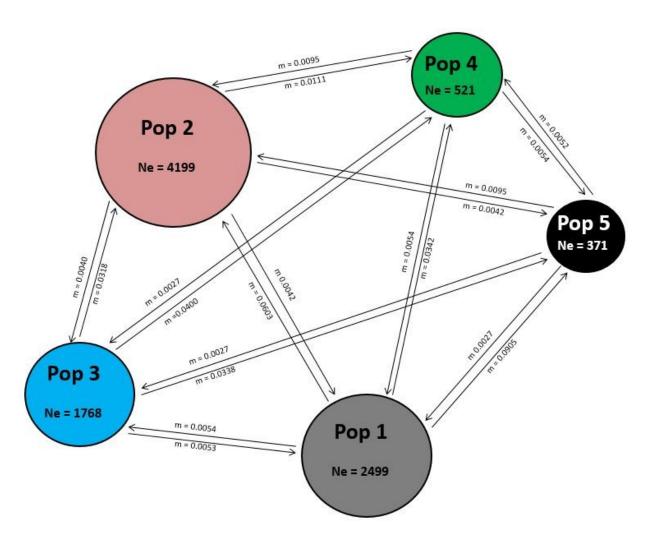
**Fig. S1.2**: **(A)** Nineteen landmarks used to quantify body shape of lake trout from Mistassini Lake: (1) tip of snout, (2) posterior tip of maxilla, (3) posterior edge of operculum, (4) most anterior part of eye, (5) most posterior part of eye, (6) top of cranium at mid of eye, (7) posterior of cranium above dorsal limit of operculum, (8) anterior insertion of dorsal fin, (9) posterior insertion of dorsal fin, (10) anterior insertion of adipose fin, (11) dorsal position above the narrowest part of caudal peduncle, (12) ventral position below the narrowest part of caudal peduncle, (13) dorsal insertion of caudal fin, (14) mid of the hypural plate, (15) ventral insertion of caudal fin, (16) posterior insertion of anal fin, (17) anterior insertion of anal fin, (18) insertion of pelvic fin, (19) insertion of pectoral fin. **(B)** Twenty-two semi-landmarks (white circles, numbers 4-25) and three landmarks (black circles, numbers 1-3) were used to quantify head shape.



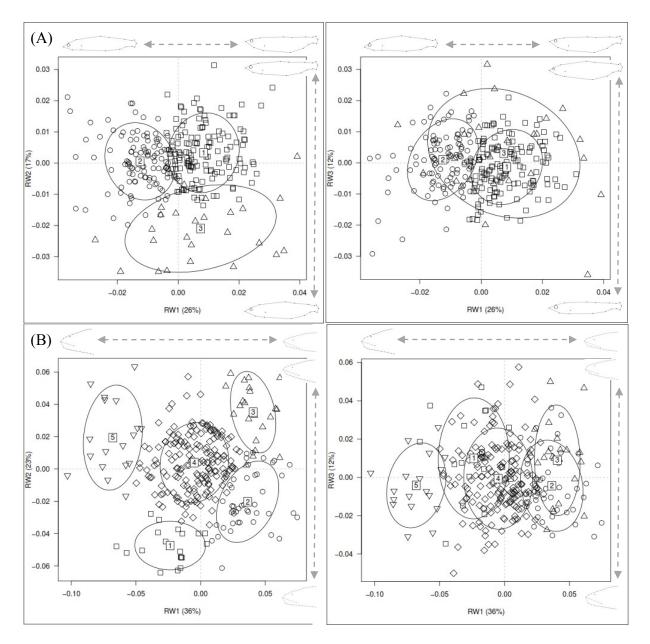
**Fig. S1.3(A)**: Global  $F_{ST}$  (hatched circles),  $R_{ST}$  (open circles),  $pR_{ST}$  (black circles) and their respective 95% confidence intervals at all three thresholds.  $R_{ST}$  is significantly greater than  $pR_{ST}$  across all three thresholds and therefore reveals that the differentiation observed in Mistassini Lake trout populations is due to stepwise mutation and thus indicative of a phylogeographic signal.



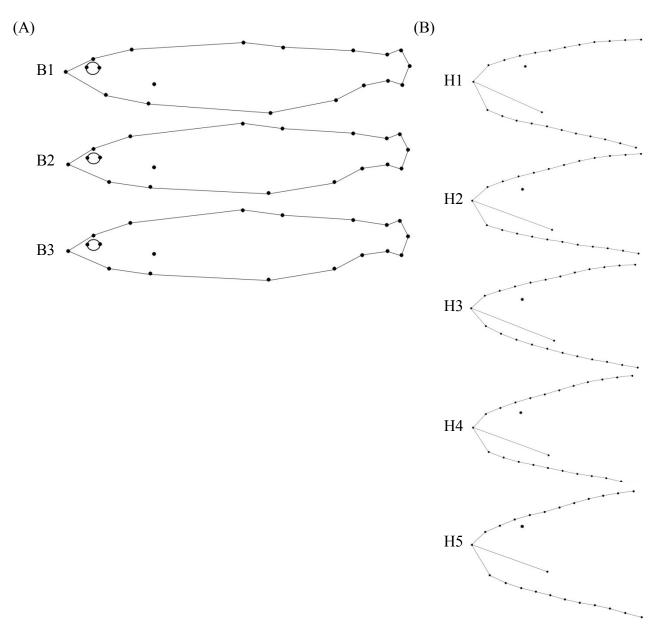
**Fig. S1.3:**  $F_{ST}$  (hatched circles),  $R_{ST}$  (open circles) and  $pR_{ST}$  (black circles) with 95% confidence intervals where **(B)** all individuals were assigned to the highest q, **(C)** q > 0.5 and **(D)** q > 0.7.



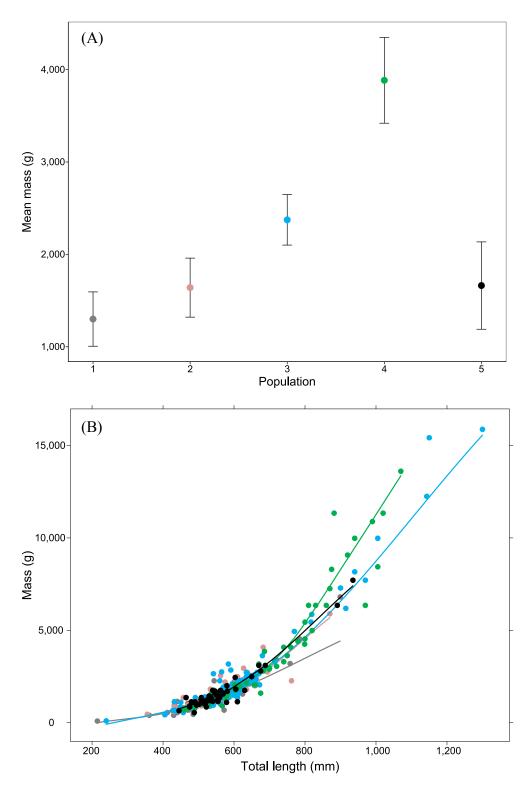
**Fig. S1.4:** Schematic summary showing recent gene flow (m) between lake trout populations present in Mistassini Lake based on individuals assigned to the highest q value (n = 636).



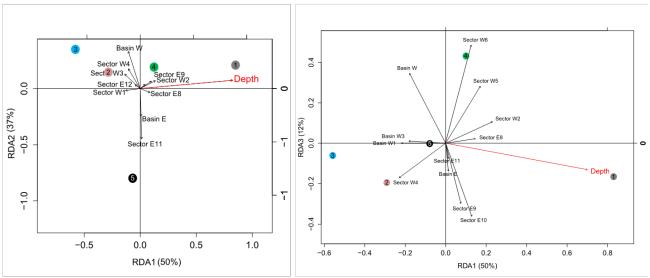
**Fig. S1.5**: 55% of body **(A)** and 71% of head **(B)** morphological variation. Numbers represent a morphological cluster **(A**: B1 - 3 for body and **B**: H1 - 5 for head) and ellipses corresponds to 67% of each cluster's variation. Inset images are visualizations of the extreme shape differences corresponding to each relative warp.



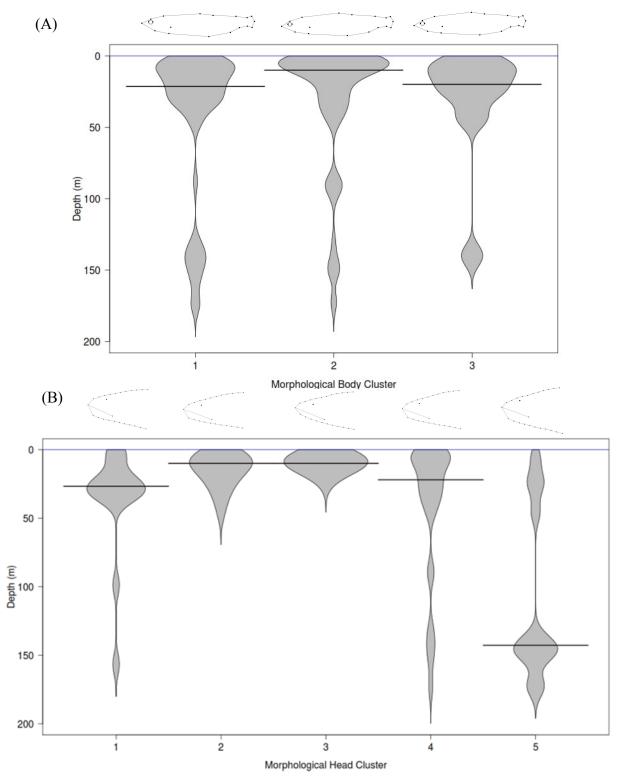
**Fig. S1.6**: The consensus shape for each one of the identified morphological clusters detected in Mistassini Lake for both body ( $\mathbf{A}$ : B1 – B3) and head ( $\mathbf{B}$ : H1 – H5).



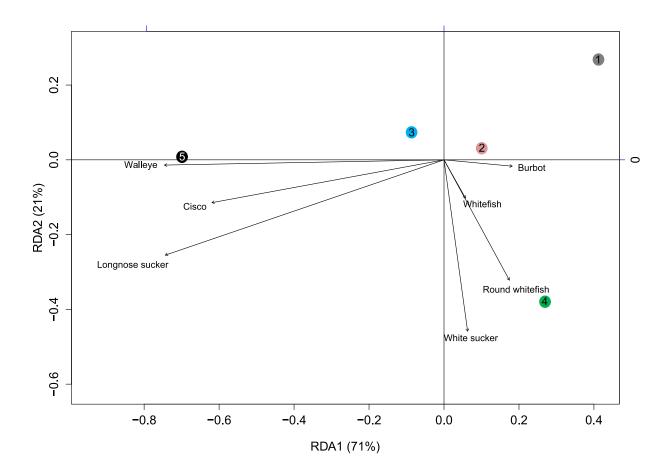
**Fig. S1.7**: The difference in mean mass for each genetically-distinct population **(A)**. The length/weight curve for each population **(B)**.



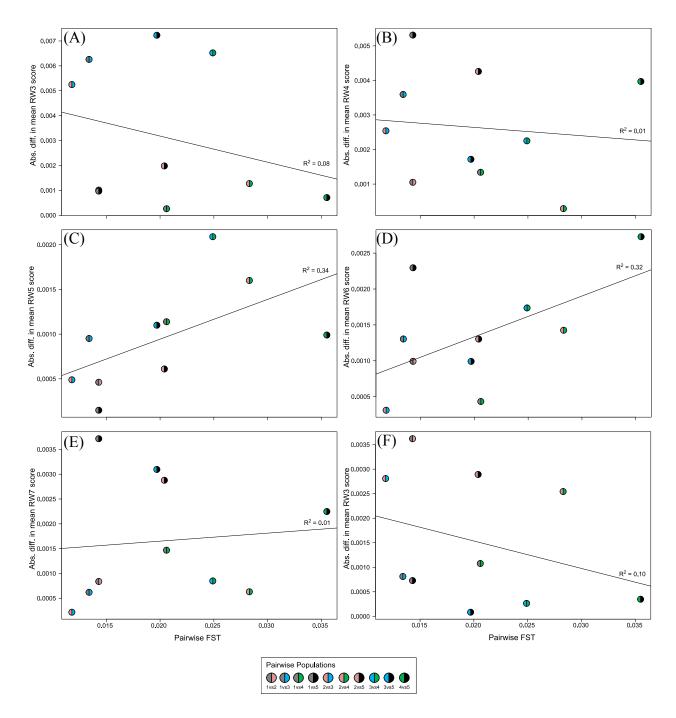
**Fig. S1.8**: Results of redundancy analysis (RDA) for the first three axes (99% of variation), which show that depth is significant with respect to the observed genetic population structuring. Coloured circles represent the 5 genetically-distinct lake trout populations present in Mistassini Lake. Ecological variables (depth, basin and sector) and their associated arrows represent the nature of the relationship with respect to populations.



**Fig. S1.9**: Depth variation for each morphological (A) body cluster and (B) head cluster. Black line represents the median.



**Fig. S1.10**: Visualization of bycatch species association with genetically-differentiated populations.



**Fig. S1.11**: Visualization of the remaining Mantel tests, which shows genetic distance (pairwise  $F_{ST}$ ) and the absolute difference in mean relative warp (RW) score for RW3 – 7 for body (**A** – **E**) and RW3 for body morphology (**F**).

**Table S1.1**: Basic descriptive statistics for 19 loci across all 5 genetically-differentiated populations where all individuals were assigned (n=636) showing the average number of alleles per locus  $(N_A)$ , observed  $(H_O)$  and expected  $(H_E)$  heterozygosities, and allelic richness  $(A_R)$ .

	Sco202	Sfo226	Sfo308	SfoD75	Sna02	Sna03	Sna06	Sna07	Sna08	Sna09	Sna10	Sco200	Sco215	Sna11	Smm22	Sna01	Sna12	Sna13	SSsp22	Avg.
Populat	tion 1 (n=1	68)																		
$N_A$	13	29	26	13	13	29	36	21	12	55	26	32	12	27	16	23	22	21	19	23.42
$H_{E}$	0.83	0.86	0.92	0.86	0.82	0.89	0.93	0.93	0.49	0.96	0.89	0.94	0.56	0.85	0.67	0.90	0.88	0.88	0.90	0.84
$H_{O}$	0.83	0.82	0.95	0.86	0.82	0.90	0.96	0.84	0.49	0.92	0.90	0.96	0.45	0.85	0.66	0.89	0.85	0.85	0.87	0.82
$A_R$	12.38	23.58	20.79	11.79	10.05	23.74	27.33	19.23	9.71	40.43	21.05	26.86	8.98	20.45	77.88	19.11	18.16	17.61	15.80	18.89
Populat	tion 2 (n=1	<b>135</b> )																		
$N_A$	12	24	25	12	12	26	35	22	15	47	22	31	12	22	15	20	19	22	17	21.58
$H_{E}$	0.80	0.83	0.92	0.86	0.79	0.87	0.94	0.92	0.67	0.97	0.81	0.93	0.48	0.80	0.81	0.89	0.86	0.89	0.90	0.84
$H_{O}$	0.78	0.79	0.91	0.84	0.73	0.86	0.88	0.82	0.64	0.97	0.85	0.91	0.45	0.82	0.81	0.88	0.83	0.85	0.87	0.82
$A_R$	10.40	20.68	21.48	10.93	11.53	20.51	28.68	18.84	12.95	40.65	19.26	26.27	8.82	17.68	12.63	17.35	16.32	18.96	15.98	18.42
Populat	tion 3 (n=1	,																		
$N_A$	13	27	25	14	13	30	43	27	15	61	25	30	11	26	16	17	22	22	21	24.11
$H_{E}$	0.84	0.72	0.91	0.85	0.76	0.88	0.95	0.92	0.68	0.97	0.92	0.93	0.48	0.82	0.79	0.87	0.92	0.90	0.88	0.84
$H_{O}$	0.81	0.72	0.93	0.87	0.72	0.85	0.92	0.81	0.69	0.96	0.90	0.93	0.48	0.78	0.78	0.84	0.88	0.85	0.86	0.82
$A_R$	12.08	20.09	19.66	10.94	10.38	21.47	31.75	21.72	12.24	45.85	19.89	24.48	7.92	20.29	13.31	14.16	19.25	19.37	16.87	19.04
	ion 4 (n=6	,																		
$N_A$	11	14	18	10	7	24	28	17	6	33	15	21	7	16	12	17	14	13	13	15.58
$H_{E}$	0.81	0.73	0.89	0.86	0.63	0.88	0.93	0.89	0.35	0.95	0.90	0.91	0.62	0.84	0.71	0.89	0.87	0.85	0.80	0.81
$H_{O}$	0.83	0.65	0.88	0.80	0.65	0.80	0.92	0.81	0.36	0.85	0.85	0.95	0.68	0.83	0.78	0.97	0.85	0.86	0.86	0.80
$A_R$	10.99	13.64	17.81	9.94	6.88	23.75	27.38	17.00	5.94	32.38	14.95	20.84	6.91	15.58	11.95	17.00	13.88	12.94	12.81	15.40
_	ion 5 (n=7	,				4.0	• 0	4.0		• •	4.0						4.0	10		
$N_A$	11	19	23	9	12	19	28	19	11	39	18	23	9	16	11	16	18	18	15	17.58
$H_{E}$	0.80	0.89	0.91	0.83	0.83	0.85	0.91	0.92	0.49	0.95	0.89	0.93	0.52	0.78	0.70	0.87	0.85	0.85	0.88	0.82
H <sub>O</sub>	0.81	0.83	0.92	0.85	0.79	0.77	0.93	0.86	0.54	0.92	0.90	0.94	0.57	0.75	0.65	0.81	0.76	0.82	0.89	0.80
A <sub>R</sub>	10.56	18.44	22.33	9.00	11.56	18.27	26.30	18.87	10.44	37.36	17.49	22.46	8.70	15.36	10.44	15.77	17.54	17.63	14.30	16.99
Global	1.2	2.5	22	1.5	1.5	2.5	60	2.1	1.0	70	20	20	1.7	27	1.0	2.4	2.5	2.4	22	20.52
N <sub>A</sub>	13	35	32	15	15	35	60	31	18	72	30	38	17	37	18	24	25	24	22	29.53
$H_{E}$	0.84	0.82	0.93	0.87	0.80	0.89	0.95	0.93	0.59	0.97	0.90	0.94	0.53	0.83	0.77	0.90	0.90	0.89	0.89	0.85
$H_{O}$	0.81	0.76	0.92	0.85	0.75	0.84	0.92	0.83	0.55	0.92	0.88	0.94	0.53	0.81	0.74	0.88	0.84	0.84	0.87	0.81
$A_{R}$	13.00	34.75	31.83	14.99	14.92	34.93	59.55	30.83	17.91	71.22	29.73	37.67	16.59	36.27	17.84	24.00	24.84	24.00	21.93	29.30

**Table S1.2**: Estimation of exact p-values from Hardy-Weinberg exact tests for heterozygote deficiencies for all 19 loci under the null hypothesis of no population structuring and alternative hypothesis of five populations as identified by STRUCTURE (highest q, q > 0.5, q > 0.7). All analyses were carried out using GENEPOP (v.4.2; Rousset 2008). Under the null hypothesis bolded p-values indicate significance where p < 0.05, whereas bolded p-values under the alternative hypothesis indicate significance after Bonferroni correction (p < 0.0005).

	Pop	n	Sco202	Sfo226	Sfo308	SfoD75	Sna02	Sna03	Sna06	Sna07	Sna08	Sna09	Sna10	Sco200	Sco215	Sna11	Smm22	Sna01	Sna12	Sna13	SSsp22
Null	NA	636	0.001	0.000	0.171	0.047	0.000	0.000	0.025	0.000	0.351	0.000	0.091	0.078	0.000	0.002	0.049	0.034	0.000	0.002	0.001
Alt.																					
Highest q	1	168	0.134	0.234	0.951	0.262	0.500	0.191	1.000	0.000	0.117	0.017	0.148	0.570	0.000	0.141	0.059	0.022	0.054	0.012	0.118
	2	135	0.006	0.000	0.218	0.073	0.003	0.099	0.075	0.000	0.302	0.146	0.958	0.088	0.259	0.390	0.254	0.553	0.371	0.013	0.189
	3	195	0.106	0.000	0.449	0.772	0.102	0.011	0.000	0.000	0.846	0.399	0.030	0.265	0.002	0.133	0.167	0.060	0.131	0.071	0.210
	4	66	0.027	0.037	0.158	0.052	0.709	0.008	0.107	0.000	0.821	0.000	0.042	0.915	0.919	0.567	0.788	0.985	0.178	0.504	0.504
	5	72	0.312	0.000	0.190	0.172	0.000	0.015	0.414	0.000	0.710	0.061	0.823	0.479	0.980	0.129	0.393	0.311	0.000	0.080	0.044
q > 0.5	1	141	0.067	0.193	0.848	0.842	0.252	0.314	1.00	0.000	0.505	0.022	0.237	0.459	0.000	0.042	0.026	0.486	0.064	0045	0.290
	2	102	0.300	0.000	0.285	0.014	0.028	0.035	0.024	0.023	0.319	0.296	0.983	0.112	0.295	0.392	0.317	0.499	0.092	0.121	0.077
	3	163	0.134	0.018	0.262	0.818	0.252	0.10	0.111	0.000	0.972	0.646	0.067	0.448	0.000	0.231	0.568	0.050	0.171	0.154	0.453
	4	60	0.803	0.012	0.331	0.025	0.772	0.014	0.311	0.000	0.797	0.013	0.029	0.889	0.992	0.516	0.761	0.978	0.130	0.369	0.502
	5	58	0.186	0.309	0.484	0.327	0.013	0.011	0.160	0.006	0.548	0.146	0.651	0.397	0.951	0.393	0.293	0.255	0.101	0.056	0.282
q > 0.7	1	81	0.332	0.543	0.743	0.534	0.257	0756	0.772	0.007	0.431	0.145	0.033	0.993	0.000	0.121	0.163	0.808	0.118	0.445	0.219
	2	73	0.505	0.000	0.378	0.131	0.167	0.014	0.016	0.180	0.343	0.007	0.969	0.126	0.422	0.664	0.434	0.373	0.089	0.243	0.554
	3	110	0.318	0.000	0.787	0.858	0.107	0.030	0.527	0.000	0.971	0.028	0.585	0.619	0.007	0.591	0.432	0.103	0.152	0.161	0.254
	4	49	0.954	0.024	0.260	0.019	0.615	0.048	0.488	0.000	0.667	0.013	0.029	0.968	0.995	0.472	0.604	0.880	0.131	0.647	0.893
	5	48	0.212	0.402	0.641	0.234	0.625	0.000	0.940	0.009	0.500	0.201	0.783	0.358	0.914	0.209	0.419	0.143	0.103	0.046	0.315

**Table S1.3**: Linkage disequilibrium results, which shows the number of significant locus pairs for all 19 loci under the null hypothesis of no population structuring and alternative hypothesis of five populations as identified by STRUCTURE (highest q, q > 0.5, q > 0.7).

	Pop	n	Level of	significance
			0.05	Bonferroni
Null hypothesis*	NA	636	20	5
Alternative hypothes	sis <sup>†</sup>			
Highest q	1	168	3	0
	2	135	15	3
	3	195	10	2
	4	66	34	0
	5	72	36	6
	Acros	ss all pops	23	13
q > 0.5	1	141	11	1
	2	102	8	2
	3	163	10	2
	4	60	12	2
	5	58	52	11
	Acros	ss all pops	34	18
q > 0.7	1	81	8	4
	2	73	10	1
	3	110	13	3
	4	49	12	2
	5	48	63	25
	Acros	ss all pops	47	34

<sup>\*</sup>Under the null hypothesis there were a total of 171 comparisons.

<sup>&</sup>lt;sup>+</sup>Under the alternative hypothesis there were a total of 855 comparisons.

**Table S1.4**: Results for the detection of any recent bottlenecks across all loci and populations for each threshold under the stepwise (SMM) and two-phase models (TMP) of mutation. The number of loci with heterozygosity excess ( $H_E$ ) and expected number of loci with heterozygosity excess ( $H_{EQ}$ ) are reported. Statistical significance of deviation from either model is represented by P, which is a one tail Wilcoxon sign rank test for heterozygosity excess across 19 loci for each population.

		TPM			SMM	
Population	$H_{\rm E}$	$H_{EQ}$	P	$H_{E}$	$H_{EQ}$	P
Highest $q$ (n =	636)					
1	7	11.21	0.82	2	11.29	0.99
2	8	11.22	0.89	2	11.18	1.00
3	8	11.18	0.75	3	11.34	0.99
4	6	11.13	0.86	5	11.24	0.99
5	8	11.26	0.79	4	11.34	0.99
q > 0.5  (n = 524)	4)					
1	9	11.18	0.70	2	11.21	0.99
2	9	11.36	0.57	5	11.21	0.99
3	9	11.17	0.60	3	11.24	0.99
4	7	11.12	0.74	4	11.31	0.99
5	10	11.20	0.42	4	11.29	0.99
q > 0.7 (n = 361	1)					
1	12	11.30	0.55	5	11.21	0.99
2	8	11.28	0.72	4	11.26	0.99
3	12	11.17	0.47	5	11.26	0.99
4	9	11.17	0.72	4	11.28	0.99
5	10	11.25	0.45	4	11.26	0.99

**Table S1.5:** Statistical results from STRUCTURE (20 iterations) for 636 individuals across 19 loci. Both the mean and standard deviations (SD) of the log-likelihood values of the data (LnP[D]) for a given number of clusters (K). In addition, results from the ad hoc statistic of Evanno et al. 2005 show the second-order rate of change in LnP[D] and is reported as mean  $\Delta K$ . Both test statistics (bolded) indicate that the most likely number of genetic clusters is 5.

K	meanLnP[D]	SDLnP[D]	ΔK
1	-59327.66	0.51	NA
2	-58945.29	5.24	29.46
3	-58717.37	7.49	10.01
4	-58414.33	5.24	9.70
5	-58060.42	8.37	57.03
6	-58184.06	92.73	11.00
7	-59328.24	1023.45	0.87
8	-59578.83	966.59	0.83
9	-60637.82	1127.27	1.38
10	-60132.61	1132.78	0.28

**Table S1.6 (A):** Pairwise  $F_{ST}$  for all three datasets: a 'high' assignment threshold of q > 0.7, a 'low' threshold of q > 0.5, and the highest q value to any one cluster, regardless of the value.

		$\mathbf{F}_{\mathbf{ST}}$	
<b>Populations</b>	q > 0.7	q > 0.5	Highest q
1 vs. 2	0.0249	0.0176	0.0143
1 vs. 3	0.0227	0.0163	0.0134
1 vs. 4	0.0278	0.0225	0.0206
1 vs. 5	0.0243	0.0181	0.0143
2 vs. 3	0.0206	0.0149	0.0118
2 vs. 4	0.0382	0.0324	0.0283
2 vs. 5	0.0312	0.027	0.0204
3 vs. 4	0.0362	0.0291	0.0249
3 vs. 5	0.0292	0.0251	0.0197
4 vs. 5	0.0481	0.0415	0.0355

**Table S1.6 (B)**: Pairwise  $R_{ST}$  for all three datasets: a 'high' assignment threshold of q > 0.7, a 'low' threshold of q > 0.5, and the highest q value to any one cluster, regardless of the value.

		$\mathbf{R}_{\mathbf{ST}}$	
<b>Populations</b>	q > 0.7	q > 0.5	Highest q
1 vs. 2	0.0544	0.0342	0.0217
1 vs. 3	0.0437	0.0235	0.0167
1 vs. 4	0.0841	0.0758	0.0681
1 vs. 5	0.0819	0.0642	0.0419
2 vs. 3	0.0598	0.0305	0.0239
2 vs. 4	0.0586	0.0499	0.0453
2 vs. 5	0.0791	0.0706	0.0461
3 vs. 4	0.1023	0.0800	0.0688
3 vs. 5	0.1389	0.1027	0.0709
4 vs. 5	0.0798	0.0717	0.0579

**Table S1.7**: Results from allele permutation test for each population pair, across all 19 loci for each threshold. Under the null hypothesis observed  $R_{ST}$  is equal to the mean value after permutation; and under the alternative hypothesis the observed  $R_{ST}$  is greater than the mean value after permutation. Therefore, significant p-values (reported below) are indicative of a phylogeographic signal. Bolded p-values indicate significance after Bonferonni correction (< 0.005).

		Threshold	
<b>Populations</b>	q > 0.7	q > 0.5	Highest q
1 vs. 2	0.0066	0.0241	0.0693
1 vs. 3	0.0062	0.0443	0.0923
1 vs. 4	0.0000	0.0003	0.0000
1 vs. 5	0.0041	0.0036	0.0117
2 vs. 3	0.0012	0.0330	0.0418
2 vs. 4	0.0730	0.0657	0.0492
2 vs. 5	0.0019	0.0010	0.0054
3 vs. 4	0.0002	0.0002	0.0002
3 vs. 5	0.0000	0.0000	0.0000
4 vs. 5	0.0172	0.0085	0.0135

**Table S1.8:** Effective population size ( $N_e$ ) estimates and associated 95% confidence interval (CI) for each genetically-differentiated population identified in Mistassini Lake. All 636 samples and their respective sample sizes per population (n) were used for this analysis. Critical values ( $P_{crit}$ : allele frequencies greater than) 0.01 were used for larger (> 100 individuals) populations and 002 was used for smaller (< 100 individuals).

Pop	n	$N_{ m e}$	95% CI
1	168	2499	1471 – 7888
2	135	4199	$1744-\infty$
3	195	1768	1246 - 2997
4	66	521	328 - 1209
5	72	371	274 - 566

**Table S1.9:** The genetic differentiation ( $F_{ST}$ ), mean gene flow into each population (m), mean effective population size ( $N_e$ ), the time, in generations, required for  $F_{ST}$  to reach halfway ( $t_{1/2}$ ) and completely ( $\sim$  t) to a new equilibrium for each population pair and globally, based on all individuals assigned to the highest q value (n = 636).

Population pair	$\mathbf{F}_{\mathbf{ST}}$	mean <i>m</i>	mean $N_{ m e}$	$t_{1/2}$	~ t
1 – 2	0.0143	0.0151	3349	22.69	46
1 – 3	0.0134	0.0038	2134	88.31	177
1 – 4	0.0206	0.0133	1510	25.64	45
1 – 5	0.0143	0.0197	1435	17.31	35
2-3	0.0118	0.015	2984	22.82	35
2 – 4	0.0283	0.0245	2360	13.94	22
2 – 5	0.0204	0.0308	2285	11.03	51
3 – 4	0.0249	0.0132	1145	25.73	51
3 – 5	0.0197	0.0196	1070	17.35	28
4 – 5	0.0355	0.029	446	11.55	23
Global	0.017	0.0184	1872	18.55	37

**Table S1.10**: The number of relative warps (RWs) for both body and head shape used to assign lake trout to morphological clusters.

RWs	% variation	MCLUST	No. of	Mean uncertainty ±					
used	explained	model	clusters	SE	BIC				
Body shape									
2	43	EII	1	$0\pm0$	3334				
		VII	1		3334				
3	55	EII	3	$0.22 \pm 0.01$	5148				
		VII	3		5160				
4	63	EII	2	$0.19 \pm 0.01$	7044				
		VII	3		7064				
5	69	EII	3	$0.16 \pm 0.01$	9030				
		VII	3		9043				
6	74	EII	3	$0.14 \pm 0.01$	11050				
		VII	3		11071				
7	78	EII	4	$0.12 \pm 0.01$	13095				
		VII	3		13137				
		Hea	ad Shape						
2	58	EII	2	$0.05 \pm 0.01$	2402				
		VII	1		2396				
3	70	EII	5	$\boldsymbol{0.17 \pm 0.01}$	3811				
		VII	2		3805				

**Table S1.11 (A)**: Model selection for the multinomial regression analysis based on Akaike information criterion (AIC).

Model	AIC
Pop ~ log(Depth) + Sector	1159.173*
$Pop \sim log(Depth) + (Basin/Sector)$	1159.173
$Pop \sim log(Depth) + Basin + Sector$	1159.173
$Pop \sim log(Depth) + Basin$	1177.086
$Pop \sim log(Depth) + log(Depth):Basin$	1178.213

<sup>\*</sup>Most parsimonious model

**Table S1.11 (B)**: Coefficients of multinomial regression analysis across all three q thresholds where population 1 is the reference.

Pop	Log (depth)	E8	Е9	E10	E11	W1	W2	W3	W4	W5	W6
High	est q										
2	-1.7	-2.6	-2.1	6.1	-1.8	11.3	-0.6	-1.8	-0.9	-0.5	-28.2
3	-2.0	-1.4	-1.7	6.5	-1.9	12.2	-0.1	-1.7	0.2	0.4	-1.1
4	-0.7	14.0	-11.8	-13.1	13.3	27.6	15.1	14.9	14.5	15.8	15.8
5	-1.4	-0.7	-2.1	4.2	0.7	12.6	-26.2	-2.2	-0.6	-0.2	0.0
q > 0.	5										
2	-1.9	-2.5	-2.4	7.1	-2.2	10.8	-0.2	-2.1	-0.9	-0.1	-37.5
3	-2.4	-1.7	-1.9	7.7	-2.4	11.8	0.2	-2.1	-0.1	0.4	-2.3
4	-0.9	15.9	-11.6	-14.2	15.2	28.9	17.2	16.6	16.5	18.0	17.7
5	-1.6	-1.2	-2.5	5.3	-1.2	11.9	-37.7	-3.1	-1.1	-0.9	-1.1
q > 0.	7										
2	-2.9	-3.0	-2.9	10.2	-2.7	14.6	0.6	-2.5	-0.5	-0.8	-55.7
3	-3.6	-1.7	-2.9	11.6	-2.7	15.0	1.2	-2.9	0.8	-0.5	-0.8
4	-1.4	18.8	-17.3	-15.3	17.5	35.7	20.7	19.4	19.8	20.8	22.2
5	-2.9	11.9	10.5	<b>-</b> 4.1	13.0	28.9	-5.9	9.9	13.1	-12.0	14.3

**Table S1.12:** Results from Mantel tests at all three thresholds which shows genetic distance (pairwise  $F_{ST}$ ) and (i) the absolute difference in mean relative warp (RW) score for the first seven RWs for body and first three RWs for head morphology; (ii) the absolute different in prey abundance; and (iii) the absolute difference in median depth (in metres). Bolded p-values indicate significance. The Mantel R statistic is based on Pearson's product-moment correlation.

	Highest q		<i>q</i> >	0.5	q > 0.7	
Pairwise F <sub>ST</sub> vs.	p-val	r stat	p-val	r stat	p-val	r stat
Body RW1	0.14	0.63	0.13	0.57	0.08	0.73
Body RW2	0.23	0.54	0.23	0.43	0.23	0.43
Body RW3	0.64	-0.28	0.65	-0.25	0.63	-0.25
Body RW4	0.60	-0.11	0.51	0.00	1.00	-0.44
Body RW5	0.16	0.58	0.17	0.31	0.36	0.20
Body RW6	0.08	0.57	0.07	0.64	0.02	0.79
Body RW7	0.38	0.10	0.38	0.17	0.40	0.06
Head RW1	0.25	0.34	0.21	0.48	0.14	0.55
Head RW2	0.11	0.77	0.12	0.71	0.10	0.75
Head RW3	0.67	-0.32	0.43	-0.06	0.57	-0.03
Bycatch	0.37	0.13	0.28	0.29	0.28	0.23
Depth	0.40	0.10	0.58	0.02	0.39	0.11

## Appendix 2: Loci and polymerase chain reaction (PCR) information

The DNA from the 636 individual lake trout by amplifying 19 microsatellite loci (*SfoD75*; T.L. King, US Geological Survey, unpublished, *Sfo308Lav Sfo226Lav*; Perry et al. 2005, *SnaMSU01*, *SnaMSU02*, *SnaMSU03*, *SnaMSU06*, *SnaMSU07*, *SnaMSU08*, *SnaMSU09*, *SnaMSU10*, *SnaMSU11*, *SnaMSU12*, *SnaMSU13*; Rollins et al. 2009, *Sco215*, *Sco202*, *Sco200*; DeHaan and Arden 2005, *Smm22*; Crane et al. 2004 and *Sssp2201*; Paterson et al. 2004) using multiplexed polymerase chain reactions (PCRs). Each 10 µl multiplex PCR contained 5 to 25 ng DNA template, 1 µl Taq buffer (1x), 0.2 mM dNTP, 2.0 mM MgSO4, 0.8 mg BSA, and forward (fluorescently labelled) and reverse primers at varying concentrations. Amplifications were performed using a T100 Thermal Cycler (BioRad) with an initial four minutes denaturing step at 95°C, followed by 35 cycles of denaturation at 95°C for 20 seconds, annealing at 58°C for 20 seconds and extension at 72°C for 15 seconds followed by a final extension at 72°C for five minutes.

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