

## *chapter two*

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# *History and evolution of lake trout in Shield lakes: past and future challenges*

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### *Introduction*

Evidence suggests that lake trout likely evolved in response to environmental changes caused by glaciation events during the Pleistocene era. Following the retreat of the last ice sheets, lake trout recolonized their present range from multiple refugia. Populations in Boreal Shield lakes are descended from at least six refugial groups, with the greatest contributions from Mississippian and Atlantic sources. Secondary contact among these separate lineages was a significant source of genetic diversity, enabling adaptation to local environments.

Surprisingly little is known about the diversity and adaptive structure of inland lake trout populations. There is some evidence of local adaptation among inland populations and stocking strains as well as differential fitness between native and stocked lake trout.

However, many issues regarding lake trout adaptation and fitness remain unresolved. In addition, the biological characteristics of lake trout make them extremely vulnerable to natural and anthropogenic disturbances, which present significant management challenges to ensure their persistence.

Lake trout have often been described as a “glacial relict,” a holdover from the Ice Age that lives primarily in deep, cold-water habitats. The species has certainly been intimately associated with glacial events and is perhaps better adapted to the past than the present. The fascination of anglers and biologists with lake trout may in part stem from the prehistoric mystique of this giant, primitive-appearing freshwater salmonid. In fact, however, lake trout are anything but ancient and primitive, having evolved no more than 3 million years ago and being specialized for habitats that did not exist before the Pleistocene glaciations.

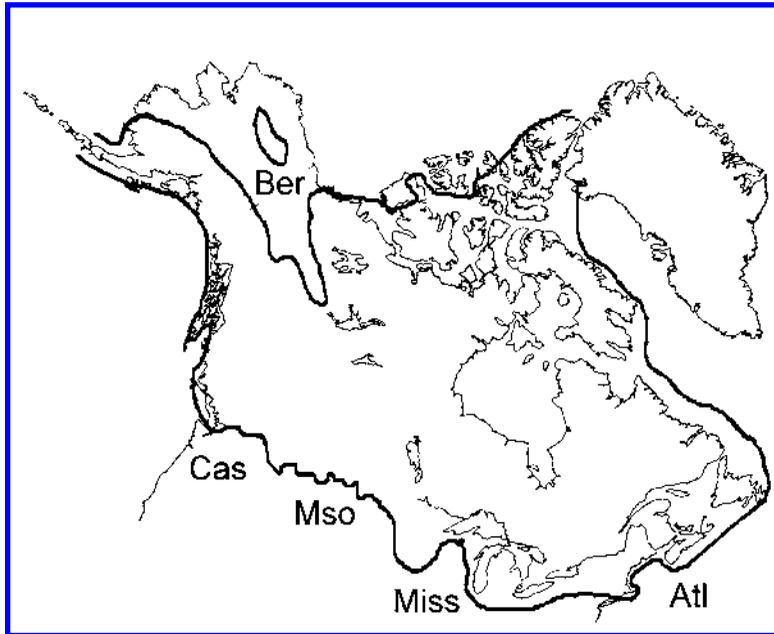
Based on morphologic systematic and genetic data, lake trout are thought to have diverged from other species of *Salvelinus* approximately 1 to 3 million years ago (Behnke, 1972; Grewe et al., 1990; Phillips et al., 1992), roughly coincident with the onset of the Pleistocene glaciations (Dawson, 1992). Lake trout have the most extensive freshwater distribution of any salmonine: the species' natural distribution closely matches the North American limits of the recent (Wisconsinan) glaciation (Lindsey, 1964), where it is largely restricted to lakes carved out by glacial scouring. Lake trout also differ from all other members of the genus by lacking the ability to live in salt water, suggesting their evolution in a purely freshwater environment. Taken together, these facts suggest that the species evolved in response to altered habitat and ecological conditions caused by Pleistocene glacial events.

The purpose of this chapter is to describe the historical influences that underpin the evolutionary biology of lake trout populations in small lakes on the southern Canadian Shield. Beginning with the historical origins of lake trout (when they first appeared and where they came from), and postglacial history (how they arrived where they are today), we examine the influence of these events on modern populations. As well as reconstructing past events that influenced the current structure and diversity of lake trout, this chapter attempts to summarize both what is known and what needs to be learned about the present biology and potential future of these populations. As well as developing some suggested research themes, some recommendations for sustainable management are presented.

## *Evolutionary history*

The early details of lake trout evolution will likely remain unknown. The close relationship between lake trout distribution and formerly glaciated areas (Lindsey, 1964; Scott and Crossman, 1973) suggests that fossil remains preceding the Wisconsinan glaciation were destroyed long ago by advancing glaciers. However, the roughly coincident divergences of the three subgenera of *Salvelinus* (*Salvelinus*, *Cristivomer*, and *Baione*) approximately 2 to 3 million years ago (Behnke, 1972, 1980; Grewe et al., 1990; Phillips et al., 1992) indicate a short burst of evolutionary diversification and selection, potentially in response to major environmental or biotic pressures. The placement of lake trout in its own subgenus (*Cristivomer*) indicates the extent of its divergence from other charr species in response to Pleistocene events (Behnke, 1972).

The nature of glacial disturbances makes it impossible to reconstruct the complete Pleistocene history of lake trout. Each glaciation effectively bulldozed continental landscapes under a wall of ice, wiping clean the geologic and biologic traces of preceding events. Because of this, the exact number of Pleistocene glaciations in North America is uncertain, with estimates ranging between 4 and 20 cycles (Pielou, 1991; Dawson, 1992; Gunn and Pitblado, Chapter 1, this volume). Each of these undoubtedly had major impacts



**Figure 2.1** Present-day distribution of lake trout, *Salvelinus namaycush*, in relation to geographic coverage of glacial ice at the maximum of the Wisconsin glacial period, approximately 23,000 years ago. Recognized glacial refugia for northern fishes are shown along the glacial margins (Atl = Atlantic; Ber = Beringia; Cas = Cascadia; Miss = Mississippi; Mso = Missouri). Glacial coverage taken from Dyke and Prest (1987b); lake trout distribution from Lee et al. (1980); glacial refugia from Crossman and McAllister (1986).

on the distribution and genetic structure of lake trout, based on the species' present distribution in relation to glacial coverage (Figure 2.1). During each glacial interval, fish populations were extirpated or displaced, in some cases by thousands of kilometers. Those fish that survived were limited to a handful of refugial habitats along the periphery of the ice sheets.

Four main southern and one northern Wisconsin glacial refugia have been hypothesized (Bailey and Smith, 1981; Crossman and McAllister, 1986; Figure 2.1). The Atlantic Coastal refugium existed along the coastal plain east of the Appalachians, south of present-day Long Island. Smaller Atlantic Coastal Uplands and Grand Banks refugia were also present along the east coast of North America (Schmidt, 1986). The Mississippi basin, south of the ice sheets, was the largest Wisconsin glacial refugium and was separated from the Missouriian refugium by a lobe of ice. Several small refugia (e.g., Nahanni, Banff-Jasper, Waterton) also existed between the Cordilleran and Laurentide ice sheets (Crossman and McAllister, 1986; Lindsey and McPhail, 1986). The Pacific Coastal (or Cascadia) refugium existed along the coastal plain west of the Rockies, south of present-day Vancouver Island. Part of present-day Alaska and land now covered by the Bering Sea formed the Beringian refugium in northwestern North America (Figure 1.1).

Very little is known about the habitat or ecological conditions in these peripheral glacial refuges, including their exact locations. On a local scale, ice movements and shifting glacial margins would have changed the locations of meltwater impoundments. The weight of the ice sheets depressed the landscape, so that water draining downhill would have been dammed by the glaciers themselves (Pielou, 1991). These periglacial aquatic habitats, which were both dammed and fed by the ice sheets, have no parallel today. Pielou (1991) gives an excellent description of ice-dammed lakes to the south of the glaciers, with icebergs and deep, cold water next to the ice walls, gradually becoming

shallower to the south. These proglacial lakes probably stratified in summer, and received a variety of substrates from rock flour to boulders from the ice and meltwater. As a result, these lakes may have contained a variety of habitats that supported diverse aquatic communities. Although lake trout probably thrived under these conditions, they were nonetheless confined to a small number of fringe habitats or regional metapopulations for tens of thousands of years during each glaciation (Bailey and Smith, 1981).

As the glaciers retreated at the end of each glacial cycle, huge volumes of meltwater were released, creating giant lakes that dwarfed any lake that exists today. These lakes were only temporary, however, and constantly changed their size, shape, and location in response to the retreating ice (Dyke and Prest, 1987b). As the glaciers receded and the newly exposed landscape rose up through isostatic rebound, the lakes followed the retreating glacial margins. Further retreat uncovered progressively lower drainage outlets, often causing dramatic drainage events and emptying or connection of water bodies (Mandrak and Crossman, 1992). The size, mobility, and interconnectedness of these proglacial lakes provided unprecedented opportunities for dispersal and colonization of the newly exposed landscape. These postglacial drainage events permitted movement of lake trout over hundreds and perhaps thousands of kilometers, potentially within a single generation.

Ecological conditions within the proglacial lakes changed considerably over time and may have varied significantly within each lake as well. For example, the Champlain Sea — a marine incursion of the St. Lawrence Lowlands between 11,800 and 8800 years ago — underwent dramatic ecological change, going from a fresh, meltwater lake (glacial Lake Vermont) to an inland sea to fresh again (Lampsilis Lake) in just a few thousand years (Dyke and Prest, 1987a; Pielou, 1991). There is also some evidence for spatial variation in habitat conditions within the major lakes, which is not surprising considering their enormous sizes. Thermal gradients, glacial till, and varying depth as a result of crustal deformation may have effectively segregated species within these lakes based on their ecological requirements.

The huge volumes of cold-water habitat and diverse prey community would have been ideal for lake trout, and it may be assumed that lake trout populations expanded rapidly in these proglacial habitats. As the glaciers continued to retreat northward, new drainage outlets were exposed, which enabled the meltwater lakes to drain over newly deglaciated terrain. This provided new connections and colonization opportunities among the proglacial lakes but also decreased the remaining habitat volume. As the volume of meltwater declined with continued glacial retreat, the proglacial lakes gradually disappeared, leaving most of the modern drainage systems in place by about 5000 to 6000 years ago (Dyke and Prest, 1987a).

Most of the present lake trout lakes on the Shield began as basins excavated by the glaciers. Many of these depressions were covered by glacial lakes, which facilitated extensive colonization. Other basins that were isolated from the large glacial lakes provided reduced opportunities for colonization. As a result, the timing and extent of colonization were highly variable and strongly influenced by lake elevation, distance from source pools (proglacial lakes), and type of access (lake source, outlet, postglacial connections) (Mandrak, 1995). As a result of their different origins and histories, lakes on the Shield were isolated for varying lengths of time, with considerably variable colonization opportunities. Lakes covered by proglacial meltwaters were likely colonized by more species and by greater numbers within species than uncovered lakes, leading to variation in the composition and size of the founding gene pools and assemblages. Conversely, areas that were not covered by the meltwater lakes had reduced colonization opportunities, which led to lower species diversity, smaller founding numbers, and reduced biodiversity at community, population, and genetic levels. As water levels dropped and

colonization opportunities ended, the immigrant populations and assemblages were forced to adapt to local abiotic and biotic conditions in the diverse mosaic of smaller inland lakes that exists today.

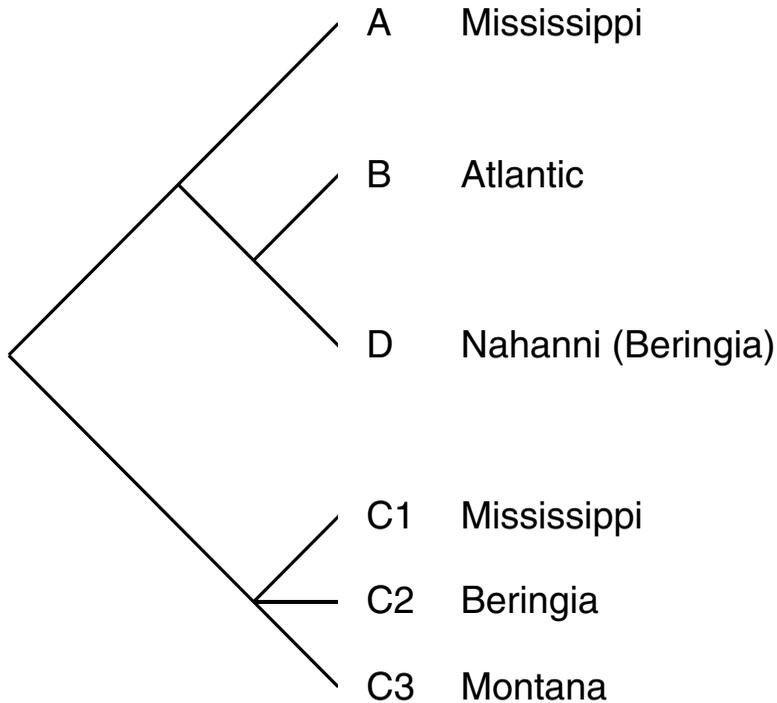
### *Glacial refugia and historical genetics: peering into the past*

The number and locations of refugia used by lake trout during the last (Wisconsinan) glacial event have been debated for half a century. The many, often-conflicting views have been summarized elsewhere (Martin and Olver, 1980; Crossman and McAllister, 1986; Wilson and Hebert, 1996, 1998) and need not be repeated here. The debate over the species' Quaternary history has largely been resolved by recent genetic evidence, which indicates that lake trout colonized their modern range from multiple refugia. Ihssen et al. (1988) detected two genetic groups of lake trout in Ontario and Manitoba based on allozyme data, which they interpreted as being Mississippian and Atlantic in origin. In addition, they inferred a third, distinct source for several lake trout populations in the Haliburton area of eastern Ontario (Ihssen et al., 1988). Analysis of mitochondrial DNA (mtDNA) among eastern hatchery strains similarly revealed three distinct lineages, which were interpreted as having Atlantic, Mississippian, and Beringian origins (Grewe and Hebert, 1988). Geographic surveys of mtDNA variation among native lake trout populations across the species' range confirmed the existence of multiple refugial groups (Wilson and Hebert, 1996, 1998). In addition to the three major lineages identified by Grewe and Hebert (1988), genetic and geographic substructure within these lineages suggested their dispersal from multiple glacial refugia (Figure 2.2; Wilson and Hebert, 1996, 1998). Based on the geographic distribution of the different mtDNA lineages, it appears that lake trout survived the Wisconsinan glaciation in at least six different refugia: two Beringian, two Mississippian, one Atlantic, and one in southern Alberta or northern Montana (Wilson and Hebert, 1996, 1998). The postglacial scenario described here largely relies on these latter studies while also drawing on data from earlier studies and complementary sources (Dyke and Prest, 1987a,b; Mandrak and Crossman, 1992).

Although much of the species' genetic history and diversity has undoubtedly been lost because of prehistoric (Pleistocene) events, the mode and tempo of genetic differentiation among the different lineages was largely influenced by the timing and extent of glacial cycles. The mtDNA C lineage mostly likely diverged from other lake trout during the mid-Pleistocene, at least 600,000 years ago (Figure 2.2; Wilson and Hebert, 1998). Separation of fish with A mtDNA types from groups B and D probably occurred roughly 300,000 years ago, and the latter two groups diverged during subsequent glaciations (Wilson and Hebert, 1998). Divergence within the C mtDNA group was probably caused by the displacement of ancestral populations into separate Beringian, Montana, and Mississippian refugia during the Wisconsinan glaciation, where they subsequently diverged (Wilson and Hebert, 1998). Similar processes within each glacial cycle (population displacement and subdivision by advancing glaciers, allopatric divergence in separate refugia, and subsequent expansion/recolonization) were probably responsible for much of the geographic genetic structure that exists among lake trout populations today.

### *Postglacial dispersal*

The major mtDNA lineages show clear differences in their geographic distribution despite considerable overlap in some regions (Figure 2.3). Populations in Quebec, eastern Ontario, the maritime provinces, and New England were primarily colonized by lake trout from an Atlantic refuge, with some Atlantic fish reaching as far west as Lake Superior and Lake Nipigon. Fish from two Mississippian sources (lineages A and C1) colonized areas south



**Figure 2.2** Simplified cladogram showing *S. namaycush* mitochondrial DNA lineages (A–D) detected by Wilson and Hebert (1996, 1998) and their association with glacial refugia during the most recent glaciation. Branch lengths are not proportional to genetic divergence among lineages.

of the Great Lakes, virtually all of Ontario, parts of Quebec, and northwestward through central Canada to Great Slave Lake. Lake trout from two separate Beringian refugia dispersed south and east but primarily contributed to areas west of the Canadian Shield. For southern Shield lakes, Beringian lake trout contributed to populations in western Ontario and Quebec as well as the upper Great Lakes. Lake trout from the Montana refuge also made minor contributions to western Ontario populations, but the Mississippian and Atlantic refugia were the major contributing sources for establishing populations in most of the study area (Figure 2.3).

The detailed geologic record left by the glaciers and proglacial lakes has enabled the reconstruction of postglacial drainage and colonization events (Figure 2.4; see also Mandrak and Crossman, 1992). Fish communities in the study area were greatly influenced by the formation of giant proglacial lakes in and near what is now the Great Lakes basin between 14,500 and 7900 years ago (Dyke and Prest, 1987a; Mandrak and Crossman, 1992). Lake Agassiz, which lasted for most of this period, covered much of Manitoba and large portions of Saskatchewan, North Dakota, Minnesota and Ontario during its existence, providing dispersal and colonization opportunities for many species that were present in the Mississippian and Missourian refugia (Teller and Clayton, 1983; Mandrak and Crossman, 1992).

Lake Agassiz drained southward into the Mississippi basin, briefly to the northwest, then southeastward into the Superior basin, and finally eastward into Lake Barlow-Ojibway (Mandrak and Crossman, 1992). Lake Barlow-Ojibway extended across northeastern Ontario and northwestern Quebec, and drained into the Ottawa River before abruptly emptying into James Bay 7900 years ago (Dyke and Prest, 1987b). A series of proglacial

and glacial lakes also drained into Lake Agassiz from the west, facilitating immigration of lake trout from western refugia (Wilson and Hebert, 1998).

The fossil evidence suggests that lake trout were able to closely follow the retreating glacial margins: the species was present in northern Wisconsin (Hussakof, 1916) 12,500 to 16,000 years ago (Lindsey 1964) and in eastern Ontario approximately 10,000 years ago (Gruchy, 1968, in Crossman and McAllister, 1986). This close connection among lake trout movements, glacial retreat, and proglacial lake positions and connections is also supported by the genetic data (Wilson and Hebert, 1996, 1998). Colonization of the study area by lake trout with Mississippian and Atlantic origins occurred initially through glacial lakes in the lower Great Lakes basin, roughly 14,000 to 13,500 years ago (Wilson and Hebert, 1996). Although dispersal from the Atlantic refuge may have been hindered by the Champlain Sea, eastern lake trout were probably able to effectively colonize southern Shield lakes by 10,000 years ago (Wilson and Hebert, 1996). A series of proglacial lakes (Lakes Peace, McConnell, Agassiz, and Barlow-Ojibway) extending from the Yukon southeast through to Quebec allowed colonization by lake trout with Atlantic, Beringian, Mississippian, and, to a lesser extent, Montanan affinities (Wilson and Hebert, 1996, 1998; [Figure 2.4](#)). Lake trout from these western refugia did not reach the Canadian Shield until 9500 years ago (Wilson and Hebert, 1996). It is possible that these groups did not make greater contributions because of early colonization by Mississippian and Atlantic fish (Wilson and Hebert, 1996, 1998). Early populations would have expanded rapidly, creating a strong priority effect. Alternatively, isolation in separate refugia may have resulted in differences in fitness among lineages under varying conditions, although this has not been tested.

### *Secondary contact among refugial groups*

Secondary contact among the different refugial groups occurred throughout the central portion of the species range, particularly within areas covered by the proglacial lakes ([Figures 2.3](#) and [2.4](#)). In the principal study area, contact was most extensive between the Mississippian and Atlantic refugial groups, with both lineages occurring through southern Quebec and Ontario as well as northern New York State (Wilson and Hebert, 1996).

This extensive contact and interbreeding among refugial groups accounts for some disagreements or conflicts among earlier studies of lake trout postglacial history. This is clearly illustrated by previous morphologic analyses: although differences among geographic populations were recognized by Lindsey (1964) and quantified by Khan and Qadri (1971), the extensive contact among refugial groups prevented discrimination of postglacial history among most populations examined (Crossman and McAllister, 1986). It is also possible that adaptation to local conditions resulted in morphologic differentiation, further confounding historical analyses.

Other data sources also show evidence of secondary contact among refugial groups. The parasitic nematode *Cystidicola stigmatura* uses lake trout and the opossum shrimp *Mysis relicta* as its primary and alternate hosts and occurs in many lake trout populations in Ontario and southwestern Quebec (Black, 1983). Although originally used to infer dispersal from a Mississippian refuge (Black, 1983), the distribution of *C. stigmatura* likely also reflects colonization events by other lake trout that came into contact with infected Mississippian-origin hosts. Mixed-origin ancestry of Shield lake trout populations was also shown by Ihssen et al. (1988) using allozyme data. Although their data were initially interpreted as showing the allopatric distribution of lake trout from Atlantic versus Mississippian refugia (Ihssen et al., 1988), it actually provides detailed information on the extent of two contact zones in Ontario. The majority of populations surveyed east of 82°W show shared ancestry from Mississippian and Atlantic fish, whereas Atlantic-refuge fish



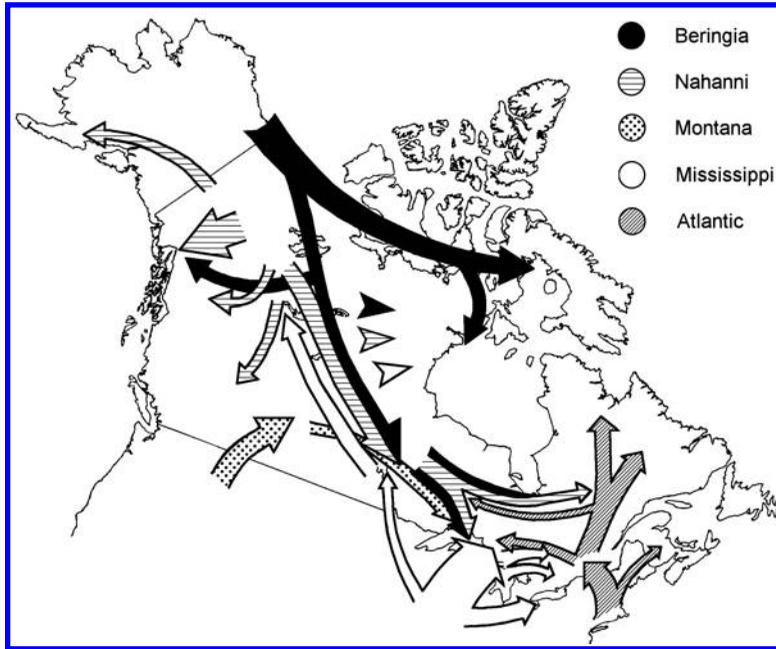
**Figure 2.3** Geographic distributions of *S. namaycush* refugial groups, as evidenced by distribution of mitochondrial DNA lineages (modified from Wilson and Hebert 1996, 1998).

are largely absent from more western populations (Ihssen et al., 1988). Rather than representing purely Mississippian fish, however, these western populations resulted from contact of Mississippian lake trout with those from the three western refugia (Figures 2.3 and 2.4). Ironically, the “glacial relict” populations of lake trout identified by Ihssen et al. near Haliburton, Ontario appear to be isolated descendants of Mississippian fish that did not come into contact with lake trout from other refugia (Wilson and Hebert, 1996), probably because of the brief time window for colonization as the glaciers retreated (Mandrak and Crossman, 1992).

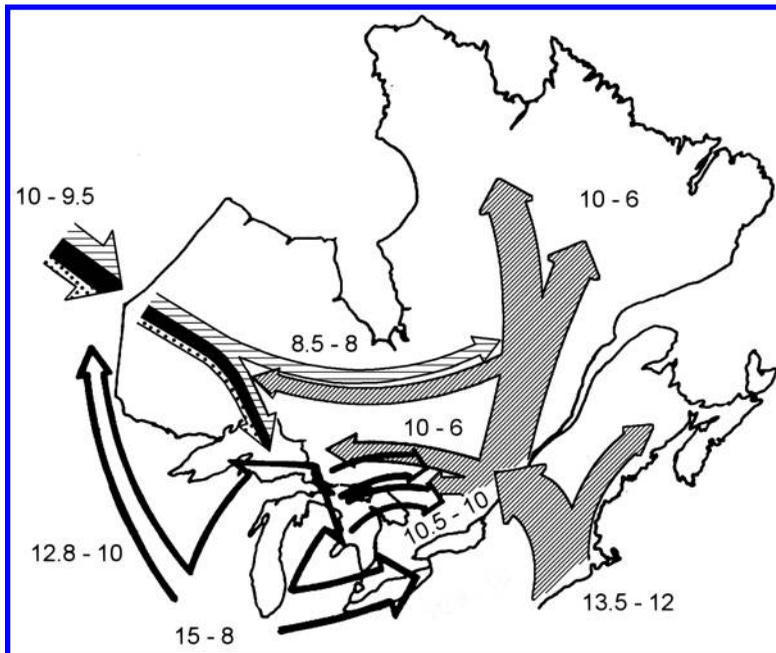
### *Genetic structure of modern populations*

Although historical events played a major role in structuring the genetic and phenotypic diversity of lake trout, populations in southern Shield habitats have been adapting to local conditions for over a thousand generations and now reflect the joint influence of historical and ecological factors. The low levels of genetic diversity that have been observed in lake trout (Ihssen et al., 1988; Wilson and Hebert, 1996, 1998) are similar to those observed in other species from northern climes (Bernatchez and Dodson, 1991; Billington and Hebert, 1991; Wilson et al., 1996; Bernatchez and Wilson, 1998). This is most likely a result of constrained or bottlenecked refugial populations during glaciations (Avise et al., 1984). In addition, it is possible that genetic diversity of lake trout has been further reduced by demographic constraints on populations such as large-bodied, long-lived top predators that generally live in low productivity environments.

Levels of diversity within populations are likely constrained by a combination of historical and ecological factors. For example, lake trout populations that occur within areas formerly covered by proglacial lakes have relatively high levels of mtDNA diversity as a result of secondary contact of refugial groups. Conversely, populations outside the



(a)



(b)

**Figure 2.4** Dispersal of lake trout from glacial refugia during the late Pleistocene and Holocene (18,000 years ago to the present). (a) Recolonization of the species range; (b) timing of colonization events in the principal study area. Modified from Wilson and Hebert (1996, 1998).

former lake borders have very low levels of genetic (mtDNA) diversity, which likely reflect the more restricted opportunities for colonization and smaller sizes of founding populations (Wilson and Hebert, 1998).

In addition, genetic diversity of populations may be limited by volume of suitable habitat (lake area vs. diversity) and habitat age (time since deglaciation vs. diversity). This is largely speculative, although Ihssen et al. (1988) observed a significant correlation between lake area and the proportion of allozyme loci that were polymorphic in the resident lake trout population ( $p < 0.01$ ). Larger lakes in their survey also had more alleles per locus than did small inland lakes, although this may have been partly confounded by historical (colonization) factors. Ihssen et al. attributed their findings to population size effects, as large populations may be expected to contain greater genetic diversity than smaller populations.

Although many existing populations of lake trout have been in place for less than 10,000 years, there have been ample opportunities for local adaptation to occur. The areas of secondary contact among the different refugial groups contained huge potential for selection and local adaptation, as the coming together of lake trout that had been isolated and exposed to different ecological conditions for tens of thousands of years would have provided plenty of raw material for natural selection to act on. This would have been compounded as the different lineages began to interbreed, as their offspring would have possessed entirely new combinations of genes and adaptive abilities. Recent evidence that significant evolutionary change can occur in short ecological time spans in some species (Thompson, 1998) may indicate that selection and adaptation to local environments occurred within the first few centuries following colonization. This is supported by the residual genetic structure of lake trout in Lac des Chasseurs, Quebec, where the entire population carries an mtDNA haplotype that may have provided a selective advantage in the early stages of population formation (Wilson and Bernatchez, 1998).

There is anecdotal evidence for multiple locally adapted stocks within the Great Lakes, although many of these disappeared as lake trout stocks declined (Brown, 1981; Goodier et al., 1981). For populations in inland lakes, there is less evidence for local adaptation. It must be emphasized, however, that this lack of evidence reflects the different focus of past research efforts and the difficulties involved in measuring local adaptation, rather than the lack of local adaptation itself. Ecological data such as life history, growth rates, and spawning preferences certainly suggest that inland populations are well adapted to their particular surroundings (Martin and Olver, 1980). Most evidence of local adaptation is indirect, such as examples of native populations having higher fitness than stocked lake trout (described below). One clear example of local specialization was the subspecies *Salvelinus namaycush huronicus*, which was described by Hubbs (1929) from Rush Lake in northern Michigan. This dwarf subspecies or morph coexisted with normal lake trout by inhabiting deeper waters and living as a benthic feeder (Hubbs, 1929). In addition to being at most one-quarter the size of the more pelagic regular form, these fish had broader, blunt heads and large fins (Hubbs and Lagler, 1959). Hubbs (1929) also reported that *huronicus* spawned in mid- to late summer, at a depth of about 120 feet. Hubbs was of the opinion that the two forms did not interbreed and were very distinct ecologically. Sadly, this unique subspecies is now presumed to be extinct (Hubbs and Lagler, 1959).

There is surprisingly little evidence dealing with adaptive variation of lake trout populations from small inland lakes despite abundant anecdotal data about individual populations. Given the diverse history, sources, and length of isolation of many Shield lakes, however, adaptation to local conditions has most likely led to considerable genotypic and phenotypic variation among resident populations. Numerous color variants have been identified in Shield lake trout populations, including black fins (e.g., Redstone Lake) and pale or dark background coloration (e.g., Lost Dog Lake and Canisbay Lake in Algonquin Park). One unique population that is both visually and genetically distinct from neighboring populations is Kingscote Lake in southern Algonquin Park: lake trout native to

this lake lack any spotting pattern and have a uniform silvery-gold body coloration (C. Wilson, unpublished data). In general, however, it would be inadvisable to assign too much importance to color variants because coloration of lake trout may be influenced by diet (Scott and Crossman, 1973; Martin and Olver, 1980). Greater variability is exhibited in other morphologic characteristics such as pyloric caecae and head morphology (Martin and Olver, 1980; P. Ihssen, Ontario Ministry of Natural Resources, unpublished data). It is likely that lake trout populations exhibit substantial genetic variation at both neutral marker systems and functional gene loci as the result of their varying histories and subsequent adaptation. Identifying and assessing the significance of potentially adaptive genetic diversity both within and among populations is an urgent need for both research and management.

In contrast to other salmonids, lake trout show very little tendency to diversify into specialized sympatric morphs or subspecies, although the Rush Lake *S. namaycush huronicus* and the siscowet, *S. namaycush siscowet*, are notable exceptions. Interestingly, mtDNA from at least four refugial groups has been observed in siscowet, indicating that this morph has evolved from mixed origins within the last 14,000 years, since the last glacial retreat (Burnham-Curtis, 1993; Wilson and Hebert, 1996, 1998). As an aside, it is worth noting that both examples of subspecific differentiation in lake trout come from extremely deep lakes that may allow for vertical partitioning of predator niches. It may be that what are generally considered normal conditions for lake trout (cold, low productivity, well-oxygenated lakes) provide stable ecological environments that limit or constrain ecological diversification and differentiation within the species.

For many years it was thought that lake trout had preprogrammed developmental tendencies for piscivory or planktivory, and many populations were classified as large-growing (piscivorous) or small (planktivory). The contrast between lake trout in Lake Opeongo and those in Lake Louisa in Algonquin Park provided a widely touted example of this (Martin and Olver, 1980). Recent data, however, indicate that either feeding/growth type may be expressed by the same population under different circumstances. Using stable isotope analysis, Vander Zanden et al. (1999) demonstrated that formerly piscivorous lake trout populations switched to planktivory after their lakes were invaded by rock bass.

Although lake trout have been intensively studied for decades, recent studies may indicate that we do not yet understand its ecological niche. The strong historical focus on Great Lakes populations has created a perception of lake trout as having narrow ecological tolerances for ecological factors such as temperature and oxygen levels (e.g., Behnke, 1972). Work done on lakes in Ontario's Experimental Lakes Area, however, has demonstrated that thermal characteristics of utilized habitats can vary considerably among lakes (Sellers et al., 1998). Similarly, Snucins and Gunn (1995) have shown that lake trout may have adaptive behavioral mechanisms and thermal tolerances that do not fall within stereotypic confines. An intriguing possibility is that Great Lakes and inland lake trout have become qualitatively different organisms over the past 10,000 years as a result of divergent selective and evolutionary trajectories despite their recent (in evolutionary time) shared history. If so, a great deal of what we think we understand about lake trout biology may need to be revisited. It may also be that the historical niche of lake trout in inland lakes was broader than we now recognize but that most "unusual" populations such as those described above disappeared soon after human colonization because of exploitation and eutrophication. Models that attempt to describe the niche and ecological characteristics of lake trout, such as Ryan and Marshall (1994) and Shuter et al. (1998), should broaden our understanding and provide greater appreciation for the species' adaptive abilities.

## *Species interactions and anthropogenic disturbances*

The close relationship between the distribution and biology of lake trout and Pleistocene glacial events highlights the interplay between historical and ecological processes in structuring modern populations. It should be noted that many communities or species assemblages in formerly glaciated areas are not in equilibrium in terms of species composition (Mandrak, 1995). Instead, many of these communities represent subsets of the species assemblages that were present just before the drainage or disappearance of the giant proglacial lakes. As communities became constrained to smaller and more restrictive environments, ecological suitability to the available habitats and interactions between species have resulted in the species assemblages now present.

Perhaps the best known set of species associations for lake trout is the deepwater “glaciomarine relict” community (deepwater sculpin, *Mysis relicta*, and several other invertebrate species) (Dadswell, 1974). More recently, Evans and Olver (1995), in an analysis of lake trout introductions among 183 inland populations, found that resident fish communities had a significant effect on the success or failure of introductions. Examination of the Ontario Ministry of Natural Resources Lake Inventory database has also suggested the possibility of both positive and negative associations between lake trout and a surprising number of species (N. Mandrak, unpublished data). Many of these potential relationships, however, have yet to be experimentally or critically examined. Recent alarming data from rock bass range expansions indicate that lake trout can be quite sensitive to community perturbations (Vander Zanden et al., 1999; J. Casselman, Ontario Ministry of Natural Resources, personal communication). In addition, data from recovering acidified lakes suggest that differential species response to recovery may prevent or deter lake trout from reassuming their role as dominant top predator (Mills et al., 2000). Resolving the biologic relationships between inland lake trout and co-occurring species continues to be a significant research and management need.

The geographic and genetic structures of existing lake trout populations have been strongly influenced by historical and ongoing human activities. Past activities such as overexploitation, habitat degradation, stocking, and transplants have undoubtedly had major impacts on the structure and fitness of native populations (OMNR, 1991). Although such activities sometimes resulted in short-term socioeconomic gains, they also regularly incurred significant long-term ecological and economic costs such as habitat rehabilitation, population reestablishment and restoration, and long-term stocking programs to compensate for the absence of naturally reproducing native fish. Given the lake trout’s ecological characteristics (top predator, long generation time, restrictive habitat requirements, etc.), we strongly recommend that the species be managed as conservatively as possible.

Of the major impacts that humans have had on lake trout populations (overexploitation, habitat loss/degradation, species introductions, and stocking), stocking has perhaps had the most insidious effect. Although each of the other factors has long been known to cause populations to disappear, stocking has only recently been recognized as having the potential to do the same (Evans and Willox, 1991). The luxury of having native populations with no stocking history is becoming scarce, and realistic management decisions must be made in a complex multiuser environment (Waples, 1991). Stocking has and will continue to be a potent management tool for a variety of purposes (Powell and Carl, this volume). For the dwindling number of native lake trout populations on the Shield, however, it carries considerable genetic risks, particularly in small lakes where the native population may have been progressively fine-tuned to local conditions over literally hundreds or thousands of generations. It is also worth noting that these same populations may be less adaptable than when they were first founded, as they no longer have a massive gene pool (mixed-origin founding population) from which to begin.

## Research needs

Many important questions remain to be addressed, such as potential fitness differences between populations and/or ecotypes under different conditions. Some particular knowledge gaps that need to be filled are to:

- Characterize the genetic structure and diversity of Boreal Shield populations to assess effective population sizes and historical demographics from lakes of different sizes and ecological attributes
- Build a “genetic map” of lake trout populations in high-use areas to identify native, mixed, and hatchery populations in order to establish mixed-use management plans that balance conservation with resource use
- Assess the adaptive potential of populations from different histories and habitat sizes in terms of plasticity in life history traits, growth and maturation rates, thermal tolerance, etc.
- Assess the effects of exploitation and/or other anthropogenic stressors on long-term diversity and viability of inland lake trout populations

## Conclusion

The long-term sustainability of wild lake trout populations requires that we conserve not only enough fish to catch but enough that populations can continue to evolve and adapt to future climatic and ecological conditions. The preservation of resident biodiversity is essential for ensuring the long-term viability of populations as well as maintaining their heritage value. This is particularly important for deepwater species such as lake trout, where isolated Shield populations are unlikely to be rescued or rejuvenated by immigration from other lake populations (Meffe, 1995). Given the species’ ecological vulnerability, lake trout management must be governed from the perspective of resource health rather than being harvest-oriented. With changing times, this has largely been achieved in most of the jurisdictions within the Boreal Shield, but continuing angler demands, species invasions, and decreasing habitat quality and quantity will continue to make this a significant challenge.

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