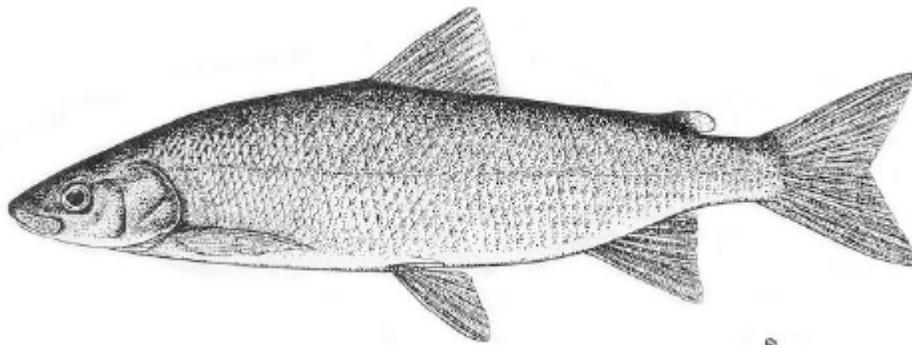


COSEWIC Special Report
Designatable units at an appropriate scale

for the

Lake Whitefish
Coregonus clupeaformis

in Canada



prepared for

**COMMITTEE ON THE STATUS OF ENDANGERED
WILDLIFE IN CANADA**

By

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COSEWIC
Committee on the Status
of Endangered Wildlife
in Canada



COSEPAC
Comité sur la situation
des espèces en péril
au Canada

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EXECUTIVE SUMMARY

The Lake Whitefish (*Coregonus clupeaformis*, Mitchill) is a broadly distributed freshwater fish in Canada. It is referred to as the '*Coregonus clupeaformis* species complex' in recognition of taxonomic problems existing across the country. The objective of this special report was to carry out an evaluation of designatable units (DUs) for *Coregonus clupeaformis* in Canada. This report examines the species complex with respect to genetics, ecology, morphology, distribution, range disjunction, as well as presence in different biogeographic zones for over eighty populations. These sources of information were used to evaluate and identify putative DUs (PDUs) under COSEWIC's guidelines for recognizing DUs below the species level.

Thirty two DUs were identified in the Lake Whitefish species complex. The Eurasian Lake Whitefish (*Coregonus lavaretus*) was identified as a distinct taxonomic entity and designated as a DU. Seven limnetic and benthic sympatric species pairs were recognized as distinct biological species and designated as 14 DUs. Three additional limnetic and benthic species pairs were given provisional status (6 DUs). Lake Whitefish populations were recognized as encompassing five genetically distinct groups reflecting geographic isolation during the Pleistocene glaciations. National Freshwater Biogeographic Zones (NFBZs) that capture these significant major phylogeographic groupings of the species complex were identified as 11 DUs. These PDUs will require closer inspection and this report should be considered as a first approximation before COSEWIC assessments can be undertaken.

I. GENERAL INTRODUCTION

Coregonines are cold-water fishes common throughout the Holarctic in North America, Europe and Asia (Lindsey and Woods 1970). They support important commercial and recreational fisheries and are the focus of significant worldwide aquaculture operations (Eckmann et al. 1996). Coregonines are a dynamic example of evolutionary change, with numerous species, sub-species, and forms evolving during and after the Pleistocene glaciations throughout their entire distribution (e.g., Kirkpatrick and Selander 1979, Morin et al. 1982, Bodaly et al. 1991, Vuorinen et al. 1993, Bodaly et al. 1994, Svaerdson 1998, Turgeon et al. 1999, Bernatchez 2004, McDermid et al. 2005, Ostbye et al. 2006). Their broad distribution and successful colonization of lake and river environments following the retreat of glacial ice has contributed to the significant interest of Coregonines as a model system for understanding evolution. However, the broad distribution and dynamic evolutionary histories of many coregonine species have also resulted in inconsistent taxonomies and disagreements in the nomenclature, commonly referred to as the 'Coregonine problem' (Svårdson 1957, 1965 Lindsey et al. 1970, Scott and Crossman 1973, Nikolsky and Reshetnikov 1970, Douglas et al. 2005, McPhail 2007).

The Lake Whitefish (*Coregonus clupeaformis*) is a broadly distributed freshwater Coregonine in Canada (Scott and Crossman 1973). The species is the most valuable commercial freshwater fish in the country (Bodaly 1986, DFO 2005) and has been studied extensively as an important aquaculture resource (Flüchter 1980, Bodaly 1986, Drouin et al. 1986, Zitzow and Millard 1988, Harris and Hulsman 1991, Champigneulle and Rojas-Beltran 1990). Variation among populations across its distribution has resulted in a confusing taxonomic picture referred to as the '*Coregonus clupeaformis* complex' (McPhail and Lindsey 1970, Scott and Crossman 1973). An explicit evaluation of designatable units (DUs) is therefore required for *Coregonus clupeaformis* within Canada before COSEWIC assessments can be undertaken.

The objectives of this special report were to: (1) assess Canadian Lake Whitefish populations to determine if they meet the guidelines for DUs, 2) for each PDU, assess the criteria that substantiated the delineation, 3) when an assessment cannot be made, determine the information lacking that compromised the identification, and (4) synthesize overall results in a context that facilitates the evaluation of various conservation scenarios towards ultimately adopting appropriate DUs for use in subsequent status assessments for Lake Whitefish as a whole.

The following methodology was used to identify DUs. First, an extensive Lake Whitefish literature was reviewed for relevant information about the species with respect to genetics, ecology, morphology, distribution, range disjunction, and presence in different biogeographic zones. A comprehensive list of the current Canadian Lake Whitefish populations requiring DU consideration was generated from this literature (Table 1). When lakes were sampled multiple times, data from all studies were integrated towards assessing DU status (e.g., multiple DNA markers in phylogenetic studies). These populations were then applied to a key for assessing PDUs (Taylor 2006), with criteria based on those in the COSEWIC Guidelines for Recognizing DUs below the species level (<http://www.cosewic.gc.ca/eng/>). The key was applied as a series of questions to attempt identification of DUs that have not yet been proposed and to establish whether the identification of Lake Whitefish DUs is necessary within a complex of populations, i.e., evaluated for DU status at one time. The final result is a DU decision chart and summary illustrating the proposed DUs for the Lake Whitefish species complex in Canada (Table 1, Figure 2).

Table 1. Lake Whitefish populations sampled in Canada and relevant regions of the United States of America. ID: locations (see Figure 2). Site: river or lake with provincial/state abbreviations (AK = Alaska, YT = Yukon Territory, NT = Northwest Territory, NU = Nunavut, BC = British Columbia, AB = Alberta, SK = Saskatchewan, MB = Manitoba, ON = Ontario, MI = Michigan, QC = Quebec, ME = Maine, NB = New Brunswick, NS = Nova Scotia. Taxonomic entity: presence of the *C. lavaretus* DU from Section 1 of the key. SP: presence of a species pair. PG: major phylogeographic groupings; B=Beringian, E=Eurasian, N=Nahanni, At=Atlantic, Ac=Acadian, and NA=not applicable. BZ: National Freshwater Biogeographic Zones (see Figure 2 for details). PDU: Putative Designatable Unit identification, see Figure 1 for complete list. Ref: citation for sampled populations.

ID	Site		Taxonomic entitv	SP	PG	BZ	PDU	Ref
1	Yukon R.	AK	<i>C. lavaretus</i>		B, E	6	1,23	5, 6
2	Minnesota L.	AK	<i>C. lavaretus</i>		B, E	n/a		5, 6
3	Chatanika R.	AK	<i>C. lavaretus</i>		B, E	n/a		5, 6
4	Davis L.	YT			B	6	23	7
5	Hanson L.	YT			NA	6	23	12
6	Tatchun L.	YT			B	6	23	3
7	Squanga L.	YT	<i>C. lavaretus</i> (limnetic)	Y	B, E	6	1,2-3,23	3, 5-7
8	Little Teslin L.	YT	<i>C. lavaretus</i> (lim + ben)	Y	B, E	6	1,4-5,23	5, 6
9	Dezadeash L.	YT	<i>C. lavaretus</i> (limnetic)	Y	B, E	6	1,6-7,23	7, 3
10	McClintock L.	YT			B	13	22	7
11	Aishihik L.	YT			B	6	23	5 – 7
12	Kluane L.	YT			B	6	23	7, 3
13	Margaret L.	YT			B	13	22	7
14	Dease L.	BC			B	13	22	7
15	Finlayson L.	YT			B	13	22	7
16	Frances L.	YT			B	13	22	3, 7
17	Simpson L.	YT			B	13	22	7
18	Watson L.	YT			B	13	22	3, 7
19	Wheeler L.	BC			B	13	22	7
20	Toobally L.	YT			B,N	13	22	7
21	Crooked L.	BC			B,N	13	22	7
22	Upper Liard R.	BC	<i>C. lavaretus</i>		B,N,M	13	22	7
23	Fisherman's L.	NT			N	13	22	7
24	Bovie L.	NT			N	13	22	7
25	Seaplane L.	NT			N	13	22	7
26	Divide L.	NT			N	13	22	7

ID	Site		Taxonomic entitv	SP	PG	BZ	PDU	Ref
27	Little Doctor L.	NT			N	13	22	7
28	Crooked R.	BC			B or N	13	22	5, 6
29	Quesnel L.	BC			NA	11	24	2
30	Fraser L.	BC			N	11	24	7
31	Aleza L.	BC			N	11	24	7
32	Lac la Hache	BC			N	11	24	3, 7
33	Williams L.	BC			N	11	24	3, 7
34	Summit L.	BC			N	11	24	3, 7
35	McLeod L.	NT			N	11	24	3, 7
36	Moberly L.	BC			N	13	22	3, 7
37	Utikuma L.	AB			N	13	22	7
38	Talbot L.	AB			N	4	25	3, 7
39	Lesser Slave L.	AB			M	13	22	7
40	Athabasca R.	SK			M	13	22	7
41	Athabasca L.	AB			M	13	22	7
42	Great Slave L.	NT			M	13	22	3, 5 – 7
43	Wabamum L.	AB			N, M	4	25	3, 5 – 7
44	Waterton L.	AB			M	7	26	7, 3
45	Fort Simpson	NT			B,N,M	13	22	7
46	Fort Good Hope	NT			B,N,M	13	22	7
47	East Channel	NT			B,N,M	13	22	7
48	Arctic Red R.	NT			B, M	6	23	5, 6
49	Mackenzie Delta	YK	<i>C. lavaretus</i>		B,N,M	13	22	7
50	Fort McPherson	NT			M	13	22	5, 6
51	Cox L.	NU			B,N,M	13	22	7
52	McEvoy L.	YT	<i>C. lavaretus</i>		B	13	1,22	5, 6
53	Jack Fish L.	SK.			M	4	25	5, 6
54	South Indian L.	MB			M	5	27	5, 6
55	Lake Superior	ON		Y	M	10	28	5, 6
56	Lake Michigan	MI			M	10	28	5, 6
57	Lake Michigan	MI			M	10	28	5, 6
58	Lake Huron	MI			M	10	28	5, 6
59	Lake Ontario	ON			M	10	28	5, 6

ID	Site		Taxonomic entitv	SP	PG	BZ	PDU	Ref
60	Como Lake	ON		Y	M	10	16-17,28	5, 6
61	Res. Kipawa	QC			M	10	28	5, 6
62	Rupert R.	QC			M	3	29	5, 6
63	Eastmain R.	QC			M	3	29	5, 6
64	La Grande R.	QC			M	3	29	5, 6
65	Great Whale R.	QC			M	3	29	5, 6
66	Inukjuak R.	QC			M	2	30	5, 6
67	Povungnituk R.	QC			M	2	30	5, 6
68	Koksoak R.	QC			M	2	30	5, 6
69	Squaw L.	QC			M	2	30	5, 6
70	Altikamagen L.	QC			M	2	30	5, 6
71	Res. ManicV	QC			M	2	30	5, 6
72	Caniapiscau	QC			M	2	8-9,30	4, 8
73	Manicouagan	QC			M	9	10-11,31	4, 8
74	Outardes II	QC			M	9	12-13,31	4, 8
75	St – Lawrence R.	QC			M	10	28	5, 6
76	L. Champlain	QC			M	9	31	5, 6
77	L. St-Francois	QC			M	9	31	5, 6
78	East L.	QC		Y	Ac	9	20-21,31	8 – 10
79	L. Témiscouata	QC		Y	At, Ac	1	18-19,32	4 – 6, 8- 11
80	Spider L.	ME			At, Ac	n/a		5, 6
81	Musquacook L.	ME			At, Ac	n/a		5, 6
82	Cliff L.	ME		Y	At, Ac	n/a		4 – 6, 8 – 10
83	Grand L.	NB			Ac	1	32	5, 6
84	Mira River	NS			Ac	1	32	5, 6
85	Opeongo Lake	ON		Y	M	10	14-15, 28	5, 6

¹ Kennedy 1943, ² McPhail and Lindsey 1970, ³ Franzin and Clayton 1977, ⁴ Bernatchez and Dodson 1990, ⁵ Bernatchez and Dodson 1991, ⁶ Bodaly et al. 1991, ⁷ Foote et al. 1992, ⁸ Pigeon et al. 1997, ⁹ Lu et al. 1999, ¹⁰ Lu et al. 2001, ¹¹ Rogers et al. 2001, ¹² Scott and Crossman 1973

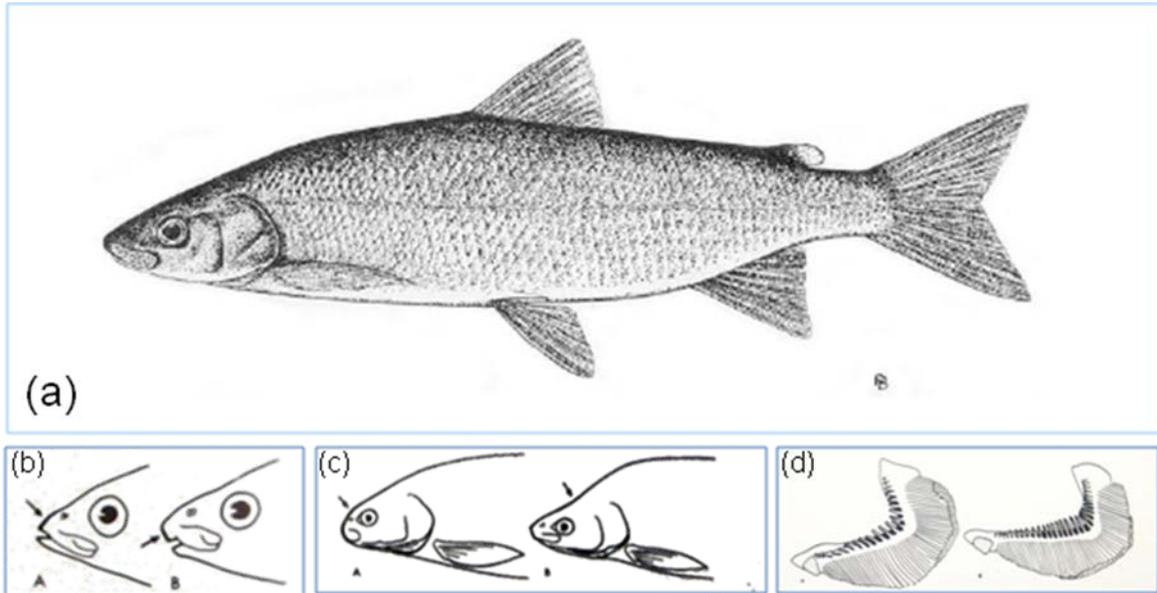


Figure 1. (a) Lake Whitefish (Scott and Crossman 1973) (b) the head of a cisco (left) versus the head of a whitefish (right) where the head of the jaw projects beyond, or is equal to, the upper jaw. In *C. clupeiformis*, the profile of the upper lip slopes backwards in line with the forehead. (c) Convex brow of a broad whitefish (*C. nasus* on left) versus the concave head profile of Lake Whitefish (*C. clupeiformis*, on right). (d) *C. nasus* gill raker (on left) with the longest gill raker measuring one-fifth the inter-orbital width and *C. clupeiformis* gill raker (on right) with the longest gill raker measuring more than one fifth the inter-orbital length. (Key and images modified from McPhail and Lindsey, Journal of the Fisheries Research Board of Canada, 1970)

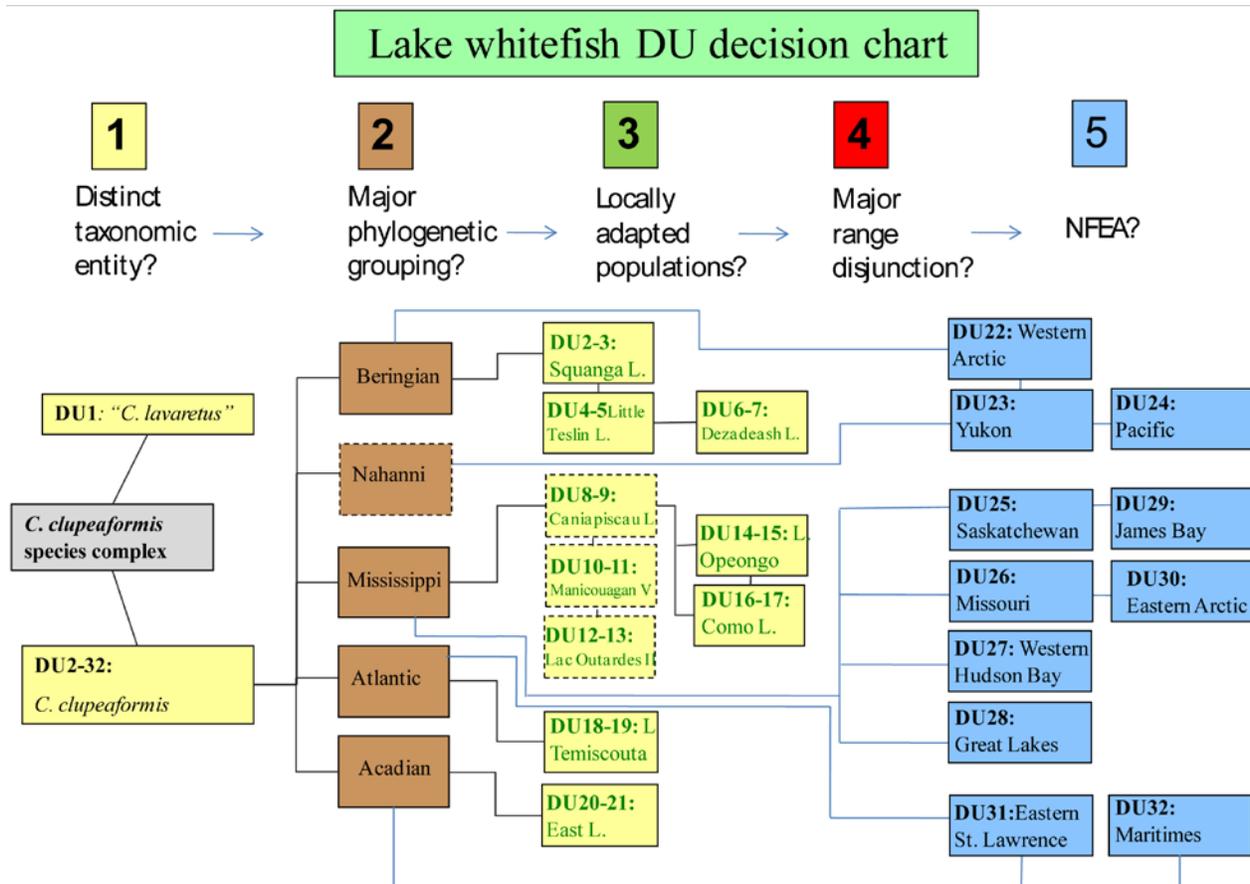


Figure 2. A Lake Whitefish species complex DU decision chart. The numbers on the top, from left to right, reflect the steps used in the key used to identify putative designatable units (DUs). The boxes show DUs identified for each of these steps. Lines connecting DUs reflect different stages of the decision process. For example, DU2-3 (Squanga Lake species pair) is connected to the Beringia DU as well as the Yukon NFEA DU. Dashed boxes and lines indicate provisional DU status. Species Pair DUs of Lake Whitefish are shown in yellow because the initial DU status designation occurred in stage 1 (see section 1.1), but was further supported in stage 3 of the key (local adaptation).

Specific cases of DUs will require closer inspection and therefore the key is considered as a first approximation. For instance, Taylor (2006) suggested that if a diagnostic character was identified in step 3 of the key, but was resolved after only limited sampling, DU status might be deferred or made provisional until the diagnostic nature of the trait was confirmed after more extensive sampling. Alternatively, if the presence of a DU was suspected based on inductive/deductive reasoning, but for which no direct evidence of distinction was available, that group may be given “provisional” or “deferred” DU status. In these cases, provisional is defined as a tentative DU status, reserved for populations that meet only some of the data requirements specified in the key. Deferred refers to a postponement in DU status, reserved for populations where the presence of a DU was suspected based on inductive/deductive reasoning, or no published data was available. At the end of each question in the key, evidence for DU status was summarized for use in a “Lake Whitefish Decision Chart” for reference (Figure 2).

Description and biology of Lake Whitefish

Lake Whitefish (Class: Actinopterygii, Order: Salmoniformes, Family: Salmonidae, Sub-family: Coregoninae, Genus: *Coregonus*, Species: *clupeaformis*, as the Greek name *clupeaformis* implies, are “herring shaped”, referring to their short head but elongate, laterally compressed body (Scott and Crossman 1973) (Figure 1a). Common names for the species include “le Grand Corégone” and “humpback whitefish” (McPhail and Lindsey 1970, Scott and Crossman 1973, Alt 1979). Lake Whitefish are silvery (but in some lakes can have a relatively dark green/brown dorsal surface) and attain an average length of 380 mm (Scott and Crossman 1973). They possess a single, soft dorsal fin plus an adipose fin, and have a scaly process at the base of each pelvic fin (McPhail and Lindsey 1970) (Figure 1a). They have 70 to 97 large, cycloid scales along the lateral line. An inferior mouth reflects an adaptation to bottom feeding and distinguishes Lake Whitefish from cisco species within the same genus (McPhail and Lindsey 1970, Scott and Crossman 1973, Figure 1b). Distinguishing characters from other closely related whitefish (e.g., broad whitefish, *Coregonus nasus*, Pallus, or Mountain Whitefish, *Prosopium williamsoni*, Pennant) include a concave, smaller profile of the head and a smaller ratio of maxillary length to interorbital width (Lindsey 1962, McPhail and Lindsey 1970, Scott and Crossman 1973, Figure 1c). The Lake Whitefish can typically be distinguished from the broad whitefish by its smaller size, longer gill rakers and a longer snout (Figure 1d).

Lake Whitefish prefer cold water (8 – 14 degrees Celsius) and spawn in the fall, with more northern populations generally spawning earlier (Scott and Crossman 1973, McPhail 2007). Females are deeper bodied than males, while males have significantly longer jaws and pectoral/pelvic fins (Lindsey 1963b, Casselman and Schulte-Hostedde 2004). Breeding males develop epidermal structures (tubercles) that protrude as sharp bumps from the scales and are located repeatedly along the dorsal and lateral sides shortly before their spawning season (Wedekind et al. 2001). Several species of benthic organisms make up the diet of Lake Whitefish, including copepods, cladocerans, chironomid larvae, amphipods, gastropods, and sometimes small fish (Brown and Taylor 1992, Davis and Todd 1998, Chouinard et al. 1996, Cucin and Faber 1985, Landry et al. 2007).

Distribution of Lake Whitefish

Coregonines (including whitefishes, vendace, ciscoes) are distributed over cooler regions of the northern hemisphere, reflecting both the species' preference for coldwater habitats as well as their dispersal ability. In Canada, the broad distribution of *Coregonus clupeaformis* extends from Yukon to Labrador. Lake Whitefish inhabit the lakes and rivers of every province except PEI and Newfoundland, extending southward into the New England and Great Lake States (USA) (Figure 3). The northern limit of its range is Victoria Island in the NWT near Cambridge Bay and the Arctic Archipelago. In these northern regions (e.g., Ungava, the Hudson Bay region, and Arctic Ocean drainages in the Northwest Territories, the species also enters brackish water (Scott and Crossman 1973). Collections from Canadian lakes have been extensive (Table 1, Figure 3). For

example, Bodaly et al. (1992b) report an impressive 119 lake and river populations sampled between 1968 and 1986. Scott and Crossman (1973) report over 166 locations known to inhabit the species in Canada and the United States. Genetic data have been collected from over 100 Canadian lakes and rivers, rendering this species uniquely informative as a model system reflecting the Canadian zoogeographic history of postglacial freshwater fish dispersal (Figure 3). This list is also by no means exhaustive, with many more bodies of water inhabited by native populations (see McPhail 2007).

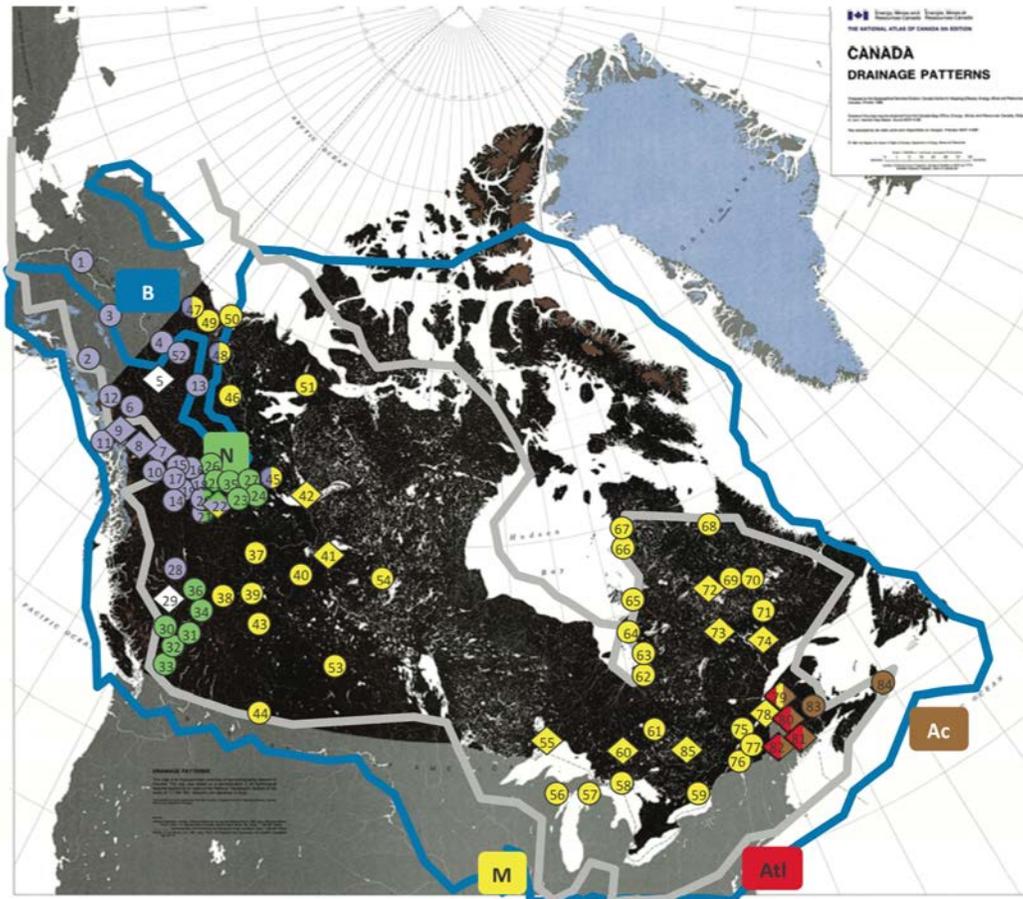


Figure 3. Distribution and phylogeography of Lake Whitefish in Canada. The grey line shows the overall distribution of the Lake Whitefish species complex while the blue line represents the maximum extent of glacial ice during the ice age (modified from Bernatchez and Dodson 1991). Locations of Lake Whitefish populations are colour coded according to their major phylogenetic groupings representative of their ancestral glacial refugia (see Section 2 of the key). Blue = Beringian, Green = Nahanni, Yellow = Mississippi, Red = Atlantic, Brown = Acadian. Locations of species pairs are labelled as diamonds. See Table 1 for details about the samples and Figure 2 for their status as putative DUs.

Additionally, there have been several instances of Lake Whitefish introductions into several lakes. For example, McPhail (2007) identified 20 introduced populations in southern British Columbia, of which nine failed. Most of the failures were in small lakes, while introductions into larger, deeper lakes appear to have been largely successful (e.g., Shuswap, Okanagan, Kootenay, and Arrow lakes) (McPhail 2007). This pattern of introductions has also been recorded in Ontario (Lasenby et al. 2001) and Nova Scotia (DFO 2006). Scott and Crossman (1964) also report an introduced population in Hogan's Pond, Newfoundland, originally from Lake Erie.

Taxonomy of Lake Whitefish

During the Pleistocene glaciation (1 800 000 to 12 000 years before present) Coregonines were isolated in meltwater lakes and rivers around the margins of ice in the northern hemisphere (Lindsey 1970, McPhail and Lindsey 1970). This extended period of allopatric isolation between populations in areas free of glacial ice led to significant levels of evolutionary divergence, complicating resolution of taxonomic relationships (Bernatchez and Wilson 1998, Reist et al. 1998). Moreover, morphological characters commonly used to describe the species are also highly subject to modification by the conditions under which fish develop, so the same population may appear quite different among lakes (Lindsey et al. 1970, Loch, 1974, Woodger, 1976, Lindsey, 1981, Sandlund, 1992). The broad distribution of the species has consequently led to the same Coregonine species having been given different names in North America, Russia, and Europe (McPhail and Lindsey, Lindsey 1988). For this reason, it has been argued that species names and descriptions remain tentative until more information is available across their distribution (McPhail and Lindsey 1970, McPhail 2007).

Phylogenetic studies have been largely successful in resolving the Coregonine tree at the species level (Bodaly et al. 1991, Bernatchez and Dodson 1991, Bernatchez et al. 1991a, Bernatchez and Dodson 1994). There are 28 extant species recognized in the sub-family Coregoninae. The major grouping of whitefishes in this family include three genera; *Stenodus*, *Prosopium*, and *Coregonus* (Reshetnikov 1988). Genetic data suggests that while *Prosopium* diverged in the order of 10 million years ago (mya) during the Miocene – early Pliocene period, *Stenodus* is more closely related sharing a common ancestor with *Coregonus* approximately 2.5 mya (Bernatchez et al. 1991a). The entire radiation of extant Coregonine species has been rapid, occurring during and since the Pleistocene glaciation dating back approximately 1.5 mya (Bernatchez et al. 1991a). Phylogenetic analyses based on different DNA markers have shown congruence in their findings with respect to branching patterns, suggesting that the Coregonine tree is an accurate representation of the evolutionary history of the sub-family Coregoninae. (Bodaly et al. 1991b, Bernatchez et al. 1991a)

One of the most complex nodes of the tree represents two widespread forms of Lake Whitefish in the northern hemisphere, *Coregonus clupeaformis* in North America and *Coregonus lavaretus* in Eurasia (Bodaly et al. 1991, Bernatchez and Wilson 1998, Reist et al. 1998, McPhail 2007). Several lines of evidence from phylogenetic analyses suggest that Beringia (Northwestern North America) was recolonized by populations of *Coregonus lavaretus* that dispersed extensively in Eurasia and into Beringia, and subsequently merged with an endemic Beringian whitefish group (Bodaly 1977, Bodaly et al. 1991, Bernatchez and Dodson 1994). However, two reproductively isolated populations, one Eurasian and one Beringian, persist in the region.

In North America, the Lake Whitefish was first described by Mitchill in 1818 as *Salmo clupeaformis* (from Lake Huron) (Koelz 1929, Lindsey et al. 1970, Scott and Crossman 1973). Three taxonomically described species currently fall within the *Coregonus clupeaformis* species complex; (*C. clupeaformis*, Mitchill; *C. pidschian*, Gmelin; and *C. nelsonii*, Bean) (Lindsey 1963a, McPhail and Lindsey 1970, Alt 1971, Lindsey 1988, Bean 1884). Details about the description, distribution, and PDU status of these additional species within the complex are described in section 1.1.1.

The taxonomic issues in whitefish are not unique to North American *Coregonus clupeaformis* complex. Indeed, taxonomic confusion also persists for *Coregonus lavaretus* in regions of Europe and Russia (Bodaly et al. 1994, Beaumont et al. 1995, Svaerdson 1998, Douglas et al. 2005). Several populations of *Coregonus lavaretus* in these regions exhibit phylogeographic patterns of reproductive isolation as well as ecological speciation similar to their counterparts in North America (Luczynski et al. 1995, Sandlund et al. 1995, Reist et al. 1998, Svaerdson 1998, Bernatchez and Wilson 1998, Bernatchez et al. 1999, McDermid et al. 2005, Ostbye et al. 2005, Ostbye et al. 2006). These studies suggest that similar ecological and evolutionary processes reported in *C. clupeaformis*, namely isolation during periods of glaciation followed by ecological opportunity in post glacial environments, have also resulted in cases of rapid population divergence in *C. lavaretus* (Ostbye et al. 2006). Consequently, the criteria used to assign DUs in *C. clupeaformis* may be useful for other Coregonine populations. This report seeks to identify designatable units at the appropriate level only in Canadian Lake Whitefish populations, therefore only taxonomic designations (past and present) for whitefish within the complex will be considered within this assessment.

II. KEY FOR ESTABLISHING DESIGNATABLE UNITS FOR COSEWIC

1. The putative designatable unit (PDU) is a distinct taxonomic entity or qualifies as a distinct biological species?

1.1. Taxonomic entities in the Lake Whitefish species complex

Lake Whitefish exhibit tremendous phenotypic variation in morphological and life history characteristics. Consequently, the species has been split into several distinct, albeit phenotypically based taxa as a result of these differences (McPhail and Lindsey 1970, Loch 1974, Woodger 1976, Lindsey and McPhail 1986, Lindsey 1988). Gill rakers have traditionally been the marker used to address taxonomy in most Coregonine populations (Lindsey 1981). As gill raker variation is heritable, it was thought to give generalized information about the genetic status of the population concerned (Svårdson 1957, Svårdson 1965). For example, North American members of the genus *Coregonus* that are not ciscoes (i.e., have fewer than 33 gill rakers and have the snout overhanging the tip of the lower jaw, Figure 1b) were deemed either broad whitefish, *Coregonus nasus*, (classified as having short gill rakers and a wide head) or “humpback” whitefishes, *Coregonus clupeaformis* (McPhail and Lindsey 1970). Despite the perceived utility of this morphological marker towards differentiating populations of whitefish, interpretations of *Coregonus* taxonomic classification have remained confusing, contributing to its general classification as a species complex (McPhail and Lindsey 1970, Woodger 1976, Alt 1979, Lindsey 1988). Below, species that remain taxonomically classified within the Lake Whitefish species complex are described. It is important to note that most of these species have been identified primarily on the basis of gill raker and other morphometric data. Thus, the current genetic and historical information that may support or refute their classification as a distinct biological species warranting DU consideration is also discussed.

1.1.1 *Coregonus lavaretus* and *Coregonus pidschian*

Lake Whitefish in northwestern Canada consist of some populations that colonized the lakes and rivers postglacially from Siberia. These Lake Whitefish, referred to as *C. lavaretus* (common name Alaska Lake Whitefish) and *C. pidschian* (common name Humpback Lake Whitefish) are routinely described as part of the *C. clupeaformis* species complex (low modal gill raker counts, 20-22, named by Bean 1788 as *Salmo pidschian* from the Ob River in Siberia) (Lindsey 1963a, Lindsey 1963b, Alt 1979, Page and Burr 1991, Mecklenberg et al. 2002, McDermid et al. 2005). The distribution of the Siberian Lake Whitefish extends westward at least as far as the Ob River in Siberia and possibly into Europe (Walters 1955, Bodaly et al. 1994, Politov et al. 1999, Politov et al. 2000). It is thought the Siberian Lake Whitefish lived in huge glacial lakes that persisted through most of Siberia during the Pleistocene (Denton and Hughes 1981, Lindsey and McPhail 1986) and were able to disperse to northwestern North America via Beringian land bridges that opened during glacial maxima (Lindsey and McPhail 1986).

Allozyme and mtDNA phylogeographic analyses have since demonstrated that populations originating from the Bering Sea and inhabiting northwestern Canada (and Alaska) are much more closely related to Eurasian populations of whitefish (*C. lavaretus*) than to any other North American populations (Bodaly et al. 1991b, Bodaly et al. 1994, Bernatchez et al. 1991a, Bernatchez and Dodson 1994, Sajdak and Phillips 1997). In fact, Bernatchez et al. 1991 found that *Coregonus pidschian* sampled from Siberia had mtDNA signatures identical or very closely related to those observed in *C. lavaretus* from Europe. Consequently, populations of *C. pidschian* described in Northwestern America are most likely conspecific with Eurasian *Coregonus lavaretus* and not *Coregonus clupeaformis*. If this is indeed the case then the name *C. lavaretus* (Linnæus 1758) should have priority over *C. pidschian* (Gmelin 1789).

Such observations have important consequences for our understanding of the Lake Whitefish species complex in Canada. Conspecific populations of *Coregonus pidschian* (currently part of the *Coregonus clupeaformis* complex) with *C. lavaretus* suggest that there are two distinct species of Lake Whitefish inhabiting northwestern North America, (*C. lavaretus/C. pidschian* in the upper Liard River and *C. clupeaformis* in Mackenzie River region, Figure 2) (Smith and Todd 1984, Sajdak and Phillips 1997, McPhail 2007). Recent point distributions in northwestern Canada reported that *C. lavaretus* primarily inhabits streams and rivers (see Table 1), while *C. pidschian* is primarily anadromous and distributed in coastal areas of the Northwest Territories, namely in the Mackenzie River system from the Albertan border north to the vicinity of Great Bear River (Sawatzky et al. 2007)

This Beringian taxonomic grouping, with close affinities to Eurasian populations of *C. lavaretus/C. pidschian* should be considered a DU under *C. clupeaformis* until a more thorough assessment can be made. Future assessments to resolve this DU will clearly require additional genetic and morphometric data (Table 1, Figure 2).

1.1.2 *Coregonus nelsonii*

C. nelsonii was described as distinct from *C. clupeaformis* due to different gill raker counts from Nulato on the Yukon River in northwestern North America (Bean 1884, Lindsey 1963a). Lake Whitefish classified as *nelsonii* have now been reported for most of the Yukon River, Paxson Lake, the Copper River system, and sporadically around the coast of northern Alaska, in the Mackenzie River delta and in the Anderson River. Because of the intermediate number of gill rakers, *C. nelsonii* has also been hypothesized to represent hybrid populations between *C. clupeaformis* and *C. pidschian/C. lavaretus* (McPhail and Lindsey 1970). The most recent genetic evidence suggests that *Coregonus nelsonii* is likely conspecific with the true Beringian Lake Whitefish glacial race (Bernatchez et al. 1999, McPhail 2007) and therefore does not comprise a distinct taxonomic group in this context (but see Beringian glacial race DU below).

1.1.3 *Coregonus huntsmani*

The endangered, anadromous Atlantic whitefish, *Coregonus huntsmani*, inhabits the Tusket and Petite Riviere watersheds in Nova Scotia. The terminal mouth of the Atlantic whitefish suggests that it is not the progenitor of *C. clupeaformis* (McPhail and Lindsey 1970, but see Figure 1a). Lateral line scale numbers differs (average of 94 in Atlantic whitefish versus an average of 77 in Lake Whitefish, as does the number of vertebrae (average of 65 in Atlantic whitefish versus 61 in Lake Whitefish, Edge et al. 1991). Atlantic whitefish are also purported to have smaller teeth than Lake Whitefish (Edge et al. 1991, Hasselman 2003). Genetically, Atlantic whitefish differ from both Lake Whitefish and cisco (Bernatchez et al. 1991b, Murray 2005). In fact, Bernatchez et al. (1991) found that among 21 taxa *C. huntsmani* was the most distant in the assemblage compared to all other *Coregonus* species, including ciscoes. Thus, *C. huntsmani* is as divergent as the genus *Stenodus*, suggesting this species represents an ancestral form (Behnke 1972). Consequently, *C. huntsmani* should be treated under its own assessment and is not considered further here.

1.2. Are these taxonomic groups distinct biological species?

1.2.1 *Limnetic and benthic Lake Whitefish*

Several sympatric pairs of Lake Whitefish inhabit northern temperate lakes in Canada (e.g., Lindsey 1963b, Fenderson 1964; Bodaly 1977, Bodaly et al. 1992a, Bernatchez et al. 1996). These so-called “species pairs” are characterized by a derived form that is typically slower growing, matures at a much earlier age and size, and lives in the limnetic zone of lakes. This is compared to a larger benthic form that grows faster and to a larger size, matures at a later age, and lives sympatrically within the benthic zone of lakes. For these reasons, the derived populations are often referred to as ‘limnetic’ or ‘dwarf’ because of the distinct differences in life-history, behavioural, and morphological characters associated with the use of trophic resources (Fenderson 1964, Bernatchez et al. 1999).

How did limnetic and benthic Lake Whitefish evolve? Ecological opportunity (e.g., the absence of competitors) as well as character displacement, is thought to have led to the repeated parallel evolution and reproductive isolation of limnetic populations diverging in sympatry with the respective niches of these environments (Vuorinen et al. 1993, Schluter 1996, Taylor 1999, Schluter 2000, Pigeon et al. 1997, Bernatchez 2004, Rogers and Bernatchez 2006). Genetic evidence supports the observation that the limnetic form has evolved repeatedly and independently in several lakes, leading to the hypothesis that the ecology of the lakes has had a substantial influence on the evolution of these species pairs (Lu and Bernatchez 1999). Furthermore, limnetic whitefish are only found in sympatry with the benthic population and only in the absence of other limnetic coregonine fishes, such as the cisco (*Coregonus artedii*), suggesting that divergent natural selection resulting from ecological opportunity within the limnetic niche is the most parsimonious explanation for the evolution of the derived *limnetic* whitefish within the last 10 000 years (Pigeon et al. 1997, Bernatchez et al. 1999).

The *limnetic and benthic* Lake Whitefish dichotomy is now supported by several genetically-based phenotype environment associations (Bernatchez 2004). A phenotype-environment association is a trait that (1) differs between populations, (2) has a clear utility, (3) is genetically based, and (4) is under the influence of divergent natural selection, thereby fulfilling the “adaptive” criterion. Identifying these traits is a key step towards understanding the variation underlying differences between the species pairs and the action of selection maintaining their divergence in sympatry (Schluter 2000). Recent evidence suggests that Fenderson (1964) accurately described the evolution of *dwarfism* in Lake Whitefish as a primarily physiological adaptation. These adaptations, namely slower growth and earlier maturation, have survival value in the face of adverse conditions (e.g., increased predation) of the limnetic environment (Fenderson 1964, Chouinard and Bernatchez 1998, Rogers and Bernatchez 2005, Rogers and Bernatchez 2007). Earlier maturation at a smaller size is under genetic control and adaptive in postglacial environments, because limnetic fish that mature at a younger age likely have a higher probability of reproducing, thereby increasing fitness. Indeed, gene flow is significantly reduced at the genes underlying growth and fecundity, indicating selection has maintained differences between the species pairs at these adaptive traits (Rogers and Bernatchez 2007). Overall, these studies suggest that limnetic and benthic Lake Whitefish species pairs fulfil the definition of a biological species as groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1963).

However, the biological significance of phenotypic and genetic variation in these species pairs must be considered in light of potential limitations in lakes inhabited by species pairs that are currently “data deficient” (see Section 3). In section 1.2.2, the distribution and characteristics of species pairs are provided with potential DU designation. When considering the relevance of PDUs as “distinct biological species”, knowledge of sufficient barriers to gene flow between species will be considered adequate for DU status according to the key. The key further states that under the assumption that two or more populations of a single taxonomic unit are found in reproductive sympatry and demonstrate significant reproductive isolation from one another, they should be considered as valid biological species even with the same taxonomic designation (Taylor 2006). Under this assumption, each species pair qualifies as a DU that is distinct from one another, as well as from all other populations or DUs of the species. This is required because they will have different habitat requirements, behaviour, physiology, and other biological features that are necessary to take into account in subsequent assessments. When some of the data to assess this is lacking, the putative species pair will be given provisional DU status until a more thorough assessment can be made. When only inferential reasoning or limited unpublished data is found to support their existence, the putative species pair will be given deferred DU status.

1.2.2 Distribution and characteristics of limnetic and benthic pairs in Canada

In Canada, limnetic and benthic species pairs inhabit at least 17 lakes from the Yukon to Labrador (Lindsey, 1970, McPhail and Lindsey 1970, Bernatchez and Dodson 1990) (Figure 3). However, these species pairs also exist in at least 22 lakes in the headwaters of the St. John River watershed, but most of these are in northern Maine (Fenderson 1964, Kirkpatrick and Selander 1979, Bernatchez et al. 1999). The available data for each species pair varies, but overall demonstrates parallel patterns of adaptive divergence within these environments (Table 1).

1.2.2.1 Squanga Lake, Yukon

60° 28' 60 N, 133° 37' 60 W

Limnetic and benthic Squanga Lake Whitefish differ in gill raker count, distance between gill rakers, depth selection, morphology (size of the head and size of their fins relative to their body), diet, and spawning times (Lindsey 1963b, Bodaly 1979, Lindsey and McPhail 1986, Bodaly et al. 1987, Bodaly et al. 1988, Bodaly et al. 1992, Bodaly 2007). However, they do not fall within the limnetic and benthic dichotomy with respect to size. Lindsey (1963) reported that, even after handling hundreds of specimens, it was impossible to assign a fish without first examining the gill rakers. Despite this, catch reports from gill nets suggest that the proportion of catch in the limnetic and benthic zones of the lake are highly correlated, with low gill raker fish comprising over 75% of the bottom catch and the pelagic high gill raker species comprising 61% of the limnetic catch (Bernatchez et al. 1996). The presence of this species appears to be associated with the absence of the Least Cisco (*Coregonus sardinella*). Thus, certain aspects of the Squanga Lake limnetic and benthic pair are consistent with the limnetic/benthic dichotomy observed in other parts of Canada.

Squanga Lake Whitefish are of Beringian glacial origin, but the whitefish in this lake represent a case where *C. lavaretus/pidschian* and Beringian *C. clupeaformis* overlap. This is supported by genetic data where the existence of sympatric pairs is best explained by the secondary contact of two monophyletic whitefish groups that evolved in allopatry during the last glaciation events (Bernatchez and Dodson 1994, Bernatchez et al. 1996). These results therefore support polyphyletic origins of limnetic and benthic populations, meaning the species pairs among lakes have evolved independently. Others have suggested that two distinct species inhabit the lake, *C. lavaretus/pidschian* and *C. clupeaformis* (McPhail and Lindsey 1970). Gill raker counts in Squanga Lake are higher than what is typically found in *C. lavaretus/pidschian*, but this may be due to character displacement from its low gill raker *C. clupeaformis* counterpart within the lake.

Elevated admixture of Beringian mtDNA and nuclear genes has been found between the species pair (Bodaly et al. 1992, Bernatchez et al. 1996). Nei's genetic distance between these high and low gill raker populations based on allozymes is low (0.02). In fact, the weakest support for reproductive isolation between Squanga Lake Whitefish ecotypes is observed in Squanga Lake, which exhibit significant but mild genetic differences at the PGM-2* locus only (Bodaly et al. 1992, Bernatchez et al. 1996). Nevertheless, the high and low gill raker dichotomy, in association with significant segregation for different spawning habitats, along with levels of gene flow that vary depending on the degree of trophic specialization, is suggestive of partial reproductive isolation (Bodaly et al. 1988, Bernatchez et al. 1996, Bodaly 2007).

It is also important to note that the high gill raker limnetic population is apparently unable to coexist with ciscoes, which may be more effective consumers of zooplankton. Therefore, introduction of ciscoes to a lake inhabited by Squanga Whitefish is suspected to result in the elimination of the limnetic whitefish. Similarly, a limnetic whitefish population could be significantly reduced by the addition of a piscivorous (fish-eating) fish to its lake (SARA 2006), consistent with other species pairs in Canada. The Squanga Lake Whitefish is currently listed by COSEWIC as 'special concern'.

Overall, based on the evidence of morphological and life history differentiation, this species pair represents reproductively distinct populations (Lindsey 1963, Bodaly 1979, Bodaly et al. 1988, Bodaly et al. 1992, Bernatchez et al. 1996, Bodaly 2007). Consequently, both the high gill raker and the low gill raker Squanga Lake Whitefish species pair warrant DU status. However, as detailed in section 1.1.1, more information is needed on the evolutionary history of this species pair, particularly to confirm the possibility of two distinct species (*C. lavaretus* and *C. clupeaformis*), the former exhibiting derived characters such as high gill raker number possibly due to evolutionary character displacement (Table 1, Figure 2).

1.2.2.2 Little Teslin Lake, Yukon

60° 28' 60 N, 133° 37' 60 W

The Little Teslin species pair differ significantly with respect to morphology (gill raker) and depth selection. Depth selection of high and low gill raker populations is highly significant, with the high gill raker population comprising over 98% of the surface catch (Bernatchez et al. 1996). This appears to be associated with the absence of the Least Cisco (*Coregonus sardinella*) in the four southern Yukon lakes where this species occurs.

Genetically, the more limnetic form is fixed for the Eurasian clade, whereas the Beringian clade predominates in the benthic form (Bodaly et al. 1992, Bernatchez et al. 1996). This indicates that, as in Squanga Lake, their sympatric occurrence originated from the secondary contact of two monophyletic groups of whitefish that evolved allopatrically (Bernatchez et al. 1996, Bernatchez et al. 1999).

Given the observed adaptive divergence and significant reproductive isolation (Bodaly 1979, Bernatchez et al. 1996, the Little Teslin species pair warrant DU status (Table 1, Figure 2)

1.2.2.3 Dezadeash Lake, Yukon

Dezadeash Lake is a separate catchment than Squanga or Little Teslin Lake, but the species pair inhabiting Dezadeash Lake also differ primarily with respect to depth selection and gill raker number (Lindsey 1963b). Gene flow is most restricted between the species pairs in this lake compared to other lakes harbouring the species pairs in the Yukon (Bernatchez et al. 1996). Both high and low gill raker populations were associated with the Eurasian clade of the Beringian glacial race (Bernatchez et al. 1996). This was congruent with results based on isozymes and suggested a distinct evolutionary origin for ecotypes of Dezadeash Lake compared to those found in the other two lakes (Bodaly et al. 1992b).

Based on the adaptive trait divergence and significant reproductive isolation (Bodaly 1979, Bernatchez et al. 1996, the Dezadeash Lake species pair warrants DU status (Table 1, Figure 2).

1.2.2.4 Teenah Lake, Yukon

This lake, south of Squanga lake, is known to inhabit the species pairs (Bodaly 1979, Bernatchez et al. 1996). It has not been included in the same genetic surveys and therefore remains data deficient.

Based on the existing information for the Squanga Lake species pair, Lake Whitefish inhabiting Teenah Lake should be granted deferred DU status until further genetic and phenotypic information can confirm their status.

1.2.2.5 Hanson Lake, Yukon

64.01°N 135.35°W

This lake was reported to have been inhabited by the Squanga Lake Whitefish. Their extinction occurred when the Hanson Lake fish fauna were poisoned in 1963 with toxaphene to facilitate the introduction of rainbow trout for sportfishing (Vetter et al. 1999).

1.2.2.6 Dragon Lake, British Columbia

52°59'N, 122°29'W

This lake was hypothesized to have a slow growing and a fast growing whitefish species pair (McPhail and Lindsey 1970, McPhail 2007). However, this population was also eradicated to promote trout fishing (McPhail and Lindsey 1970).

1.2.2.7 Lower Liard River, British Columbia

This system is reported to potentially be inhabited by a slow-growing and fast growing species pair (McLeod et al. 1979). As discussed in section 1.1.1, it is possible that the Liard River might inhabit a migratory population of Lake Whitefish or that the system represents contact zone between Eurasian and North American clades (McPhail 2007)

Overall, there appears to be some evidence for differential growth between the putative populations (McLeod et al. 1979). However, the data are not clearly supported by phenotypic or genetic analyses. Therefore, deferred DU status should be given to the potential species pair in this system until further information is available.

Although no mtDNA has been collected, allozymes have also suggested that this system is a zone of secondary contact between Beringian, Mississippian, Nahanni, and Eurasian Lake Whitefish (Table 1, Foote et al. 1992). This renders the Liard River system a very important and unique system towards resolving questions about the species status of these glacial races and the potential role for evolutionary reinforcement within this system.

1.2.2.7 Great Slave Lake, NWT

61°40'N, 114°00'W

This is the second largest lake in the Northwest Territories (after Great Bear Lake) and the deepest lake in North America (maximum depth = 614m). These Lake Whitefish are of Mississippian glacial origin (Foote et al. 1992). Rawson (1947) reported a dark, rounded form in sympatry with the benthic form, although the phenotypic data are inadequate and the genetic data are unknown (Scott and Crossman 1973).

As these traits are not part of the known suite of phenotype-environment associations evolving in limnetic-benthic species pairs, this putative species pair is data deficient and does not currently warrant deferred DU status.

1.2.2.8 Lake Athabasca, Alberta

59°16'N, 109°27'W

Lake Whitefish in Lake Athabasca are of Mississippian glacial origin (Foote et al. 1992). Rawson (1947) also reported a dark, distinctly rounded form in sympatry with the benthic form in this lake although the phenotypic data are inadequate and the genetic data are unknown (Scott and Crossman 1973).

As these traits are not part of the known suite of phenotype-environment associations evolving in limnetic-benthic species pairs, this putative species pair is data deficient and does not currently warrant DU status.

1.2.2.9 Lake Opeongo, Ontario

45°42'N, 78°24'W

Lake Opeongo is Algonquin Park's biggest lake with an area of 5800 ha, a mean depth of 14.6 m (maximum depth 49.4 m). Kennedy (1943) discovered that the lake contains a limnetic and benthic species pair. Limnetic whitefish apparently grow slower than benthics in the lake, although Kennedy (1943) reported that 1+ limnetic whitefish were 109 mm long while their benthic counterparts were 78 mm long at the same age. The species pair also differs with respect to age at maturity and fecundity (Kennedy 1943, Ihssen et al. 1981, Cucin and Faber 1985).

Although genetic evidence from Lake Opeongo is suggestive of differences between limnetic and benthics, the focus of the study was a stock assessment in comparison with allopatric populations in Ontario (Ihssen et al. 1981). Therefore, the level of reproductive isolation between limnetics and benthics in this environment remains inconclusive.

Based on the divergence in adaptive growth rate, age at maturity and fecundity between limnetic and benthics in a direction parallel to other species pairs, the Lake Whitefish in Lake Opeongo warrants DU status. However, in the absence of genetic data and compared to other species pairs in Canada, a provisional DU status may be more appropriate until genetic information can confirm phylogenetic grouping and/or reproductive isolation (Table 1, Figure 2).

1.2.2.10 Como Lake, Ontario

47°55'N, 83°30'W

Located in northern Ontario, Como Lake has a surface area of 1596 ha and a mean depth of 9.4 m. Significant differences in body morphometry between limnetic and benthics were found for five of nine meristic characters and 14 of 19 morphometric characters, consistent with the magnitude and direction of parallel adaptive trait divergence in other limnetic and benthic species pairs (Bodaly et al. 1991, Vuorinen et al. 1993).

Genetic differences in the frequency of mtDNA haplotypes has shown that Como Lake Whitefish have diverged into a genetically distinct, reproductively isolated limnetic and benthic species pair (Vuorinen et al. 1993). The mtDNA evidence also demonstrated that the benthic Lake Whitefish are most likely of Atlantic glacial origin (a largely diagnostic mtDNA haplotype found in southern Québec) while the limnetic population is of Mississippian glacial origin (Bodaly et al. 1991, Vuorinen et al. 1993).

Given the adaptive trait divergence between the species pairs and the secondary contact between genetically distinct Atlantic and Mississippian glacial PDUs, both limnetic and benthic Como Lake Whitefish warrant DU status (Table 1, Figure 2).

1.2.2.11 Lake Superior, Ontario

47.7°N – 87.5°W

Edsal (1960) reported a species pair within Lake Superior but phenotypic and genetic data were inadequate. A lack of phenotypic and genetic data for the putative species pair do not support DU status for Lake Whitefish inhabiting Lake Superior.

It is noteworthy that species interactions between the invasive zebra mussel and the decline of Lake Whitefish in Lake Superior have resulted in significant life history changes for the Lake Whitefish within this ecosystem (Nalepa et al. 2005). There have been observations that declines in abundance of the benthic amphipod, *Diporeia spp.*, have resulted in Lake Whitefish adopting a more limnetic life history (Nalepa et al. 2005, Bernatchez 2005). Given the rapid evolution of the derived limnetic species upon colonization of a limnetic environment, predictions can be made about the evolutionary changes this alternative life history will have on Lake Superior whitefish. Namely, this interaction may cause evolutionary changes that lead to a slower growing population that matures earlier.

1.2.2.12 Lake Simcoe, Ontario

44°26'12"N, 79°20'21"W

Lake Whitefish are an important recreational fishery within this lake which has been heavily stocked with whitefish since 1982 (Lasenby et al. 2001). MacCrimmon and Skobe (1970) reported a sympatric species pair of Lake Whitefish but subsequent evidence remains to be gathered (Scott and Crossman 1973). A lack of phenotypic and genetic data for the putative species pair do not support DU status for Lake Whitefish inhabiting Lake Simcoe.

1.2.2.13 Témiscouata Lake, Quebec

47°36'00"N, 68°45'00"W

Lac Témiscouata is a part of a series of lakes in the Allagash Basin and Saint John River Watershed in south-eastern Quebec. The lake contains one of the most extensively studied species pairs of Lake Whitefish. Significant adaptive trait divergence has evolved between populations, with the limnetics attaining an average size at maturity of 188 mm while the benthic population attains an average size of 238 mm at maturity. Limnetic and benthics within this lake also differ with respect to gill rakers, behaviour, growth, and spawning habitat (Lu et al. 1999). Limnetic forms in this lake spawn in a groundwater stream feeding the lake while benthics spawn in the lake (Lu and Bernatchez 1998).

Significant genetic differentiation and reproductive isolation exists between Témiscouata limnetic and benthic (Lu et al. 1999). Once believed to be of primarily Acadian glacial origin (Bernatchez et al. 1990), subsequent genetic analyses have revealed substantial hybridization between Atlantic and Mississippian glacial races in the benthic population while the limnetic are primarily of Acadian origin (Lu et al. 2001, Rogers 2001)

Based on the significant suite of adaptive trait divergence and genetic differentiation in Témiscouata Lake Whitefish, both the limnetic and benthic populations warrant DU status in this lake (Table 1, Figure 2).

1.2.2.14 East Lake, Quebec

47°11'00"N, 69°33'00"W

Phenotypic differentiation in size between limnetic and benthics in East Lake is highly significant, with limnetic fish averaging 153 +/- 17 mm at maturity while benthics attain an average size at maturity of 285 +/- 67 mm (Lu et al. 2001). East Lake remains one of the least phenotypically differentiated species pairs with respect to gill raker variation, but the extent of morphological differentiation (other than adult size) between ecotypes is significantly associated with trophic use (Chouinard et al. 1996, Bernatchez et al. 1999). More pronounced morphological differentiation between ecotypes in other lakes (e.g., Cliff Lake) translated into stronger trophic niche partitioning during periods of food depletion than in East Lake, where limnetic and benthic fish feed mainly on planktonic and epibenthic prey, respectively (Chouinard et al. 1996, Chouinard and Bernatchez 1998, Bernatchez et al. 1999, Landry et al. 2007). These results have been important towards demonstrating a functional link between morphology and trophic use (Bernatchez et al. 1999). These studies have also demonstrated that the persistence of ecological opportunity for differential resource use throughout their ontogeny may be the primary selective force promoting the extent of specialization reached.

Lake Whitefish in East Lake also support the hypothesis for an intralacustrine origin of the species pairs (Pigeon et al. 1997). Both limnetic and benthic Lake Whitefish are of Acadian glacial origin, more closely related to each other than other populations at both mtDNA and Amplified Fragment Length Polymorphism (AFLP) DNA markers (Bernatchez and Dodson 1990, Campbell et al. 2003, Campbell and Bernatchez 2004). The mtDNA analysis supports a single founding population characterized by an original haplotype (Bernatchez and Dodson 1990), followed by a novel mutation of another haplotype following colonization. Genetic studies between the species pair have identified candidate genes associated with growth that exhibit parallel adaptive divergence in other limnetic-benthic species pairs (Rogers and Bernatchez 2005, Rogers et al. 2007).

Altogether, the adaptive trait divergence and genetically distinct ecotypes of monophyletic origin suggests that both the limnetic and benthic Lake Whitefish of East Lake should be granted DU status (Table 1, Figure 2).

1.2.2.15 *Caniapiscau Lake, Quebec*

Fortin and Gendron (1990) reported limnetic and benthic species pairs in three Québec lakes. The first, Caniapiscau Lake, exhibits phenotypic differences in growth, maturity, and spawning. A limnetic/benthic phenotypic dichotomy in this phylogenetically distinct assemblage supported the hypothesis that similar phenotypic patterns evolved in parallel in separate, yet closely related lineages (Pigeon et al. 1997). Genetic evidence for reproductive isolation is insignificant with mtDNA (Pigeon et al. 1997, but given the young intralacustrine divergence of the species this genetic marker may not have had enough resolution and should be followed up with more appropriate genetic markers such as microsatellite DNA). Indeed, recent research on other north temperate fishes has pointed out the possibility that this region in central Quebec may have been colonized by distinct 'subglacial' races (not strictly mtDNA glacial races, but very distinct lineages within a 'traditional' mtDNA race) originating from within a Mississippian race in each species (Fraser and Bernatchez 2005).

Overall, Taylor (2006) suggested that if a diagnostic character or suite of characters was identified with limited sampling, DU status might be deferred or made provisional until the diagnostic nature of the trait was confirmed after more extensive sampling. This fits the current situation with the Caniapiscau Lake species pair. Given the parallel patterns of adaptive divergence in this limnetic and benthic dichotomy, these limnetic and benthic populations should be given provisional DU status (Table 1, Figure 2)

1.2.2.16 *Lac Outardes II, Quebec*

Fortin and Gendron (1990) reported a limnetic and benthic species pair in Lac Outardes II. This putative species pair exhibited phenotypic differences in growth, maturity, and spawning date. This group is similar to Caniapiscau Lake in that there is evidence for only the Mississippian glacial race in the lake (Bernatchez and Dodson, 1991). Genetic evidence for reproductive isolation was also insignificant with mtDNA (Pigeon et al. 1997).

DU status for this species pair should be provisional until the diagnostic nature of the traits is confirmed after more extensive sampling. Given the parallel patterns of adaptive divergence in this limnetic and benthic dichotomy, these populations should be given provisional DU status (Table 1, Figure 2)

1.2.2.17 *Lac Manicouagan V, Quebec*

Fortin and Gendron (1990) reported a limnetic and benthic species pair in Lac Manicouagan V. This putative species pair also exhibited phenotypic differences in growth, maturity, and spawning date. This group is similar to Caniapiscau Lake and Lac Outardes II in that only the Mississippian glacial race is found in this lake (Bernatchez and Dodson, 1991). Genetic evidence for reproductive isolation is also insignificant with mtDNA (Pigeon et al. 1997).

DU status should be provisional until the diagnostic nature of the trait was confirmed after more extensive sampling. Given the parallel patterns of adaptive divergence in this limnetic and benthic dichotomy, these populations should be given provisional DU status (Table 1, Figure 2).

1.2.3 Hybridization of *C. clupeaformis* with other Coregonineae

Hybridization between *C. clupeaformis* and other Coregonines is rare but continues to occur with several species in certain habitats (Smith 1992, Reist, 1992). For example, hybrids with *C. artedii*, so-called “mule whitefish”, have been documented in Lake Erie and the northwest (Koelz 1929, Scott and Crossman 1973). Mule whitefish possibly exhibit heterosis with respect to growth rate (McPhail and Lindsey 1970). Several other cases of hybridization have also been reported in the northwestern part of their range with inconnu whitefish (*Stenodus leucichthys*), least cisco, (*Coregonus sardinella*), and Arctic cisco (*Coregonus autumnalis*) (Alt 1971, Nelson and Paetz 1992, Reist et al. 1992).

1.2.4 Species status of *Coregonus clupeaformis*

Most studies suggest retaining the species status of *C. clupeaformis* populations until more data are available (Walters 1955, Lindsey et al. 1970, Smith and Todd 1984, McPhail 2007). Biogeographic and experimental data will be necessary to resolve these issues. For example, *C. clupeaformis* has been taxonomically considered as the same species as *C. lavaretus* (Walters 1955, Reshetnikov 1963). Although these species show distinct phylogenetic groupings (Bodaly et al. 1991, Bernatchez et al. 1994, Bernatchez and Wilson 1998), direct evidence for the extent of reproductive barriers between the two is unknown, leading some to suggest that perhaps the name *C. lavaretus* be applied to all Lake Whitefish populations in the northern hemisphere (Bernatchez and Wilson 1998). However, indirect evidence from genetic distance data is indicative of reduced hybridization and introgression when the species do overlap, suggesting that reproductive isolation may be considerable.

Overall, attempts to delineate subspecies status remain premature (McPhail and Lindsey 1970, Lindsey 1988, Bernatchez and Wilson 1998). Importantly, the utility of gill rakers to resolve the species' status has been largely replaced by genetic measures of population differentiation. The patterns of modal gill raker counts across Canada remain compelling, with western Lake Whitefish populations exhibiting low modal counts (20-22, conforming to observations for *C. lavaretus/C. pidschian*, described by Gmelin in 1788) while eastern and southern populations have higher modal counts (26+, agreeing with Mitchill's classification for *C. clupeaformis*). Overall, variation in this character in some populations was perhaps the first line of evidence that a combination of historical and contemporary evolutionary or environmental forces may have been driving observed differences (Scott and Crossman 1964, Loch 1974, Woodger 1976). For instance, comparable ranges of gill raker variation may be generated within each of the species classified under the *C. clupeaformis* complex via natural selection and environmental influences (Scott and Crossman 1964, Woodger 1976, Lindsey 1981).

It has been well established that traditional taxonomic methods employing phenotypic variation should not be the primary criterion used to reflect the evolutionary history or distinctness of Lake Whitefish populations (Lindsey 1981). This has been established in other systems with similar taxonomic issues (e.g., *Osmerus* sp., Taylor and Bentzen 1993, Bernatchez et al. 1999, whereby the use of genetic data for resolving taxonomic issues has increased our knowledge of evolutionary history.

1.3. Summary

Many proposed species within *C. clupeaformis* complex have been identified on the basis of morphological variation, leading to taxonomic designations not fully supported by genetic evidence.

Genetic evidence strongly supports the possibility that two species, *C. lavaretus* and *C. clupeaformis*, inhabit British Columbia and the Yukon.

Provisional DU status should be given to populations that represent distinct *Coregonus lavaretus* species (Figure 2).

Genetic evidence suggests that *C. lavaretus* inhabits the upper Yukon River and, potentially the upper Liard River system. A more thorough analysis of this latter system is needed.

Coregonus huntsmani, already listed on the endangered species list, was considered here in the context of the Lake Whitefish species complex based on previous associations with *C. clupeaformis*. Under the criteria of the key, this population's taxonomic position places it outside the scope of the current assessment.

Under the assumption that two or more populations of a single taxonomic unit found in reproductive sympatry and demonstrating significant reproductive isolation from one another are valid biological species even with the same taxonomic designation (Taylor 2006), each limnetic and benthic pair of Lake Whitefish, distinct from other such pairs, qualifies as a DU.

Of the 17 lakes known to be inhabited by the putative species pairs, seven warrant DU status for the limnetic and benthic species pairs inhabiting these lakes, leading to 14 DU designations (Figure 2).

In three lakes, where the species pairs are purported to exist, but locally adapted traits have not been assessed, or genetic differentiation between limnetic and benthic is unknown, provisional DU status was granted until the diagnostic nature of adaptive traits is confirmed after more extensive sampling (6 provisional DUs) (Figure 2).

Three additional lakes, purported to be inhabited by species pairs, remain completely data deficient and were identified as deferred DUs.

The seven PDU species pairs of limnetic and benthic Lake Whitefish are distributed throughout Canada but mainly concentrated in two regions of secondary contact between PDUs representing glacial races (Yukon and southern Quebec) (Figure 3)

The addition or invasion of other limnetic species (e.g., cisco or rainbow smelt) will likely precipitate the extinction of the limnetic Lake Whitefish.

2. The PDU represents a major phylogenetic grouping separate from other groupings within the taxon in question?

2.1. Glacial History of Canada and Postglacial dispersal of Lake Whitefish

The Pleistocene ice age was arguably the most significant event in the history of most extant northern organisms. Nowhere is this more apparent than for organisms inhabiting the Canadian landscape (McPhail and Lindsey 1970, Denton and Hughes 1981, Bodaly et al. 1991, Pielou 1991, Hewitt 1996, Schluter 1996, Dawson 2002, Power 2002, Curry 2007). North American icesheets were larger than those of Europe and Asia combined, covering most of the country. Ancient freshwater habitats were destroyed by the advancing glaciers, displacing or eradicating local populations (Pielou 1991).

Each glaciation spanned approximately 100 000 years, with the interglacial periods consisting of a duration of 10-12000 years (Dawson 2002). Subsequent retreat of the most recent glacial period (between 15000 and 8000 years ago) was equally a major environmental change. Meltwater formed large proglacial lakes affecting the dispersal of aquatic organisms. These lakes were larger than any existing lakes and changed frequently as their size and volume were largely determined by the rate of melting. For example, geological radiocarbon evidence from the Strait of Georgia has shown that approximately 10 000 years ago, a catastrophic release of impounded glacial lake water and melt water flooded the lower Fraser River Valley and the Strait of Georgia, leaving a 22cm layer of clay in the Strait of Georgia and likely resulting in less brackish surface water for a period of years (Conway et al. 2001). This may have contributed to the dispersal ability of several freshwater aquatic organisms able to tolerate the reduced salinity of the strait. Events such as these leave important signatures in the geological records for reconstructing the zoogeography of the time.

Glaciations affected Lake Whitefish populations in two major ways. First, advancing ice sheets resulted in a reduction of available habitat for the species. Second, the ice sheets resulted in extreme geographic and temporal isolation of whitefish populations. In fact, as discussed below, Lake Whitefish could have only survived in a limited range of habitats that were not iced over during the repeated advances and retreats of glacial ice during the Pleistocene. These areas were limited to regions not affected by the glacial advances, providing refuge for terrestrial and aquatic organisms. In North America, three large areas served as the primary refugia for organisms during the Wisconsin glaciation (Pielou 1991). These areas included an ice-free corridor that formed a northward pointing peninsula of ice – free land just east of the Rocky Mountains. Beringia, consisting of most of Alaska and Yukon, formed a huge refuge along the beds of two shallow seas – the Bering and the Chukchi seas. Third, the coastal plains, east of the ice sheet, which are now submerged and form the continental shelves of the Atlantic Provinces. Several smaller refugia, so-called *nunataks*, persisted primarily on coasts and at the summit of mountain peaks. Several nunataks have been identified, including but not limited to; Vancouver Island, the Queen Charlotte Islands, and Cape Breton, Nova Scotia. Coastal refugia are believed to have been common around the Gulf of Saint Lawrence, the Gaspé Peninsula, and the coast of Newfoundland. Coastal refugia and the ecosystems within them would have migrated slowly inland as the level rose and the ice retreated. Because the current distribution of Lake Whitefish matches the areas covered by the North American glaciers, phylogeographic approaches have been highly suitable towards elucidating the postglacial history of this species complex.

2.2. Phylogeography of the Lake Whitefish species complex

In the following section the existence of five major glacial lineages within *C. clupeaformis* is discussed (Figure 3). Extensive genetic resources have been developed within the species complex over the years which are ideal towards addressing phylogeographic issues (Tsuyuki et al. 1966, Lindsey et al. 1970, Hamada et al. 1997, Sajdak and Phillips 1997, Vuorinen et al. 1998, Sendek 1999, Bernatchez et al. 1999, Politov et al. 2000, McDermid et al. 2005). Phylogenetic and genetic characteristics for each of these glacial lineages and their relationship to one another in the context of establishing DUs are described. Several important differences within each glacial race that will need to be considered for assessing status of each and particularly for deciding the relative importance for future assessments of each DU are also described.

2.2.1 Beringian Glacial Race:

This group of whitefish inhabits Alaska, Yukon and the Northwest Territories and is believed to have survived in the Beringian refuge during the last ice age (Lindsey 1975, Lindsey and McPhail 1986). Fish collected in these areas consisted largely of two significantly distinct mtDNA groupings; A and B (Bootstrap support > 80%, Bernatchez and Dodson 1991) (Figure 3). As discussed in section 1.1.1, one of these groupings is representative of *C. lavaretus* originating from Siberia when the land masses connected. The second grouping represents a population of *C. clupeaformis* that survived the Pleistocene in the Beringian refugia. The percentage of mtDNA divergence between these clades A and B suggests that these two populations diverged in the order of 360 000 years ago, representing the deepest phylogenetic split compared to all glacial races, with the major genetic break between whitefish inside and outside of Beringia during the Kansan ice advance. Interestingly, *C. lavaretus/pidschian* and Beringian *C. clupeaformis* overlap and are sympatric in only three regions; the Yukon River, Chatanika Lake, and Squanga Lake. Within these regions, there is some evidence of reproductive isolation between populations (Lindsey 1963b).

The effective population size (N_e) for the Beringian Lake Whitefish was estimated to be 72 000 (Bernatchez and Dodson 1990), although exact values are not likely accurate (Fraser et al. 2007). However, the interesting aspect with this estimate is that the effective population size is three times higher than the rest of Canada, indicating that Lake Whitefish were more abundant in this zone during the ice age despite the relatively small surface area in this refuge. The genetic evidence offers support for the hypothesis that this region was a glacial refuge for fish fauna during the Pleistocene ice age. Bernatchez and Dodson (1990) suggest other reasons why such a major difference may persist between Beringia and other regions of the country, including the role of bottlenecks (Bernatchez et al. 1989), and gene flow between Alaska and Eurasia (Lindsey and McPhail 1986). Evidence from mtDNA suggests that this clade reached an eastern limit of the lower Mackenzie River where they overlap with Lake Whitefish from the Mississippian glacial race. This is in contrast with evidence from allozymes that Beringian whitefish dispersed towards central Canada (Franzin and Clayton 1977).

Beringian Lake Whitefish have a high level of genetic differentiation compared to other assemblages (e.g., eight mtDNA clones alone exist in the Yukon and Chatanika rivers) (Bernatchez and Dodson 1990, McDermid et al. 2005). The discontinuity of haplotypes has also been corroborated by other genetic data, namely allozyme frequencies (Franzin and Clayton 1977, Foote et al. 1992). Overall, significant differences in genetic diversity exist between Beringian Lake Whitefish and the rest of North America (McDermid et al. 2005).

Sequence divergence measured among the 46 mtDNA haplotypes comprising the Beringian Lake Whitefish and all other glacial lineages is high (1.15%) and supported by bootstrap values greater than 75% in two separate studies (Bernatchez and Dodson 1991, Bernatchez and Dodson 1994). This is compared to interspecies measures of sequence divergence of 1.8% between *C. nasus* and *C. clupeaformis* at the same genetic markers. Thus, there is little doubt that these whitefish populations corresponding to the Beringian glacial lineage represents a DU (Beringian DU) under COSEWIC's guidelines (Table 1, Figure 2).

2.2.2 Nahanni Glacial Race:

Lake Whitefish may have also survived during the ice age in an area of what is currently Nahanni National Park Reserve in the Northwest Territories (NWT) (Figure 3). This area was found to be ice-free during the Wisconsinan and Illinoian glacial periods (Ford 1974). Geological evidence suggests there was a 'corridor' between the Mackenzie mountains and the Alaskan slope which could have provided an important refuge for organisms isolated from the Beringia glacial refuge by the Mackenzie mountains (Prest 1970). Foote et al. (1992) examined 43 populations covering all of these western regions and found that a distinct assemblage, compared to the Beringian and Mississippian glacial races, inhabited waters in the southwest corner of NWT, central BC, in lakes of the lower Liard, Tetcela, Fraser, and upper Peace rivers as well as the Talbot River. Although the genetic distance between the Nahanni and its neighbouring glacial races was low (0.047, presumably significant although p-values were not estimated, private alleles (genetic variants not found anywhere but in this region) were present only within this Nahanni group. Importantly, there were no clines in allele frequencies at these markers but rather breaks in the distribution, supporting the hypothesis that this group is genetically distinct from the other glacial refugia. Evidence that Arctic grayling (*Thymallus arcticus*) and lake trout (*Salvelinus namaycush*) also appear to have similar patterns of genetic divergence for populations within the Nahanni further support the hypothesis that this region is distinct from Beringian populations (Foote 1979, Wilson and Hebert 1998, Stamford and Taylor 2004, McDermid et al. 2005).

Interestingly, not all of the variation is related to isolation of fish in separate refugia, but possibly reflects population subdivision that occurred within the Beringian refugium during the ice age. Overall, there is evidence to suggest that populations comprising the Nahanni groups are likely distinct from other glacial races, but because of continued gene flow with the Beringian Lake Whitefish and high genetic similarity to the Mississippian glacial race, this group should not be considered a distinct phylogenetic grouping until more suitable genetic data can be obtained for resolving these questions. Nevertheless, populations within the Nahanni grouping should be given provisional DU status under COSEWIC's guidelines, following the evidence for diagnostic alleles at allozyme loci from Foote et al. (1992) (Table 1, Figure 2).

2.2.3 Mississippian Glacial Race:

This was the biggest refugium responsible for most postglacial Lake Whitefish colonizations. Many species were thought to have survived in the Mississippian River drainage basin, in the southern, non-glaciated part of the continent (Crossman and McAllister 1986, Pielou 1991). Large proglacial lakes, such as Lake Agassiz, covered over 350 000 km², four times larger than Lake Superior, the largest freshwater lake in the world. Lake Agassiz drained south into the Mississippi River valley until recession of glacial ice 10 700 years ago led to the lake spilling eastward. It is likely that the majority of fishes living in the interior of Canada today originated from Lake Agassiz (Crossman and McAllister 1986). This lake was also purported to be linked to and extend as far as Beringia at times.

Indeed, mtDNA evidence suggests that many Canadian Lake Whitefish populations must have survived in the Mississippian refuge (Group C, clonal line 1, Bernatchez and Dodson 1991), diverging approximately 360 000 ya. Postglacial dispersal within this clade extends as far northwest as the Arctic Red River where Mississippian Lake Whitefish overlap with the Beringia glacial race (McDermid et al. 2005). This is the only known area of secondary contact with the Beringia glacial race (Rempel and Smith 1998). In eastern Canada, the Mississippian glacial race overlaps with the Atlantic glacial lineage (see 1.2.2.13) in several lakes in southern Quebec and Maine. Secondary contact with the Acadian glacial race is limited to a single lake sampled in south-eastern Quebec (Lac Témiscouata).

The majority of Mississippian populations (over 90%) contain the same mtDNA haplotype (Bernatchez et al. 1991). Thus, descendants of a single lineage recolonized over 5 000 000 km², from Yukon to Labrador. The phylogeny of Mississippian Lake Whitefish is complex. Indeed, the node separating this glacial race from Beringian Lake Whitefish and other Coregonines has been well supported by both mtDNA bootstrap values (97%, Bernatchez and Dodson 1991, 1994, Lu et al. 2001) and allozyme data (Bodaly et al. 1992a). Lake Whitefish from the Mississippian glacial race should therefore be considered a significant DU under COSEWIC's guidelines. However, within this DU, there are distinct assemblages exhibiting disjunct, localized distributions (see Atlantic and Acadian glacial races below) that may warrant additional DU status (Table 1, Figure 2).

2.2.4 Atlantic Glacial Lineage:

Populations in southeastern Quebec and Maine likely survived in an Atlantic refugium south of the Wisconsinian ice sheet (Schmidt 1986, Underhill 1986, Bernatchez et al. 1991, Lu et al. 2001, Curry 2007). Bernatchez and Dodson (1991) found that this group comprised a sub-assembly of the group C clade largely of the Mississippian glacial race, also supported by genetic differences in allozyme frequencies (Bodaly et al. 1992a) (Figure 3). Whitefish that survived in the Atlantic glacial refuge share two mtDNA lineages with anadromous populations from the northern Quebec peninsula and in the St. Lawrence River. These mtDNA haplotypes are absent everywhere else, suggesting that postglacial colonization in this region may have been from coastal populations that persisted in brackish water. As mentioned, this is possible if sufficient glacial melting resulted in lower salinity (de Vernal and Hillaire-Marcel 2000).

The Atlantic glacial race diverged from the Mississippian glacial race only 18-75000 ya according to the evidence from mtDNA (Bernatchez et al. 1991). Secondary contact occurs with the Acadian glacial race in three eastern lake populations, one of which (Lac Témiscouata, Table 1) while the other two are located in Maine (Table 1). The remaining Lake Whitefish populations of known Atlantic glacial race origin have been sampled in Maine (e.g., limnetic ecotype of Usaskis Lake and Ross Lake). Further mtDNA analysis of populations in this region show significant phylogenetic divergence of the Atlantic from the Acadian or Mississippian glacial races (bootstrap support = 93%, Lu et al. 2001). Furthermore, an analysis of variance of Mississippian, Atlantic, and Acadian populations in Eastern Canada found that between 65 and 82% of the total genetic variance among sympatric and allopatric populations could be attributed to genetic differences among the eastern glacial lineages (Lu et al. 2001). In some of these lakes (e.g., Lac Témiscouata), there is also evidence for reproductive isolation between Mississippian/Atlantic and Acadian glacial races (Rogers 2001, Lu et al. 2001). Overall, these results suggest the Atlantic glacial race is a distinct phylogenetic group, indicating that this assemblage be considered by COSEWIC as a DU (Table 1, Figure 2).

2.2.5 Acadian Glacial Race:

Both mtDNA (Bernatchez and Dodson 1991) and allozyme (Bodaly et al. 1992) data support evidence for a distinct glacial refuge lineage in eastern North America (Figure 3). This glacial race inhabits lakes in Maine, the Gaspé Peninsula, and New Brunswick and probably survived glaciation in a northeast banks refugium on the coastal plains of northeastern North America (Schmidt 1986, Pielou 1991, Curry 2007).

The mtDNA haplotypes (group D in Bernatchez and Dodson 1991, 1994) suggest that this group diverged from the Mississippian/Atlantic clade approximately 150 000 years ago. This split from the Mississippian clade is highly significant (bootstrap value = 89%, Bernatchez and Dodson 1994; bootstrap value = 79%, Lu et al. 2001). Consequently, these Eastern Canada Acadian glacial race populations represent a distinct DU (Table 1, Figure 2).

2.3. Population Subdivision within Glacial Races:

COSEWIC (2006) recognizes that distinct phylogenetic groupings should be inferred with genetic markers that are capable resolving population subdivision at an appropriate scale (e.g., mtDNA, nuclear genes). Population subdivision of Lake Whitefish has been studied within some glacial races, namely those of Mississippian origin of the Great Lakes Region (Imhof et al. 1980, Casselman et al. 1981, Ihssen et al. 1981, Stott et al. 2004). Studies exploring allozyme variation (e.g., Imhof et al. 1980, Ihssen et al. 1981, Casselman et al. 1981) supported the mtDNA evidence that Lake Whitefish from these regions had a single origin. While microsatellites have further resolved this variation on a microgeographic scale, there has been no evidence that any of these populations are reproductively isolated or locally adapted to the extent necessary for defining these populations as PDUs. This lack of population subdivision includes the Lake Simcoe population, which was designated distinct stock status by COSEWIC in 1987 (deemed data deficient, COSEWIC 2005). However, the genetic data of Ihssen et al. 1981 show that the whitefish of Lake Simcoe are not significantly different from the Lake Huron or Lake Ontario populations (see COSEWIC 2005a). The Mira River population in Nova Scotia was also deemed data deficient by COSEWIC in 2000 (Goodchild 1999 (unpublished report)). Mira Lake Whitefish fall within the Acadian DU designation based on phylogeny (Bernatchez and Dodson 1994). The Mira Lake population is considered in the context of the distinctive and rare traits in later sections of this report (see section 3.4).

2.5. Summary

- Isolation of Lake Whitefish during glacial refugia resulted in significant allopatric divergence during the Pleistocene ice age
- Genetic evidence (mtDNA and allozymes) from Lake Whitefish inhabiting over 100 populations across Canada strongly supports five major phylogeographic groupings (Figure 3)
- Lake Whitefish from the Beringia refuge should be granted DU status based in the distinct phylogenetic grouping and diagnostic haplotypes found for Lake Whitefish in this region (Table 1, Figure 2)
- The Nahanni warrants provisional DU status until more appropriate genetic markers can establish the significance of this population subdivision with respect to its split from the Beringian during the Pleistocene (Table 1, Figure 2)
- Lake Whitefish from the Mississippian refuge should be granted DU status based in the distinct phylogenetic grouping and diagnostic haplotypes found for Lake Whitefish in this region (Table 1, Figure 2)

- Lake Whitefish from the Atlantic refuge should be granted DU status based in the distinct phylogenetic grouping and diagnostic haplotypes found for Lake Whitefish in this region (Table 1, Figure 2)
- Lake Whitefish from the Acadian glacial race are a distinct phylogenetic group and warrants DU status (Table 1, Figure 2)
- Population subdivision within the Mississippian (Manitoba and Ontario, the Great Lakes) and Acadian glacial races (Mira River) reflect recent postglacial population divergence and significant population subdivision. Although local selection may be influencing the observed structure, this has not been established. Consequently, these populations should jointly be considered within the Mississippian/Atlantic and Acadian DUs unless further genetic or ecological evidence should prove otherwise.

3. The PDU has distinctive traits that (1) represent local adaptation and (2) identifies the PDU as not ecologically interchangeable with other known PDUs within the species, or (3) identifies the PDU as an irreplaceable component of Canada's biodiversity?

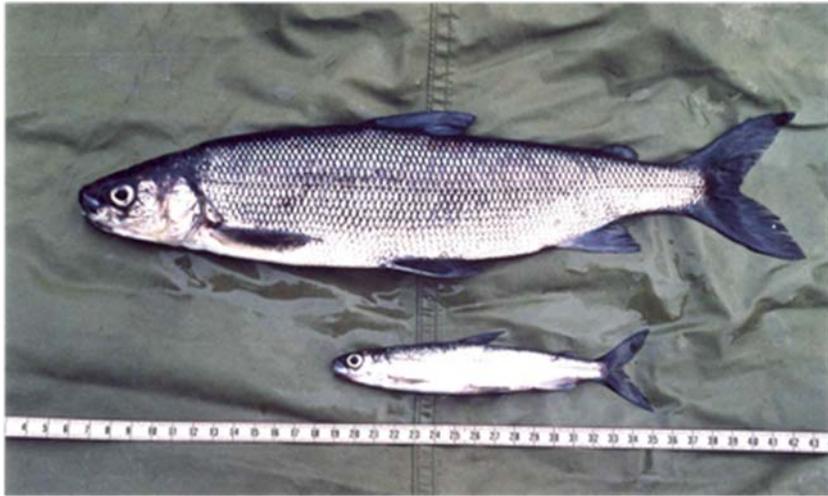
3.1. Evidence of distinctive traits that represent local adaptation in the species pairs

3.1.1 Distinctive Traits:

Sympatric species pairs composed of limnetic and benthic forms display differences in life-history, behavioural, and morphological characters associated with the use of trophic resources (Fenderson 1964, Bernatchez et al. 1999). In this section the most commonly studied characters are provided to assess (i) variation in adaptive traits between species pairs, ii) that the variation underlying adaptive traits is genetically controlled, and (iii) that the variation in adaptive traits is under the influence of divergent natural selection (thereby fulfilling the adaptive criterion).

3.1.1.1 Morphology

In the majority of sympatric pair DUs (Lake Opeongo, Como Lake, Témiscouata Lake, East Lake), a tremendous dichotomy in size between sexually mature fish is the primary trait distinguishing the species pairs within a lake environment (Figure 4a). Limnetic Lake Whitefish are rarely over 200 mm in length and 100g in weight. A sexually mature benthic Lake Whitefish, on the other hand, is almost always greater than 200 mm (usually bigger than 400 mm) and typically weighs more than 1000g. Fenderson (1964) reported that limnetic whitefish from Cliff Lake, Maine, ranged from 163 mm (age 1+) to 193 mm (age 5+) while benthic Lake Whitefish varied from 178 mm (age 1+) to 465 mm (age 12+). This was consistent with additional measurements in Cliff Lake where limnetic whitefish were on average 168 mm and benthic whitefish were on average 285 mm (Lu and Bernatchez 1999). Interestingly, although size-at-age was not known in Lu et al. (1999), those benthic Lake Whitefish were significantly smaller than those reported 30 years earlier in Fenderson (1964), suggesting that older benthic Lake Whitefish are not as frequent in this population, are growing slower, or maturing earlier. Size at maturity can differ greatly among lakes inhabiting the species pairs. In Lake Opeongo, limnetic Lake Whitefish are smaller than those in Cliff Lake, ranging from 109 mm (age 1+) to 134 mm (age 5+) while their benthic counterparts exhibit tremendous variation, from 78 mm (age 1+) to 456 mm (age 14+). However, species pairs of Lake Whitefish in Squanga Lake, Yukon, completely overlap with respect to size (Figure 4b, Lindsey 1963b)



(a)



(b)

Figure 4. Limnetic and benthic Lake Whitefish species pairs; (a) Benthic (top) and Limnetic (bottom) from Indian Lake, Maine, and (b) Limnetic (high gill raker, top) and Benthic (low gill raker, bottom) from Squanga Lake, Yukon.

Gill rakers have been found to contribute the most to significant morphological differences between lakes (Fenderson 1964, Kirkpatrick and Selander 1979, Bernatchez et al. 1996, Lu et al. 1999). Several studies on the adaptive divergence of northern temperate particulate feeding fishes have identified gill-raker characteristics as a key trait between diverging populations (Schluter and McPhail 1993, Robinson and Wilson 1994; Lu and Bernatchez, 1999, Landry et al. 2007). Gill rakers, the protuberances along the gill arches, are functional for sieving ingested prey while directing fluid movement within the buccal cavity; (Sanderson et al. 1991). Thus, gill raker number and spacing is believed to influence the efficiency of the retention of small prey (Schluter and McPhail, 1993; Robinson and Wilson, 1994; Budy and Haddix 2005) by potentially regulating fluid dynamics in the buccal cavity (Sanderson et al. 2001). Landry et al. (2007) discovered that a narrow length distribution of the planktonic invertebrate community resulted in a higher predation rate by limnetic whitefish. This was interpreted as evidence for resource limitation in the zooplanktonic structure, leading potentially to an increase in competition, which could ultimately result in a higher relative fitness for individuals with a higher efficiency in planktonic prey retention. To this end, Lindsey (1963b) and Bodaly (1979) revealed that limnetic ecotypes in southern Yukon possess more gill rakers than their counterpart benthic ecotypes. For example, limnetics have 27 or more while benthics have 26 or fewer (Lindsey 1963). However, this varies tremendously and appears to be associated with the degree of trophic resource overlap between the species (Bodaly 2007). In East Lake, for example, there is really no difference between limnetic and benthic with respect to gill raker counts (limnetic Lake Whitefish have an average of 25.5 while benthics have an average of 26, Lu et al. 1999). This finding is consistent with other Lake Whitefish species pairs in Canada and the United States (Kennedy 1943, Vuorinen et al. 1993, Lu et al. 1999, Bernatchez 2004, Landry et al. 2007).

Kennedy (1943) found differences in the number of scales in the lateral line, a finding consistent with Lu et al. (1999), but the utility of this trait is unclear. Other morphological variables rarely discriminate between populations. For example, Lu et al. (1999) found that of 19 morphometric variables measured in six sympatric populations, only four variables discriminated between limnetic and benthic populations; adipose fin length, pectoral fin length, caudal peduncle length, and maxillary width. Further studies have not found any of these traits to be under divergent selection between limnetics and benthics in nature (Rogers et al. 2002, Bernatchez 2004), although the latter three traits are known to be associated with trophic use efficiency in some fishes (Webb 1984). Caudal peduncle depth to length ratio was also found to differentiate limnetic and benthic in the Allagash Basin, where differences in blood types have also been documented (Fenderson 1964).

3.1.1.2 Behaviour

Adaptive trait differences have been observed for behavioural traits associated with habitat isolation and predator avoidance. Rogers et al. (2002) studied the genetic basis of three traits associated with swimming behaviours; depth selection, burst or 'fast start' swimming, and biased directional turns and found these behaviours differed between limnetic and benthic species pairs raised in the same environment, indicating a strong genetic basis for these traits. Analysis of the genes underlying these traits in natural populations found a significant reduction of gene flow at these genes, demonstrating that natural selection maintains differences in behavioural trait variation between the species pairs, at least in the environments examined thus far (Rogers and Bernatchez 2007).

3.1.1.3 Physiology and performance

Limnetic whitefish mature as early as one year old and seldom exceed 20 cm in length and 100 g in weight while benthic whitefish mature at an older age (greater than two years old) and commonly exceed 40 cm and 1000 g. Benthic benthic individuals typically reach sexual maturity at age 4 and may have a lifespan of up to 12 years, although Kennedy reported benthic individuals of 14 years old in Lake Opeongo, Ontario. Limnetic individuals reach sexual maturity earlier and typically do not live past 5 years (Kennedy 1943, Fenderson 1964).

Significant differences in size at maturity are associated with differences in growth (Bidgood 1973, Bidgood 1974, Beauchamp et al. 2004). Rogers and Bernatchez (2005) grew limnetic and benthic species pairs in the same environment and found that the limnetic group grew slower than the benthic group, leading to significant differences in size as early as age 1+. These differences in growth are likely due to differences in the bioenergetics of the species pairs as shown by Trudel et al. (2001). Under natural conditions, limnetic whitefish consume 40-50% more food than benthic ecotypes, yet their respective conversion efficiency of these resources is reported to be 2-3 times lower than the benthic ecotype (Trudel et al. 2001). These results were consistent with observations for lake cisco (*Coregonus artedii*, another coregonine species that feed in a limnetic environment, Trudel et al. 2001). Altogether, these findings demonstrate that inhabiting a limnetic environment has led to substantial bioenergetic differences in metabolism to the limnetic form. Differential growth is more difficult to measure in the field than size at maturity but could be an ideal trait to diagnose the species pairs if it was possible to rear specimens in a controlled environment.

3.1.1.4 Gene expression differences

Genes are the elemental units of adaptation. Genomic methods (e.g., microarrays, pyrosequencing) can measure levels of gene expression for thousands of genes, highlighting distinctive genes underlying local adaptation that can differentiate populations. Levels of differential gene expression have been measured for limnetic and benthic species pairs collected from two lakes in the Allagash Basin (Indian Lake and Cliff Lake, Maine) (Derome et al. 2006). Gene expression for over 130 genes in white muscle differed between limnetics and benthics in both lakes. Sixteen candidate genes (1.35%), belonging to energetic metabolism and regulation of muscle contraction, showed true parallelism of expression between the species pairs.

3.1.2 Evidence for local adaptation:

This key considers local adaptation in the strict sense in that variation in the trait is genetically controlled and influenced by divergent selection in distinct environments (Taylor 2006). Two methods have been applied to test the hypothesis that natural selection is maintaining differences between limnetic and benthic Lake Whitefish at the adaptive traits known to influence their survival in the limnetic and benthic trophic niches in nature. These methods include testing departures from neutrality at quantitative phenotypes ($Q_{ST} - F_{ST}$ comparisons, Rogers et al. 2002, Bernatchez 2004) and genome scans (Campbell and Bernatchez 2004, Rogers and Bernatchez 2005, 2007).

$Q_{ST} - F_{ST}$

Testing whether traits are under divergent natural selection can be tested by comparing the extent of differentiation at phenotypic traits (Q_{ST}) with that of neutral expectations (quantified at neutral molecular markers, F_{ST}) (Spitze 1993). Under the influence of neutral evolutionary forces (migration, mutation and drift) the among-population proportion of total genetic variance in phenotypic traits is expected to equal that of 'neutrally evolving' nuclear markers (Lande 1992). The prediction is that divergent selection will cause Q_{ST} to be larger than that expected from neutral expectations. Q_{ST} analyses based on the use of phenotypic variance as a surrogate for additive genetic variance must be interpreted cautiously. However, estimates derived from phenotypic and genotypic variance have not differed in their general patterns of F_{ST} - Q_{ST} relationships (Merilä and Crnokrak 2001, Lynch et al. 1999, Schluter 2000, Merilä and Crnokrak 2001, Bernatchez 2004) suggests that the approach based on phenotypic variance is not strongly biased.

In Lake Whitefish, upper departures of Q_{ST} from neutral expectations have been detected in behaviour, growth, and morphology suggesting these traits are locally adapted (Rogers et al. 2002, Bernatchez 2004, Rogers and Bernatchez 2005). Depth selection and gill-raker counts most strongly deviated from neutral expectations compared to other morphological traits. Bernatchez (2004) estimated Q_{ST} for 18 morphological characters and found that gill raker counts were the only character between limnetic and benthic whitefish to differ significantly from neutral expectations suggesting that it most likely evolved under directional selective pressures. Q_{ST} results should be interpreted with caution given that phenotypic rather than genetic variance was used. Yet, they strongly suggest that differences in behaviour, growth, and gill raker counts are driven by divergent natural selection, particularly when parallel departures from neutral expectations occur in multiple environments.

Genome Scans

A central challenge in adaptive variation is to identify genes underlying ecologically important traits and describe the fitness consequences of naturally occurring variation at these loci (Stinchcombe and Hoekstra 2007). The “genome scan” approach partially circumvent these problems through the simultaneous study of a large number of genetic markers to better understand the action of evolutionary forces on variation among populations at specific genetic markers or genes. Such studies hypothesize that the action of divergent selection should reduce gene flow at genomic regions implicated in adaptation and speciation. Empirical and simulation data strongly suggest that detecting loci subjected to directional selection is feasible on the basis of genetic differentiation estimates among genetic markers (Storz 2005, Campbell and Bernatchez 2004). In these cases, “outlier loci” exhibit much greater genetic distances than one would expect from neutral evolution alone. Genome scans must confirm the function and role of these outliers to demonstrate that the increased molecular divergence is due to selection (Luikart et al. 2003).

Lake Whitefish represent one of the first empirical examples of how genome scans identified the most likely candidate genetic markers to be under the influence of local adaptation (Campbell and Bernatchez 2004). Rogers and Bernatchez (2005, 2007) were able to demonstrate that genetic markers associated with adaptive traits such as swimming behaviour (habitat selection, predator avoidance, growth rate, morphology (condition factor and gill rakers), and life history (onset of maturity and fecundity) were outliers between limnetics and benthics in nature, providing strong support for the hypothesis that divergent natural selection is currently maintaining adaptive differentiation and promoting ecological speciation in Lake Whitefish species pairs.

3.2. Identification of the limnetic and benthic species pairs as not ecologically interchangeable with other known PDUs within the species

Recent ecological non-exchangeability may be indicative of adaptive divergence and population persistence (Crandall et al. 2000). Genetic distinctiveness alone, however, does not imply that adaptive divergence has occurred. This is the challenge associated with making the link between ecological differentiation and heritable genetic variation in the wild (Fraser and Bernatchez 2001). To answer these questions, the origin of the species pairs and the underlying forces responsible need to be considered. If species pairs have arisen independently and more than once, and we can associate parallel adaptive traits with this divergence, then this supports the hypothesis that limnetic and benthic species pairs are not ecologically interchangeable with other PDUs within the species.

3.2.1 Independent origins of the species pairs

Replicate evolution of the species pairs, a common phenomenon among other north temperate species, suggests that natural selection is the main evolutionary force driving the divergence of these forms (Taylor 1999, Robinson and Schluter 2000, Schluter and Nagel 1995, Rogers and Bernatchez 2007). However, multiple modes of speciation are involved in the divergence. Allopatric divergence of glacial races followed by subsequent secondary contact and reinforcement has been found in some lakes (e.g., Lac Témiscouata). The best genetic and ecological evidence for the allopatric scenario has been found for Lake Whitefish inhabiting Cliff Lake (St. John River Drainage, Maine, USA). Limnetic and benthic species pairs in this lake are the result of secondary contact between previously allopatric Atlantic (benthic) and Acadian (limnetic) whitefish glacial races, both of benthic phenotype when in allopatry, now coinhabiting the lake (Bernatchez and Dodson 1990). Parallel adaptive radiation and ecological speciation has also led to divergence of the species pairs in lakes colonized by a single glacial race (e.g., the Acadian glacial race that colonized East Lake). Thus, both allopatric and sympatric modes of speciation are independently involved in the evolution of the species pairs (Bernatchez et al. 1996).

Differentiation between limnetics and benthics has been shown to be associated with parallel genetic signatures of selection in natural populations, providing support for the hypothesis that divergent natural selection is currently maintaining adaptive differentiation and promoting ecological speciation in some of these Lake Whitefish species pairs, regardless of the historically contingent factors (Rogers and Bernatchez 2007). This is further supported by associations between neutral genetic data and the degree of trophic specialization. Chouinard and Bernatchez (1998) demonstrated a correlation with trophic niche overlap and gene flow between ecotypes. Lakes inhabiting the limnetic and benthic species pairs have significantly higher gene flow in the presence of overlapping trophic niches when compared to lakes with less gene flow. Traits that differentiate the two ecotypes are directly related to the specialization and availability of trophic niches, leading to a negative correlation between the extent of gene flow and morphological specialization between species pairs among lakes (Chouinard and Bernatchez 1998, Chouinard et al. 1996, Lu and Bernatchez 1999)

Limnetic Lake Whitefish are only found in sympatry with the benthic ecotype and only in the absence of other limnetic coregonine fishes such as the cisco (*Coregonus artedii*), suggesting that divergent natural selection resulting from ecological pressures within the benthic niche may explain the evolution of the derived *limnetic* whitefish (Pigeon et al. 1997). This has been supported by evidence for convergence in the expression of genes associated with the limnetic life history (metabolism and swimming efficiency) among coregonine species. Derome and Bernatchez (2006) tested whether the same genes associated with adaptive divergence in limnetic Lake Whitefish were also implicated *C. artedii*. They found that both limnetic Lake Whitefish and cisco were over-expressing the same candidate genes modulating swimming activity. Natural selection in the limnetic niche appears to act on the same genetic variation in both species. However, even greater upregulation in cisco suggested that this species had a greater physiological potential in the limnetic niche, potentially explaining why the addition of a cisco to lakes inhabiting the limnetic species would likely result in its extinction (Derome and Bernatchez 2006).

Overall, there is substantial evidence that ecological processes are a factor for the extent of reproductive isolation and contribute to the sustained differentiation between the ecotypes (Bernatchez et al. 1996, Pigeon *et al.* 1997, Lu et al. 1999, Rogers and Bernatchez 2007, Landry et al. 2007). Moreover, it has been demonstrated that divergent selection reduces gene flow at ecologically relevant genes associated with adaptive traits such as growth in multiple limnetic and benthic species pairs (Rogers and Bernatchez 2005). Adaptive traits exhibit much less gene exchange than other regions of the genome, supporting the hypothesis that divergent selection maintains adaptive differentiation despite the effects of gene flow (Rogers and Bernatchez 2007). Although there is no single trait distinguishes the PDU, these genetic data provide good evidence that a particular suite of adaptations make it very unlikely that the PDU could be replaced by recolonization or deliberate introductions from another population, consistent with the criteria set forth by Taylor (2006). However, despite the fact that similar ecological processes are involved in the parallel evolution of the species pairs, it remains difficult to establish the degree of ecological interchangeability with other PDUs within the species.

3.2.2 Evidence of reproductive isolation

Controlled crosses between limnetic and benthic species pairs have demonstrated significant intrinsic and extrinsic postzygotic isolation (Lu 1998, Rogers and Bernatchez 2006). Hybrid inviability under experimental conditions is up to five times higher in hybrids than what is observed in the pure crosses. However, this experimental design in both of these studies employed crosses originating from different glacial races which may have had a significant impact in the degree of reproductive isolation. More recent studies have isolated the genetic factors associated with this decrease in fitness and found that progeny from hybrid backcross families either died during development or hatched at a sub-optimal time, suggesting that both genetic incompatibilities and extrinsic postzygotic isolation contribute to reproductive barriers (Rogers and Bernatchez 2006). This is consistent with observations that hybrids between diverging populations are rare (1-3%) within their natural habitat (Bodaly 1979b). More studies on the degree of reproductive isolation between glacial races and species pairs are clearly needed.

3.3. Are limnetic and benthic species pairs an irreplaceable component of Canadian biodiversity?

Lake Whitefish were among the first fish species to colonize the Canadian landscape. Less than 10 000 years later they now comprise some of the youngest biological species on earth (Bernatchez et al. 1999). The evolution of these species pairs reflects rapid adaptation following colonization of a novel niche not inhabited by the ancestral form within postglacial environments (Rogers and Bernatchez 2007). The derived Eurasian limnetic form is also an important prey resource for larger salmonid predators and in some cases is their main source of food (Kahilainen et al. 2002, 2003). Predation of limnetic Lake Whitefish from large salmonid predators such as lake trout is common (Dave Basely, Maine Fish and Wildlife, personal communication), but this has not been resolved in detail.

Unique scenarios of population divergence between some species pairs (e.g., Squanga Lake Whitefish, Bodaly 2007) suggest that other historically contingent or ecological factors may affect population divergence in certain northern temperate limnetic and benthic environments. Namely, the role of historical contingency, due in part to isolation in glacial refugia, has also been shown to play a significant role in the evolution of reproductive isolation in many species pairs (Lu et al. 2001, Rogers et al. 2001). Historical contingency refers to the original assemblage, locally specific and unique selection pressures, and locally unique stochastic influences (e.g., founder effects, drift, extinctions), that may have influenced the evolutionary history of a lineage. In cases where inviability is associated with divergence in allopatry rather than sympatry, historical contingency may have primed subsequent ecological determinism (Taylor and McPhail 2000, Fraser, 2005, Rogers, 2001, Rogers and Bernatchez 2006). This is important to acknowledge given the mandate of COSEWIC to maximize the probability of protecting biological variation within a species. This requires considering both historical and ecological evolutionary forces that have given rise to isolated lineages (Fraser and Bernatchez 2001). Because evolutionary divergence in limnetic and benthic Lake Whitefish will be determined by the conditions of the lake (Bernatchez 2004), standing genetic variation of the colonizers (Rogers and Bernatchez 2005, Barrett and Schluter 2008), along with historically contingent factors that promote their differentiation (Lu et al. 2001, Rogers et al. 2001, Rogers and Bernatchez 2006), the limnetic ecotype and the conditions that led to its divergence may differ from one environment to the next. Given the data, it would likely be unwise to assume that if one limnetic population was wiped out it could be created anew. This has been reinforced in similar species pairs such as threespine stickleback (*Gasterosteus aculeatus*), whereby alterations of natural habitat, such as an invasive species, resulted in the so-called “speciation in reverse” or collapse of a species pair (Taylor et al. 2006). Indeed, the introduction of ciscoes in Squanga whitefish lakes are suspected to have resulted in the extinction of the limnetic whitefish. Similarly, a whitefish population could be significantly reduced by the addition of a piscivorous fish to its lake (SARA 2006, both factors leading COSEWIC to list the Squanga Lake Whitefish as a population of ‘special concern’. Overall, limnetic and benthic Lake Whitefish species pairs embody the process of rapid evolutionary change but their extinction in a significant number of environments is a stark reminder that conservation efforts may ultimately be necessary for their persistence.

3.3. Consideration of the Mira River population

This small population of Lake Whitefish in Nova Scotia is found in a restricted range of the Mira and Salmon rivers (less than 100 km²) and have low lateral line scale and gill raker counts (Edge et al. 1991). The Mira River population is listed by COSEWIC as data deficient (Goodchild, 1999). Consequently, there is insufficient information to assess ecological interchangeability of the Mira River with other populations.

3.5. Summary

- There is no single phenotypic trait that can be used to identify the species pairs but instead a suite of phenotype-environment associations that have been empirically tested in the lab and in nature among certain lakes inhabiting the species pairs.
- In lakes where the species pairs are purported to exist but phenotype-environment associations have not been assessed, or genetic differentiation between limnetic and benthic is unknown, DU status should be deferred until these data can be provided.
- Although ecological processes are associated with adaptive divergence, historically contingent reductions of introgression may differ among glacial races and play distinct roles during evolution in sympatry.

4. The PDU represents a major range disjunction?

Taylor (2006) defined major range disjunctions as two or more groups of populations separated widely by naturally unoccupied areas. Generally, this would include an area across which natural dispersal is not observed nor expected. Disjunctions may therefore reflect evolutionarily significant events caused by major geological transitions that now separate the species (e.g., ice sheets, change in sea level, and formation of mountains).

Lake Whitefish are the most broadly distributed freshwater fish in Canada (Figure 3). Lindsey (1970) noted that at least three sympatric pairs of whitefish species pairs exhibited range disjunction (east, west, and central Canada) as evidence that these have evolved independently. This was also considered as some of the first evidence that these populations survived in separate glacial refugia. Pigeon et al. (1997) supported these disjunctions between species pairs and proposed that five regions; St. John River Drainage, northern Quebec and Labrador, Ontario, Yukon, and British Columbia were disjunct and therefore Lake Whitefish species pairs must have evolved independently.

4.1. Summary

Based on section 2.1, the disjunct regions proposed by Lindsey (1970) and Pigeon et al. (1997) also reflect evolutionarily significant sunderings caused by the glaciations. Arguably, these disjunctions do not contribute to the existing criteria under which Lake Whitefish glacial races and species pairs are considered as PDUs, and are already depicted in the major phylogeographic groupings. Consequently, major range disjunctions alone need not be identified as PDUs. Given the limitations of applying disjunction or population separation to lacustrine species, and the purpose of this report as testing DU criteria in a representative species, there is an obvious caveat regarding geographic separation as it applies to habitat-restricted species. Although the criteria regarding disjunctions is valuable; it is worth noting that for obligatory lacustrine species historical water connections such as glacial meltwater lakes may be more relevant than contemporary watershed boundaries

5. The PDU inhabits a different biogeographic zones?

National Freshwater Ecological Areas represent different eco-geographic regions within Canada (Figure 5). These regions may be relevant to Lake Whitefish if they depict the previously described glacial history within these phylogeographic zones. Fourteen biogeographic zones have been defined in Canada (Mandrak 2003). This scheme is meant to capture the major divisions within named taxa (i.e., the phylogeographic groupings of Lake Whitefish). Indeed, the Lake Whitefish species complex exists in eleven of these biogeographic zones with the exception of the Pacific Islands (Lake Whitefish are only indigenous to mainland BC), the Arctic Archipelago, and the Atlantic Islands (although Lake Whitefish were introduced into some lakes in Newfoundland, Scott and Crossman (1964)) (Figure 5).

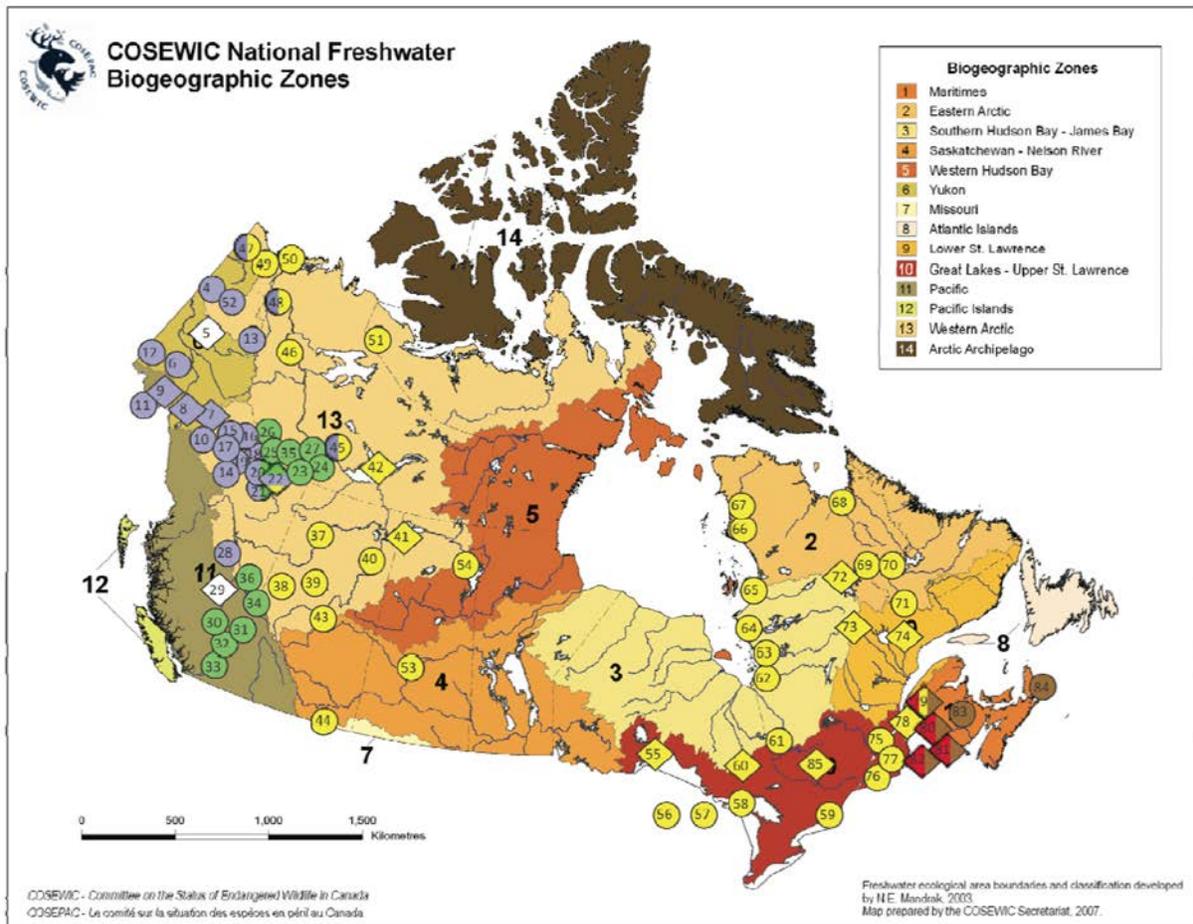


Figure 5. Distribution of samples with respect to National Freshwater Biogeographic Zones. See Table 1 for more information.

The Mississippian Glacial Race is captured by eight ecoregions, the largest number of all the putative phylogeographic DUs, while the Atlantic PDU consists of only one ecoregion, Lac Témiscouata in the Maritime NFEA (Table 1, Figure 2, Figure 5). Over thirty populations from the Mississippian, Beringian, and Nahanni groups are represented in the Western Arctic NFEA, the largest number of Lake Whitefish populations within a single NFEA. At the other end of the range, only one Mississippian Lake Whitefish population is found in the Missouri ecoregion (Table 1). However, these samples do not represent the entire distribution of the species within these regions and Lake Whitefish likely exist in other lakes and rivers within these areas.

5. 1 Summary

NFEA are identified as significant DUs that capture the significant major phylogeographic groupings of the species complex and the major range disjunctions previously described. The eleven NFEAs designated as DU for the Lake Whitefish species complex are: Maritimes, Eastern Arctic, Southern Hudson Bay-James Bay, Saskatchewan-Nelson, Western Hudson Bay, Yukon, Missouri, Eastern St. Lawrence, Great Lakes-Western St. Lawrence, Pacific and Western Arctic (Table 1, Figure 2).

6. Concluding Summary

- The taxonomic status, biology, and life history of the Lake Whitefish has been a source of taxonomic confusion for over one hundred years. Lake Whitefish have been described as several different species due to the tremendous variation it exhibits across its range. One species included in the Lake Whitefish species complex, *Coregonus pidschian*, has a genetic signature almost identical to the Eurasian whitefish, *Coregonus lavaretus*. Consequently, this species should be considered as a separate DU within the Lake Whitefish species complex.
- Ecological opportunity and divergent natural selection within postglacial lakes has led to the repeated evolution of a derived species that inhabits the limnetic zone of lakes and does not randomly interbreed with their benthic counterparts, an evolutionary pattern repeated regardless of allopatric or sympatric origin. Ecological speciation of seven Canadian Lake Whitefish populations meet the guidelines for designation of DUs (Figure 2)
- Lake Whitefish populations across Canada were significantly impacted by the Pleistocene glaciations. The phylogeography of the species across Canada demonstrates how thousands of years of separation within glacial refugia located in different areas of the country have led to contemporary reproductive isolation between populations that can be detected genetically. Four of these Canadian Lake Whitefish glacial races separated by major phylogeographic groupings caused by isolation during the Pleistocene ice age meet the guidelines for DU while one (Nahanni, Figure 2) should be granted provisional DU status.
- Adoption of NFEA DUs that encompass both the major phylogeographic groupings and the species pairs may facilitate conservation scenarios while addressing regional situations towards ultimately adopting appropriate DUs for use in subsequent status assessments for Lake Whitefish as a whole
- Conserving these differences among species pairs and glacial races as designatable units, fundamental to the biodiversity of the species, will help ensure that the evolutionary legacy of this species complex is protected in Canada.

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LITERATURE CITED

- Alt, K. 1971. Occurrence of hybrids between inconnu, *Stenodus leucichthys nelma* (Pallas), and humpback whitefish, *Coregonus pidschian* (Linnaeus) in Chatanika river, Alaska. *Transactions of the American Fisheries Society* 100: 362 – 365.
- Alt, K.T. 1979. Contributions to the life history of the humpback whitefish in Alaska. *Transactions of the American Fisheries Society* 108: 156 – 160.
- Barrett, R.D.H., and Schluter, D. 2008. Adaptation from standing genetic variation. *Trends in Ecology and Evolution* 23: 38 – 44.
- Bean, T.H. 1884. Description of a new species of whitefish (*Coregonus nelsonii*) from Alaska. *Proceedings of the U.S. National Museum*. Case Reference number 16047.
- Beauchamp, K.C., Collins, N.C., and Henderson, B.A. 2004. Covariation of growth and maturation of Lake Whitefish (*Coregonus clupeaformis*). *Journal of Great Lakes Research* 30: 451 – 460.
- Baumont, A.R., Bray, J., Murphy, J.M., and Winfield, I.J. 1995. Genetics of whitefish and vendace in England and Wales. *Journal of Fish Biology* 46: 880 – 890.
- Behnke, R.J. 1972. Systematics of Salmonid Fishes of Recently Glaciated Lakes. *Journal of the Fisheries Research Board of Canada* 29: 639
- Bernatchez, L. 2004. Ecological Theory of Adaptive Radiation: An empirical assessment from Corigonine fishes (Salmoniformes). *In Evolution Illuminated: Salmon and Their Relatives. Edited by A.P. Hendry and S. Stearns.* Oxford University Press, Oxford, U.K. pp. 176 – 207.
- Bernatchez, L. 2005. On the role of natural selection in promoting population divergence in Lake Whitefish (*Coregonus clupeaformis*): relevance for population management in the Great Lakes. *In Proceedings of a workshop on the dynamics of Lake Whitefish (Coregonus clupeaformis) and the amphipod Diporeia spp. in the Great Lakes.* Ann Arbor, MI. *Edited by Great Lakes Fisheries Commission.*
- Bernatchez, L., Chouinard, A., and Lu, G. 1999. Integrating molecular genetics and ecology in studies of adaptive radiation: whitefish, *Coregonus* sp., as a case study. *Biological Journal Of The Linnean Society* 68: 173 – 194.
- Bernatchez, L., Colombani, F., and Dodson, J.J. 1991a. Phylogenetic-Relationships among the Subfamily Coregoninae as Revealed by Mitochondrial-DNA Restriction Analysis. *Journal of Fish Biology* 39: 283 – 290.

- Bernatchez, L., and Dodson, J.J. 1990. Allopatric Origin of Sympatric Populations of Lake Whitefish (*Coregonus clupeaformis*) as Revealed by Mitochondrial-DNA Restriction Analysis. *Evolution* 44: 1263 – 1271.
- Bernatchez, L., and Dodson, J.J. 1991. Phylogeographic structure in mitochondrial-DNA of the Lake Whitefish (*Coregonus clupeaformis*) and its relation to Pleistocene glaciations. *Evolution* 45: 1016 – 1035.
- Bernatchez, L., and Dodson, J.J. 1994. Phylogenetic relationships among Palearctic and Nearctic whitefish (*Coregonus* sp.) populations as revealed by mitochondrial DNA variation. *Canadian Journal of Fisheries and Aquatic Sciences* 51(Suppl. 1): 240 – 251.
- Bernatchez, L., Dodson, J.J., and Boivin, S. 1989. Population bottlenecks: Influence on mitochondrial DNA diversity and its effect in coregonine stock discrimination. *Journal of Fish Biology*. 35: 233 – 244.
- Bernatchez, L., Edge, T.A., Dodson, J.J., and Qadri, S.U. 1991b. Mitochondrial-DNA and Isozyme Electrophoretic Analyses of the Endangered Acadian Whitefish, *Coregonus-Huntsmani* Scott, 1987. *Canadian Journal of Zoology* 69: 311 – 316.
- Bernatchez, L., Vuorinen, J.A., Bodaly, R.A., and Dodson, J.J. 1996. Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus clupeaformis*). *Evolution* 50: 624 – 635.
- Bernatchez, L., and Wilson, C. 1998. Comparative phylogeography of nearctic and palearctic fishes. *Molecular Ecology* 7: 431 – 452.
- Bidgood, B.F. 1973. Divergent Growth in two Lake Whitefish (*Coregonus clupeaformis*) Populations. *Journal of the Fisheries Research Board of Canada* 30: 1683 – 1696.
- Bidgood, B.F. 1974. Reproductive Potential of 2 Lake Whitefish (*Coregonus clupeaformis*) Populations. *Journal of the Fisheries Research Board of Canada* 31: 1631 – 1639.
- Bodaly, R.A. 1977. Evolutionary divergence between currently sympatric Lake Whitefish, *Coregonus clupeaformis*. Ph.D. thesis, University of Manitoba, Winnipeg.
- Bodaly, R.A. 1979. Morphological and Ecological Divergence within the Lake Whitefish (*Coregonus clupeaformis*) Species Complex in Yukon Territory. *Journal of the Fisheries Research Board of Canada* 36: 1214 – 1222.
- Bodaly, R.A. 1986. Biology, exploitation and culture of Coregonine fishes in Canada. *Arch. Hydrobiol. Beih., Ergebn. Limnol.* 22: 1 – 30.
- Bodaly, R.A., Vuorinen, J., Reshetnikov, Y.S., and Reist, J.D. 1994. Genetic relationships of five species of Coregonine fishes from Siberia [translated from Russian]. *Journal of Ichthyology* 34: 117 – 130.
- Bodaly, R.A. 2007. COSEWIC Status Report on Squanga whitefish *Coregonus* sp. Edited by Freshwater Fisheries Specialist Subcommittee. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca).

- Bodaly, R.A., Clayton, J.W., and Lindsey, C.C. 1987. COSEWIC status report on the Squanga whitefish *Coregonus* sp. in Canada. *Edited by* Freshwater Fisheries Specialist Subcommittee. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca). p. iv + 32 pp.
- Bodaly, R.A., Clayton, J.W., and Lindsey, C.C. 1988. Status of the Squanga whitefish, *Coregonus* sp., in the Yukon Territory, Canada. *Canadian Field Naturalist* 102: 114 – 125.
- Bodaly, R.A., Clayton, J.W., Lindsey, C.C., and Vuorinen, J. 1992. Evolution of Lake Whitefish (*Coregonus clupeaformis*) in North-America During the Pleistocene – Genetic Differentiation between Sympatric Populations. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 769 – 779.
- Bodaly, R.A., Vuorinen, J., and Macins, V. 1991. Sympatric presence of limnetic and benthic forms of the Lake Whitefish, *Coregonus clupeaformis*, in Como Lake, Ontario. *Canadian Field Naturalist* 105: 87 – 90.
- Bodaly, R.A., Vuorinen, J., Reshetnikov, Y.S., and Reist, J.D. 1994. Genetic relationships of five species of Coregonine fishes from Siberia [translated from Russian]. *Journal of Ichthyology* 34: 117 – 130.
- Bodaly, R.A., Vuorinen, J., Ward, R.D., Luczynski, M., and Reist, J.D. 1991b. Genetic comparisons of new and old world Coregonine fishes. *Journal of Fish Biology* 38: 37-51.
- Brown, R.W., and Taylor, W.W. 1992. Effects of Egg Composition and Prey Density on the Larval Growth and Survival of Lake Whitefish (*Coregonus clupeaformis* Mitchell). *Journal of Fish Biology* 40: 381 – 394.
- Budy, P., and Haddix, T. 2005. Zooplankton Size Selection Relative to Gill Raker Spacing in Rainbow Trout. *Transactions of the American Fisheries Society* 134: 1228 – 1235.
- Campbell, D., and Bernatchez, L. 2004. Genomic scan using AFLP markers as a means to assess the role of directional selection in the divergence of sympatric whitefish ecotypes. *Molecular Biology and Evolution* 21: 945 – 956.
- Campbell, D., Duchesne, P., and Bernatchez, L. 2003. AFLP utility for population assignment studies: analytical investigation and empirical comparison with microsatellites. *Molecular Ecology* 12: 1979 – 1991.
- Casselman, J.M., Collins, J.J., Crossman, E.J., Ihssen, P.E., and Spangler, G.R. 1981. Lake Whitefish (*Coregonus clupeaformis*) Stocks of the Ontario Waters of Lake Huron. 38: 1772 – 1789.
- Casselman, S.J., and A.I. Schulte-Hostedde. 2004. Reproductive roles predict sexual dimorphism in internal and external morphology of Lake Whitefish (*Coregonus clupeaformis*). *Ecology of Freshwater Fish* 13: 217 – 222.
- Champigneulle, A., and Rojas-Beltran, R. 1990. First attempts to optimize the mass rearing of whitefish (*Coregonus lavaretus* Linnaeus) larvae from L emen and Bourget lakes (France) in tanks and cages. *Aquatic Living Resources* 3: 217 – 228.

- Chouinard, A., and Bernatchez, L. 1998. A study of trophic niche partitioning between larval populations of reproductively isolated whitefish (*Coregonus* sp.) ecotypes. *Journal of Fish Biology* 53: 1231 – 1242.
- Chouinard, A., Pigeon, D., and Bernatchez, L. 1996. Lack of specialization in trophic morphology between genetically differentiated limnetic and benthic forms of Lake Whitefish (*Coregonus clupeaformis* Mitchell) in Lac de l'Est, Québec. *Canadian Journal of Zoology* 74: 1989 – 1998.
- Conway, K.W., Barrie, J.V., and Hebda, R.J. 2001. Evidence for a Late Quaternary outburst flood event in the Georgia Basin, British Columbia *Edited by Geological Society of Canada*.
- COSEWIC. 2005a. COSEWIC assessment and update status report on the Lake Whitefish (Lake Simcoe population) *Coregonus clupeaformis* in Canada. *Edited by Committee on the Status of Endangered Wildlife in Canada*, Ottawa. p. vii + 36. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca)
- COSEWIC. 2005b. Guidelines for recognizing designatable units below the species level. *Edited by Committee on the Status of Endangered Wildlife in Canada*, Ottawa. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca)
- Crandall, K., Bininda-Emonds, O., Mace, G., and Wayne, R. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* 15: 290 – 295.
- Crossman, E.J., and D.E. McAllister, 1986. Zoogeography of freshwater fishes of the Hudson Bay drainage, Ungava Bay and the Arctic Archipelago, In *The zoogeography of North American freshwater fishes*, C.H. Hocutt and E.O. Wiley (editors.), John Wiley and Sons, New York, p. 53 – 104.
- Cucin, D., and Faber, D.J. 1985. Early life studies of Lake Whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*) in lake Opeongo, Ontario. Ontario fisheries technical report series no. 16: iii-28.
- Curry, R.A. 2007. Late glacial impacts on dispersal and colonization of Atlantic Canada and Maine by freshwater fishes. *Quaternary Research* 67: 225 – 233.
- Davis, B.M., and Todd, T.N. 1998. Competition between larval lake herring (*Coregonus artedii*) and Lake Whitefish (*Coregonus clupeaformis*) for zooplankton. 55: 1140 – 1148.
- Dawson, A.G. 2002. *Ice Age Earth*. Routledge Press, London.
- de Vernal, A., and Hillaire-Marcel, C. 2000. Sea-ice cover, sea-surface salinity and halo/thermocline structure of the northwest North Atlantic: Modern versus full glacial conditions. *Quaternary Science Reviews* 19: 65 – 85.
- Denton, G.H., and Hughes, T.J. 1981. *The last great ice sheets*. John Wiley and Sons, New York.

- Derome, N., and Bernatchez, L. 2006. The transcriptomics of ecological convergence between 2 limnetic coregonine fishes (Salmonidae). *Molecular Biology and Evolution* 23: 2370 – 2378.
- Derome, N., Duchesne, P., and Bernatchez, L. 2006. Parallelism in gene transcription among sympatric Lake Whitefish (*Coregonus clupeaformis* Mitchell) ecotypes. *Molecular Ecology* 15: 1239 – 1249.
- Department of Fisheries and Oceans, Canada. 2005. Ontario-Great Lakes Area Fish Fact Sheets. Available from http://www.dfo-mpo.gc.ca/regions/central/pub/fact-fait-ogla-rglo/lakewhitefish_e.htm.
- Douglas, M.R., Brunner, P.C., and Douglas, M.E. 2005. Evolutionary homoplasy among species flocks of central alpine Coregonus (Teleostei : Salmoniformes). *Copeia* 2: 347 – 358.
- Drouin, M.A., Kidd, R.B., and Hynes, J.D. 1986. Intensive Culture of Lake Whitefish (*Coregonus clupeaformis* Mitchell) Using Artemia and Artificial Feed. *Aquaculture* 59: 107 – 118.
- Eckmann, R., Appenzeller, A., and Rösch, R. 1996. Biology and Management of Coregonine Fishes – Proceedings of the Sixth International Symposium on the Biology and Management of Coregonine Fishes, Konstanz, Germany.
- Edge, T.A., McAllister, D.E., and Qadri, S.U. 1991. Meristic and Morphometric Variation between the Endangered Acadian Whitefish, *Coregonus huntsmani*, and the Lake Whitefish, *Coregonus clupeaformis*, in the Canadian Maritime Provinces and the State of Maine, USA. 48: 2140 – 2151.
- Edsal, T.A. 1960. Age and growth of the whitefish, *Coregonus clupeaformis*, of the Munising Bay, Lake Superior. *Transactions of the American Fisheries Society* 89: 323 – 332.
- Fenderson. 1964. Evidence of subpopulations of Lake Whitefish, *Coregonus clupeaformis*, involving a dwarfed form. *Transactions of the American Fisheries Society* 93: 77 – 94.
- Flüchter, J. 1980. Review of the present knowledge of rearing whitefish (Coregonineae) larvae. *Aquaculture* 19: 191 – 208.
- Foote, C.J. 1979. A biochemical genetic study of zoogeography of Lake Whitefish, *Coregonus clupeaformis*, in western Canada in relation to their possible survival in a Nahanni glacial refugium, University of Manitoba, Winnipeg.
- Foote, C.J., Clayton, J.W., Lindsey, C.C., and Bodaly, R.A. 1992. Evolution of Lake Whitefish (*Coregonus clupeaformis*) in North-America During the Pleistocene – Evidence for a Nahanni Glacial Refuge Race in the Northern Cordillera Region. 49: 760 – 768.
- Ford, D.C. 1974. Evidences of multiple glaciation in South Nahanni National Park, Mackenzie Mountains, North West Territories, Canada. *Canadian Journal of Earth Science* 13: 1433 – 1445.

- Fortin, R., and Gendron, M. 1990. Comparative Reproduction, Growth and Morphology of Limnetic and benthic Whitefish [*Coregonus clupeaformis*] in the Outardes-2 Reservoir (Quebec). *Canadian Journal of Zoology* 68: 17 – 25.
- Franzin, W.G., and Clayton, J.W. 1977. Biochemical Genetic Study of Zoogeography of Lake Whitefish (*Coregonus clupeaformis*) in Western Canada. *Journal of the Fisheries Research Board of Canada* 34: 617 – 625.
- Fraser, D.J., and Bernatchez, L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology* 10: 2741 – 2752.
- Fraser, D.J., and Bernatchez, L. 2005. Allopatric origins of sympatric brook charr populations: colonization history and admixture. *Molecular Ecology* 14: 1497 – 1509.
- Fraser, D.J., Hansen, M.M., Ostergaard, S., Tessier, N., Legault, M., and Bernatchez, L. 2007. Comparative estimation of effective population sizes and temporal gene flow in two contrasting population systems. *Molecular Ecology* 16: 3866 – 3889.
- Gmelin, J.F. 1789. *Systema Naturae*. Ed. 13. (3). Amphibia et Pisces. Leipzig.
- Goodchild, C.D. 1999. COSEWIC status report on the Lake Whitefish *Coregonus clupeaformis* Mira River population in Canada. *Edited by Committee on the Status of Endangered Wildlife in Canada*. p. 29
- Hamada, M., Kido, Y., Himberg, M., Reist, J.D., Ying, C., Hasegawa, M., and Okada, N. 1997. A newly isolated family of short interspersed repetitive elements (SINEs) in Coregonine fishes (whitefish) with sequences that are almost identical to those of the Smal family of repeats: Possible evidence for the horizontal transfer of SINEs. *Genetics* 146: 355 – 367.
- Harris, K.C., and Hulsman, P.F. 1991. Intensive Culture of Lake Whitefish (*Coregonus clupeaformis*) from Larvae to Yearling Size Using Dry Feeds. *Aquaculture* 96: 255 – 268.
- Hasselman, D.J. 2003. Discrimination of adult and early life history stage Coregonine fishes in Maritime Canada, Acadia University, Wolfville, Nova Scotia, Canada.
- Heuts, B. 1999. Lateralization of trunk muscle volume, and lateralization of swimming turns of fish responding to external stimuli. *Behavioral Process* 47: 113 – 124.
- Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal Of The Linnean Society* 58: 247 – 276.
- Ihssen, P.E., Evans, D.O., Christie, W.J., Reckahn, J.A., and Desjardine, R.L. 1981. Life-History, Morphology, and Electrophoretic Characteristics of 5 Allopatric Stocks of Lake Whitefish (*Coregonus clupeaformis*) in the Great-Lakes Region. 38: 1790 – 1807.
- Imhof, M., Leary, R., and Booke, H.E. 1980. Population or Stock Structure of Lake Whitefish, *Coregonus clupeaformis*, in Northern Lake-Michigan as Assessed by Isoenzyme Electrophoresis. 37: 783 – 793.
- Kennedy, W.A. 1943. The whitefish *Coregonus clupeaformis* (Mitchill), of Lake Opeongo, Algonquin Park, Ontario. *Univ. Toronto Stud. Biol. Ser. No. 51 (Publ. Ontario Fish. Res. Lab. No. 62): 22 – 43.*

- Kirkpatrick, M., and Selander, R.K. 1979. Genetics of speciation in Lake Whitefishes in the Allegash basin. *Evolution* 33: 478 – 485.
- Koelz, W. 1929. Coregonine fishes of the Great Lakes. *Bulletin of the United States Bureau of Fisheries* 43: 297 – 643.
- Lande, R. 1992. Neutral theory of quantitative genetic variance in an island model with local extinction and colonization. *Evolution* 46: 381 – 389.
- Landry, L., Vincent, W.F., and Bernatchez, L. 2007. Parallel evolution of Lake Whitefish limnetic ecotypes in association with limnological features of their adaptive landscape. *Journal of Evolutionary Biology* 20: 971 – 984.
- Lasenby, T.A., Kerr, S.J., and Hooper, G.W. 2001. *Lake Whitefish Culture and Stocking: An Annotated Bibliography and Literature Review*, Peterborough, Ontario.
- Lindsey, C.C. 1962. Distinctions between the broad whitefish, *Coregonus nasus*, and other North American whitefishes. *Journal of Fisheries Research Board Canada* 19: 687 – 714.
- Lindsey, C.C. 1963a. Status of the whitefish species, *Coregonus nelsonii*, and the designation of a new type. *Copeia* 1: 173 – 174.
- Lindsey, C.C. 1963b. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. *Journal of Fisheries Research Board Canada* 20: 749 – 767.
- Lindsey, C.C. 1975. Proglacial lakes and fish dispersal in southwestern Yukon territory. *Verh. Internat. Verein. Limnol.* 19: 2364 – 2370.
- Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of Coregonine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1497 – 1506.
- Lindsey, C.C., and McPhail, J.D. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins. In . Edited by: New York. pp. 639–673. In *The zoogeography of North American freshwater fishes*. Edited by C.H. Hocutt and E.O. Wiley. John Wiley and Sons, New York.
- Lindsey, C.C. 1988. The relevance of systematics and nomenclature to Coregonine management. *Finnish Fisheries Research* 9: 1 – 10.
- Lindsey, C.C., Clayton, J.W., and Franzin, W.G. 1970. Zoogeographic problems and protein variation in the *Coregonus clupeaformis* whitefish species complex. In *Biology of Coregonine Fishes*. Edited by C.C. Lindsey and C.S. Woods. University of Manitoba Press, Winnipeg, Canada. pp. 127 – 146.
- Lindsey, C.C., and McPhail, J.D. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins. In *The zoogeography of North American freshwater fishes*. Edited by C.H. Hocutt and E.O. Wiley. John Wiley and Sons, New York. pp. 639 – 673.
- Lindsey, C.C., and Woods, C.S. 1970. *Biology of Coregonine Fishes*. University of Manitoba Press, Winnipeg.

- Linnæus, C. 1758. *Systema Naturae*, Ed. X. (*Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.*) Holmiae. *Systema Nat.* ed. 10 v. 1
- Loch, J.S. 1974. Phenotypic variation in the Lake Whitefish, *Coregonus clupeaformis*, induced by introduction into a new environment. *Journal of Fisheries Research Board Canada* 31: 55 – 62.
- Lu, G., Basley, D.J., and Bernatchez, L. 2001. Contrasting patterns of mitochondrial DNA and microsatellite introgressive hybridization between lineages of Lake Whitefish (*Coregonus clupeaformis*); relevance for speciation. *Molecular Ecology* 10: 965 – 985.
- Lu, G., and Bernatchez, L. 1998. Experimental evidence for reduced hybrid viability between limnetic and benthic ecotypes of Lake Whitefish (*Coregonus clupeaformis* Mitchill). *Proceedings of the Royal Society of London B – Biological Sciences* 265: 1025 – 1030.
- Lu, G., and Bernatchez, L. 1999. Correlated trophic specialization and genetic divergence in sympatric Lake Whitefish ecotypes (*Coregonus clupeaformis*): Support for the ecological speciation hypothesis. *Evolution* 53: 1491 – 1505.
- Lu, G.a.B., Louis. 1998. Experimental evidence for reduced hybrid viability between limnetic and benthic ecotypes of Lake Whitefish (*Coregonus clupeaformis* Mitchill). *Proc. R. Soc. Lond. B*: 1025 – 1030.
- Luczynski, M., Rösch, R., Vuorinen, J.A., and Brzunan, P. 1995. Biochemical genetic study of sympatric Lake Constance whitefish (*Coregonus lavaretus*) populations: “Blaufelchen” and “Gangfish”. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 136 – 143.
- Luikart, G., England, P.R., Tallman, D., Jordan, S., and Taberlet, P. 2003. The power and promise of population genomics: from genotyping to genome typing. *Nature Reviews Genetics* 4: 981 – 993.
- Lynch, M., Pfrender, M., Spitze, K., Lehman, N., Hicks, J., Allen, D., Latta, L., Ottene, M., Bogue, F., and Colbourne, J. 1999. The quantitative and molecular genetic architecture of a subdivided species. *Evolution* 53: 100 – 110.
- MacCrimmon, H.R., and Skobe, E. 1970. The fisheries of Lake Simcoe. *Edited by Ontario Ministry of Natural Resources, Ontario.* p. 140.
- Mandrak, N. 2003. Biogeographic zones of Canada *In* COSEWIC (2005). Guidelines for recognizing designatable units below the species level. *Edited by Committee on the Status of Endangered Wildlife in Canada, Ottawa.* Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca)
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge MA.
- McDermid, J.L., Reist, J.D., and Bodaly, J.A. 2005. Phylogeography and postglacial dispersal of whitefish (*Coregonus clupeaformis* complex) in Northwestern North America. *Arch. Hydrobiol. Special Issues Advances in Limnology* 60: 91 – 109.

- McLaughlin, R.L., A., G.J.W., and L., K.D. 1994. Foraging movements in relation to morphology, water-column use, and diet for recently emerged brook trout (*Salvelinus fontinalis*) in still-water pools. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 268 – 279.
- McLeod, C., O'Neil, J., Hildebrand, L., and Clayton, T. 1979. An examination of fish migrations in the Liard River, British Columbia, relative to proposed hydroelectric development at site A,R,L,and L., Edmonton, Alberta. Environmental Services, Ltd. Edmonton, Alberta. 199 pages.
- McPhail, J.D. 2007. *The Freshwater Fishes of British Columbia*. University of Alberta Press.
- McPhail, J.D., and Lindsey, C.C. 1970. *Freshwater Fishes of Northwestern Canada and Alaska*. Fisheries Research Board of Canada, Ottawa.
- Mecklenberg, C.W., Mecklenberg, T.A., and Thorsteinson, L.K. 2002. *Fishes of Alaska*. American Fisheries Society, Bethesda, Maryland.
- Merila, J., and Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology* 14: 892 – 903.
- Murray, K.D. 2005. Population genetic assessment of the endangered Atlantic whitefish, *Coregonus huntsmani*, and the Lake Whitefish, *C. clupeaformis* in Atlantic Canada, Dalhousie University, Halifax, Nova Scotia, Canada.
- Nalepa, T.F., Mohr, L.C., Henderson, B.A., Madenjian, C.P., and Schneeberge, P.J. 2005. Lake Whitefish and Diporeia spp. in the Great Lakes: An Overview. *In* Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod Diporeia spp. in the Great Lakes. Ann Arbor, MI. Edited by Great Lakes Fisheries Commission. pp. 3 – 19.
- Nelson, J.S., and Paetz, M.J. 1992. *The Fishes of Alberta*. University of Alberta Press/University of Calgary Press, Edmonton/Calgary.
- Nikolsky, G.V., and Reshetnikov, J.S. 1970. Systematics of Coregonine fishes in the USSR; Intraspecific variability and difficulties in taxonomy. *In* Biology of Coregonine Fishes. Edited by C.C. Lindsey and C.S. Woods. University of Manitoba Press, Winnipeg.
- Ostbye, K., Amundsen, P.A., Bernatchez, L., Klemetsen, A., Knudsen, R., Kristoffersen, R., Naesje, T.F., and Hindar, K. 2006. Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. *Molecular Ecology* 15: 3983 – 4001.
- Ostbye, K., Naesje, T.F., Bernatchez, L., Sandlund, O.T., and Hindar, K. 2005. Morphological divergence and origin of sympatric populations of European whitefish (*Coregonus lavaretus* L.) in Lake Femund, Norway. *Journal of Evolutionary Biology* 18: 683 – 702.
- Page, L.M., and Burr, B.M. 1991. *A field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Co., Boston.
- Pielou, E.C. 1991. *After the ice age*. The University of Chicago Press, Chicago.

- Pigeon, D., Chouinard, A., and Bernatchez, L. 1997. Multiple modes of speciation involved in the parallel evolution of sympatric morphotypes of Lake Whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* 51: 196 – 205.
- Politov, D.V., Gordon, N.Y., and Makhrov, A.A. 1999. Genetic identification and taxonomic relationships of six Siberian species of *Coregonus*. In *Biology and Management of Coregonine Fishes – Proceedings of the Seventh International Symposium on the Biology and Management of Coregonine Fishes*.
- Politov, D., Gordon, N., Afanasiev, K., Altukhov, Y., and Bickham, J. 2000. Identification of palearctic Coregonine fish species using mtDNA and allozyme genetic markers. *Journal Of Fish Biology* 57: 51 – 71.
- Power, G. 2002. Charrs, glaciations and seasonal ice. *Environmental Biology of Fishes* 64: 17 – 35.
- Prest, V.K. 1970. Quaternary geology of Canada. In *Geology and Economic Minerals of Canada. Edited by R.J.W. Douglass*. Geological Survey of Canada, Ottawa. pp. 676 – 764.
- Rawson, D.S. 1947. Great Slave Lake. In *North West Canadian Fisheries Surveys in 1944-1945. Edited by Fisheries Research Board of Canada*. p. 94.
- Reist, J.D., Lianne, D., Maiers, R.A., Bodaly, J.A., Vuorinen, J., and Carmichae, T.J.I. 1998. The phylogeny of new – and old-world coregonine fishes as revealed by sequence variation in a portion of the d-loop of mitochondrial DNA. In *Biology and Management of Coregonine Fishes. Edited by R. Eckmann, A. Appenzeller and R. Rosch*. pp. 323 – 339.
- Reist, J.D., Vuorinen, J., and Bodaly, R.A. 1992. Genetic and morphological identification of Coregonine hybrid fishes from Arctic Canada. *Polish Archives of Hydrobiology* 39: 551 – 561.
- Rempel, L., and Smith, D. 1998. Postglacial fish dispersal from the Mississippi refuge to the Mackenzie River basin. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 893 – 899.
- Reshetnikov, J.S. 1988. Coregonine fishes in recent conditions. *Finnish Fisheries Research* 9: 11 – 16.
- Robinson, B.W., and Schluter, D. 2000. Natural selection and the evolution of adaptive genetic variation in northern freshwater fishes. In *Adaptive Genetic Variation in the Wild. Edited by T. Mousseau, B. Sinervo and J.A. Endler*. Oxford University Press, Oxford.
- Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: A neglected literature. *The American Naturalist* 144: 596 – 627.
- Rogers, S.M., Gagnon, V., and Bernatchez, L. 2002. Genetically based phenotype-environment association for swimming behavior in Lake Whitefish ecotypes (*Coregonus clupeaformis* Mitchill). *Evolution* 56: 2322 – 2329.

- Rogers, S.M., and Bernatchez, L. 2005. Integrating QTL mapping and genome scans towards the characterization of candidate loci under parallel selection in the Lake Whitefish (*Coregonus clupeaformis*). *Molecular Ecology* 14: 351 – 361.
- Rogers, S.M., and Bernatchez, L. 2006. The genetic basis of intrinsic and extrinsic postzygotic reproductive isolation jointly promoting speciation in the Lake Whitefish species complex (*Coregonus clupeaformis*). *Journal of Evolutionary Biology* 19: 1979 – 1994
- Rogers, S.M., and Bernatchez, L. 2007. The genetic architecture of ecological speciation and the association with signatures of selection in natural Lake Whitefish (*Coregonus* Sp. Salmonidae) species pairs. *Molecular Biology and Evolution* 24: 1423 – 1438.
- Rogers, S.M., Campbell, D, Baird, S. J. E., Danzmann, R.G., and Bernatchez, L. 2001. Combining the analyses of introgressive hybridisation and linkage mapping to investigate the genetic architecture of population divergence in the Lake Whitefish (*Coregonus clupeaformis*, Mitchill). *Genetica* 111: 25 – 41.
- Sajdak, S.L., and Phillips, R.B. 1997. Phylogenetic relationships among *Coregonus* species inferred from the DNA sequence of the first internal transcribed spacer (ITS1) of ribosomal DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1494-1503.
- Sanderson, S.L., Cech, J.J., and Patterson, M.R. 1991. Fluid Dynamics in Suspension-Feeding Blackfish. *Science* 251: 1346 – 1348.
- Sanderson, S.L., Cheer, A.Y., Goodrich, J.S., Graziano, J.D., and Callan, W.T. 2001. Crossflow filtration in suspension-feeding fishes. *Nature* 412: 439 – 441.
- Sandlund, O.T., Næsje, T.F., and Jonsson, B. 1992. Ontogenetic changes in habitat use by whitefish, *Coregonus lavaretus*. *Environmental Biology of Fishes* 33: 341 – 349.
- Sandlund, O.T., Næsje, T.F., and Saksgård, R. 1995. Ecological diversity in whitefish *Coregonus lavaretus*: ontogenetic niche shifts and polymorphism. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 46: 49 – 59.
- Schluter, D. 1996. Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351: 807 – 814.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, New York.
- Schluter, D., and McPhail, J.D. 1993. Character displacement and replicate adaptive radiation. *Trends in Ecology and Evolution* 8: 197 – 200.
- Schluter, D., and Nagel, L.M. 1995. Parallel Speciation by Natural-Selection. *American Naturalist* 146: 292 – 301.
- Schmidt, R.E. 1986. Zoogeography of the Northern Appalachians. *In Zoogeography of North American Freshwater Fishes. Edited by C.H. Hocutt and E. Wiley.* John Wiley and Sons, New York. pp. 137 – 159.
- Scott, W.B., and Crossman, E.J. 1964. Fishes occurring in the freshwaters of insular Newfoundland. *Edited by Ontario Department of Fisheries, Ontario, Canada.* p. 124.

- Scott, W.B., and Crossman, E.J. 1973. Freshwater Fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Ottawa 184. 966 pages.
- Sendek, D.S. 1999. Electrophoretic studies of Coregonine fishes from across Russia. *In* Biology and Management of Coregonine Fishes – Proceedings of the Seventh International Symposium on the Biology and Management of Coregonine Fishes. Todd, T. Fleischer, G., Ann Arbor, Michigan, U.S.A. p. 689.
- Smith, G.R. 1992. Introgression in Fishes: Significance for Paleontology, Cladistics, and Evolutionary Rates. Taylor and Francis, Ltd. for the Society of Systematic Biologists. pp. 41 – 57.
- Smith, G.R., and Todd, T.N. 1984. Evolution of species flocks of fishes in North Temperate Lakes. *In* Evolution of Fish Species Flocks. Edited by A.A. Echelle and I. Kornfield. University of Maine at Orono Press, Orono, Maine. pp. 45 – 68.
- Spitze, K. 1993. Population Structure in *Daphnia obtusa*: Quantitative Genetic and Allozymic Variation. *Genetics* 135: 367 – 374.
- Stamford, M.D., and Taylor, E.B. 2004. Phylogeographical lineages of Arctic grayling (*Thymallus arcticus*) in North America: divergence, origins and affinities with Eurasian *Thymallus*. *Molecular Ecology* 13: 1533-1549.
- Stinchcombe, J.R., and Hoekstra, H.E. 2007. Population genomics and quantitative genetics: combined approaches for finding the genes underlying ecologically important traits. *Heredity* 100: 158-170.
- Storz, J.F. 2005. Using genome scans of DNA polymorphism to infer adaptive population divergence. *Molecular Ecology* 14: 671-688.
- Stott, W., Todd, T.N., and Kallemeyn, L. 2004. Genetic variability among Lake Whitefish from Isle Royale and the Upper Great Lakes. *Annales Zoologici Fennici* 41: 51-59.
- Svaerdson, G. 1998. Postglacial Dispersal and Reticulate Evolution of Nordic Coregonines. *Nordic Journal of Freshwater Research* 74: 3-32.
- Svärdson, G. 1957. The Coregonine problem. VI. The palearctic species and their intergrades. Report of the Institut of Freshwater Research, Drottningholm 38: 261-356.
- Svärdson, G. 1965. The Coregonine Problem VII. The isolating mechanisms in sympatric species. Report of the Institut of Freshwater Research, Drottningholm 46: 95-123.
- Sawatzky, C.D., D. Michalak, J.D. Reist, T.J. Carmichael, N.E. Mandrak, and L.G. Heuring. 2007. Distributions of freshwater and anadromous fishes from the mainland Northwest Territories, Canada. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 2793: xiv + 239 p.
- Taylor, E. 1999. Species pairs of north temperate freshwater fishes: Evolution, taxonomy, and conservation. *Reviews In Fish Biology And Fisheries* 9: 299 – 324.
- Taylor, E., and McPhail, J. 2000. Historical contingency and ecological determinism interact to prime speciation in sticklebacks, *Gasterosteus*. *Proceedings Of The Royal Society Of London Series B-Biological Sciences* 267: 2375 – 2384.

- Taylor, E.B. 2006. Guidelines for Recognizing Designatable Units Below the Species Level. *Edited by* Freshwater Fisheries Specialist Subcommittee. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca).
- Taylor, E.B., and Bentzen, P. 1993. Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in Northeastern North America. *Evolution* 47: 813 – 832.
- Taylor, E.B., Boughman, J.W., Groenenboom, M., Sniatynski, M., Schluter, D., and Gow, J.L. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a threespined stickleback (*Gasterosteus aculeatus*) species pair *Molecular Ecology* 15: 343 – 355.
- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J.B. 2001. Why are limnetic fish so small? An energetic analysis of polymorphism in Lake Whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences* 58: 394 – 405.
- Tsuyuki, H., Uthe, J.F., Roberts, E., and Clarke, L.W. 1966. Comparative Electropherograms of *Coregonus clupeaformis*, *Salvelinus namaycush* *S. alpinus* *S. malma* and *S. fontinalis* from family Salmonidae. *Journal of the Fisheries Research Board of Canada* 23: 1599
- Turgeon, J., Estoup, A., and Bernatchez, L. 1999. Species flock in the North American Great Lakes: Molecular ecology of Lake Nipigon Ciscoes (Teleostei: Coregonineae : *Coregonus*). *Evolution* 53: 1857 – 1871.
- Underhill, J.C. 1986. The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador. *In Zoogeography of North American Freshwater Fishes. Edited by* C.H. Hocutt and E. Wiley. John Wiley and Sons, New York.
- Vamosi, S., and Schluter, D. 2002. Impacts of trout predation on fitness of sympatric sticklebacks and their hybrids. *Proceedings Of The Royal Society Of London Series B-Biological Sciences* 269: 923 – 930.
- Vetter, W., Bartha, R., Stern, G., and Tomy, G. 1999. *Environ. Toxicol. Chem.* 18: 2775 – 2781.
- Vuorinen, J.A., Bodaly, R.A., Reist, J.D., Bernatchez, L., and Dodson, J.J. 1993. Genetic and Morphological-Differentiation between Limnetic and benthic Size Forms of Lake Whitefish (*Coregonus clupeaformis*) in Como Lake, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 210 – 216.
- Vuorinen, J.A., Bodaly, R.A., Reist, J.D., and Luczynski, M. 1998. Phylogeny of five *Prosopium* species with comparisons with other Coregonine fishes based on isozyme electrophoresis. *Journal of Fish Biology* 53: 917 – 927.
- Walters, V. 1955. Fishes of western arctic America and eastern arctic Siberia. *Taxonomy and zoogeography. Bull. Am. Mus. Nat. Hist.* 106: 259 – 368.
- Webb, P.W. 1983. Speed, acceleration and manoeuvrability of two teleost fishes. *J. Exp. Biol.* 102: 115 – 122.

- Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* 24: 107 – 120.
- Wedekind, C., Muller, R., and Spicher, H. 2001. Potential genetic benefits of mate selection in whitefish. *Journal of Evolutionary Biology* 14: 980 – 986.
- Weihs, D., and Webb, P.W. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. *Journal of Theoretical Biology* 106: 189 – 206.
- Wilson, C., and Hebert, P. 1998. Phylogeography and postglacial dispersal of lake trout (*Salvelinus namaycush*) in North America. 55: 1010 – 1024.
- Woodger, C.D. 1976. Morphological variations as induced by environment in Coregonines. *Environmental Biology of Fishes* 1: 101 – 105.
- Zitzow, R.E., and Millard, J.L. 1988. Survival and Growth of Lake Whitefish (*Coregonus clupeaformis*) Larvae Fed Only Formulated Dry Diets. *Aquaculture* 69: 105 – 113.