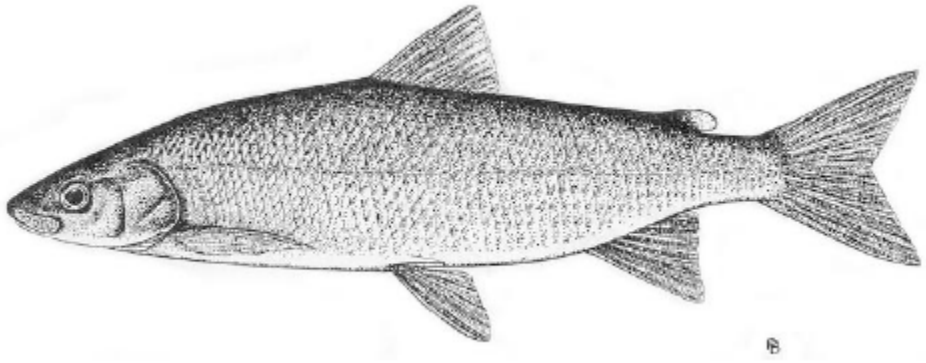
COSEWIC Executive Summary
Designatable units at an appropriate scale

for the

Lake Whitefish
Coregonus clupeaformis

in Canada



prepared for

COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA

By

Sean M. Rogers
Department of Biological Sciences
University of Calgary

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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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INTRODUCTION

Species conservation requires consideration of populations below the species level to prevent wildlife from becoming extinct or extirpated (COSEWIC 2005). This includes considering subspecies and “geographically or genetically distinct” populations defined within the federally legislated Species at Risk Act (SARA). COSEWIC's recognition of populations below the species level (i.e., designatable units that are significant and irreplaceable units of biodiversity, DUs) is also directed by these same general conservation objectives. To this end, COSEWIC has developed guidelines with uniform criteria that can determine the most appropriate DUs on a case by case basis (see COSEWIC 2009a, Taylor 2006). However, achieving a uniform interpretation of DUs for populations below the species level remains challenging, as patterns of population structure and life history can often differ dramatically across taxonomic groups.

These problematic issues are exemplified by freshwater fishes. With over 240 freshwater fish species in Canada (Scott and Crossman 1973), and 15% of these species already at risk and listed in SARA (2 extirpated, 21 endangered and 13 threatened), the ability to apply DU guidelines effectively requires consideration of numerous complex scenarios (Taylor 2006). These complex scenarios may include species represented by different taxonomic groups (e.g., Westslope vs. Coastal Cutthroat Trout within *Oncorhynchus clarkii*) or phylogenetic lineages (e.g., coastal and interior Bull Trout within *Salvelinus conflentus*). Species may have distinct locally adapted traits that identify a DU as not likely to be ecologically interchangeable with other known DUs within the species (e.g., unarmoured sticklebacks on the Queen Charlotte Islands or girdle-less sticklebacks in Paxton Lake, B.C). These guidelines may also identify species as irreplaceable components of Canada’s biodiversity or include species with major range disjunctions (e.g., Pygmy Whitefish (*Prosopium coulterii*) from western Lake Superior and Alberta/BC). Finally, the distribution of species may overlap the over 13 different aquatic ecoregions that COSEWIC recognizes as warranting different DU status (e.g., Arctic Grayling (*Thymallus arcticus*) in Yukon River inhabit a distinct freshwater biogeographic region than those in the Pacific or Western Arctic biogeographic regions and therefore qualify as separate DUs).

To help increase the ability of the Freshwater Fisheries Special Subcommittee to achieve a uniform interpretation of DUs, Taylor (2006) developed a key with criteria based on the COSEWIC Guidelines for Recognizing DUs below the species level (http://www.cosewic.gc.ca/eng/). This key applies a series of questions to test the identification and validity of DUs within a complex of populations, i.e., concurrent evaluation of DU status under several criteria. The final result is a DU decision chart which can be used by a Specialist Sub-Committee (SSC) to guide and prioritize conservation efforts.

This key was used to determine DUs at an appropriate scale for the Lake Whitefish (*Coregonus clupeaformis*), a species with innumerable taxonomic problems and multiple species pairs across Canada (COSEWIC 2009b). The objective of this special report was to assess the entire range of Canadian Lake Whitefish populations with Taylor's key to determine a uniform interpretation of DUs for Lake Whitefish populations below the species level. This assessment used relevant information about the species with respect to genetics, ecology, morphology, distribution, range disjunction, and presence in different aquatic biogeographic zones.

This executive summary of the Special Report provides an abbreviated version of the main results as well as final recommendations to the Freshwater Fisheries Specialist Subcommittee regarding future assessments based on these data that will increase the conservation of our Lake Whitefish resources in Canada. The successful application of the key towards delineating Lake Whitefish DUs below the species level also demonstrates how uniform DU considerations in a species complex will improve the ability of the SSC to prioritize candidate species for assessment.

RESULTS

Information from over 82 lakes was used to assess the number of DUs in the Lake Whitefish species complex within Canada (Table 1). These DUs below the species level are presented following a series of questions as they appear in the key (Taylor 2006), from the "most significant" criterion (distinct taxonomic units) to the least significant (inhabiting distinct biogeographic zones). Criteria 1-2 reflect largely pre-glacial (long time frame) processes while 3-5 postglacial (short time frame) processes (Taylor 2006). Fulfilling any criterion is sufficient for a DU, but fulfilling more criteria increases the importance of the DU. Justification or rationale behind DU delineation is not provided in this executive summary, but can be found in the full Special Report (COSEWIC 2009b).

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. Taxonomic entity: presence of the *C. lavaretus* DU from Section 1 of the key (otherwise *C. clupeaformis*). SP: presence of a species pair. PG: major phylogeographic groupings; B=Beringian, E=Eurasian, N=Nahanni, M = Mississippi, 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: References for the source of the populations sampled.

ID	Site		Taxonomic entity	SP	PG	BZ	PDU	Ref
1	Yukon R.	AK	*C. lavaretus*		B, E	6	1,23	[5, 6]
2	Minnesota L.	AK	*C. lavaretus*		B, E	n/a		[5, 6]
3	Chatanika R.	AK	*C. lavaretus*		B, E	n/a		[5, 6]
4	Davis L.	YT			B	6	23	[7]

ID	Site		Taxonomic entity	SP	PG	BZ	PDU	Ref
5	Hanson L.	YT			NA	6	23	[12]
6	Tatchun L.	YT			B	6	23	[3]
7	Squanga L.	YT	*C. lavaretus* (limnetic)	Y	B, E	6	1,2-3,23	[3, 5-7]
8	Little Teslin L.	YT	*C. lavaretus* (lim + ben)	Y	B, E	6	1,4-5,23	[5, 6]
9	Dezadeash L.	YT	*C. lavaretus* (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.	YT			B	13	22	[7]
20	Toobally L.	YT			B,N	13	22	[7]
21	Crooked L.	BC			B,N	13	22	[7]
22	Liard R.	BC	*C. lavaretus* (upper)		B,N,M	13	22	[7]
23	Fisherman's L.	BC			N	13	22	[7]
24	Bovie L.	BC			N	13	22	[7]
25	Seaplane L.	BC			N	13	22	[7]
26	Divide L.	BC			N	13	22	[7]
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.	YT			N	11	24	[3, 7]

ID	Site		Taxonomic entity	SP	PG	BZ	PDU	Ref
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			B,N,M	13	22	[7]
50	Fort McPherson	NT			M	13	22	[5, 6]
51	Cox L.	NT			B,N,M	13	22	[7]
52	McEvoy L.	YT	*C. lavaretus*		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]
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]

ID	Site		Taxonomic entity	SP	PG	BZ	PDU	Ref
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

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

DU designations based on taxonomic entities or distinct biological species were given for 21 populations (Figure 1, DU1-21). One DU was identified on the basis that genetic evidence supported the possibility that what is now recognized as one taxon of Lake Whitefish actually comprises two distinct taxa, *C. lavaretus* and *C. clupeaformis,* that exist in British Columbia and Yukon. However, provisional DU status should be given to populations that represent distinct *Coregonus lavaretus* species (see Table 1). These populations have also been classified as *C. pidschian* and are routinely described as part of the "*C. clupeaformis* species complex". Conspecific populations of *Coregonus pidschian* 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, Table 1). Future assessments will require additional data to resolve the issue and would have important consequences for our understanding of the Lake Whitefish species complex in Canada.

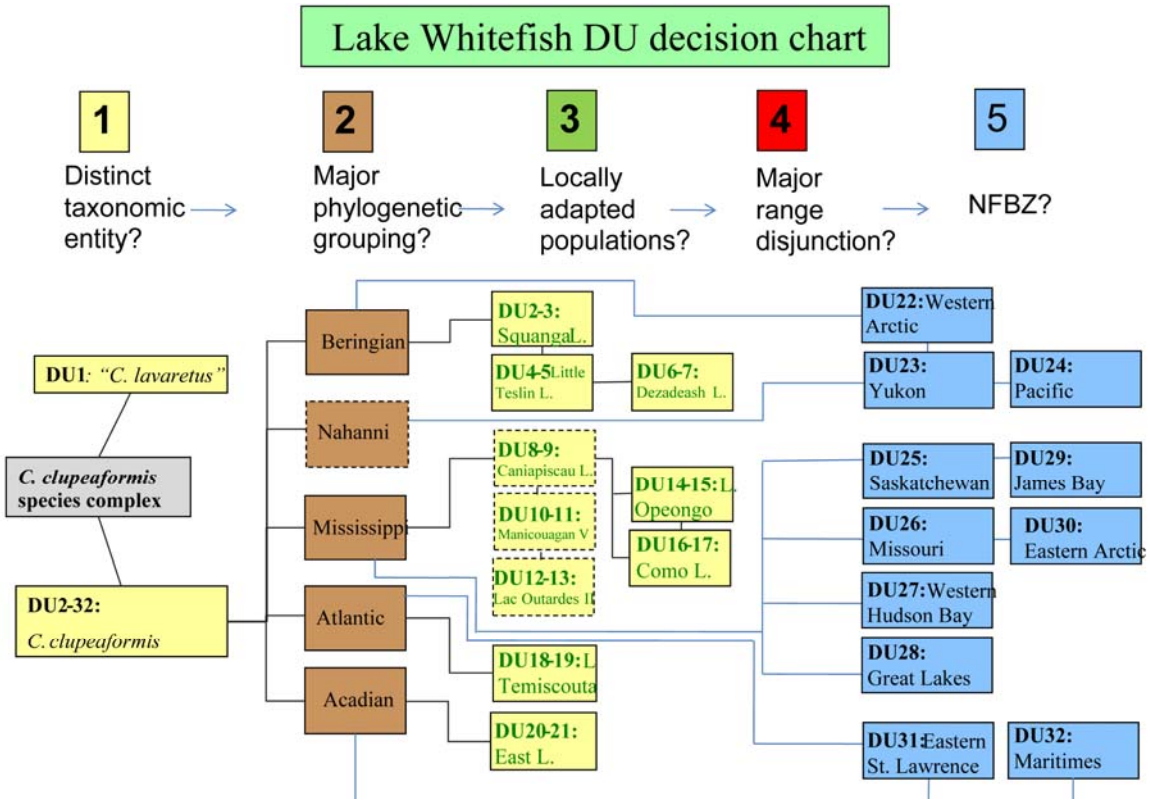

Figure 1. A Lake Whitefish species complex DU decision chart. The numbers on the top, from left to right, reflect the steps used in the key used to identify putative designatable units (DUs) following Taylor (2006). The boxes show DUs identified for each of these steps. Lines connecting DUs reflect different stages of the decision process. For example, DU2-3 (Squanga Lake species pair) is connected to the Beringia DU as well as the Yukon River NBGZ 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).

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 population pair of Lake Whitefish qualifies as a DU. Although 17 lakes are known or suspected to be inhabited by putative species pairs, only seven species pairs have sufficient data to warrant DU status, leading to 14 DU designations (Table 1, Figure 1). These 14 DUs consists of species pairs in which both genetic and morphological information support the occurrence of limnetic and benthic Lake Whitefish with the lake. An additional 6 provisional DU designations were granted until the diagnostic nature of adaptive traits can be confirmed following more extensive sampling (Figure 1).

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

Isolation of Lake Whitefish during glacial refugia resulted in significant allopatric divergence during the Pleistocene ice age. Genetic evidence from Lake Whitefish in over 100 populations across Canada strongly supports five major phylogeographic groupings representative of distinct glacial refugia (Figure 2). Lake Whitefish populations from each of these phylogenetic groups represent distinct DUs (Table 1), but because of their broad distribution these DUs are adequately captured within eight National Freshwater Biogeographic Zones (Figures 1 and 2).

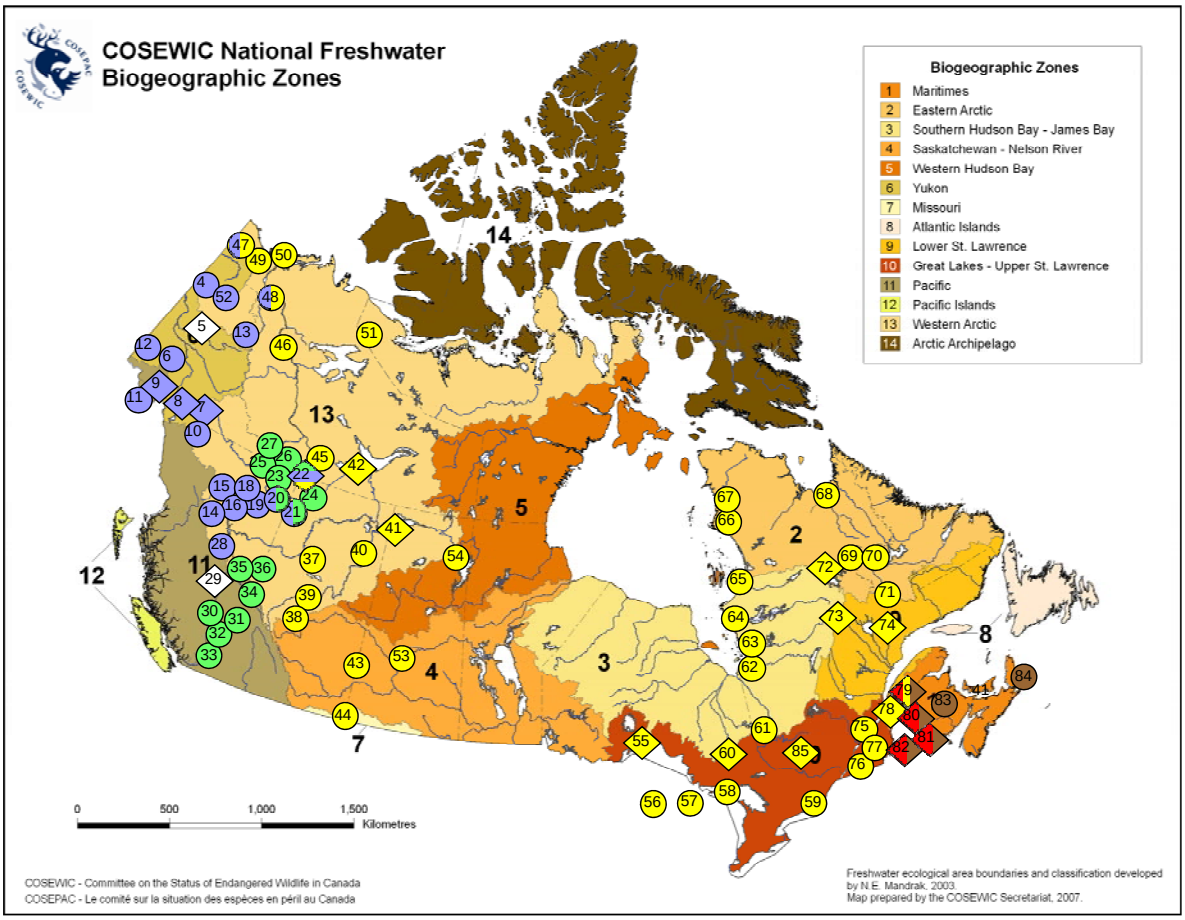

Figure 2. Distribution and of Lake Whitefish in Canada with respect to National Freshwater Biogeographic Zones. See Table 1 for more information. Locations of Lake Whitefish populations are colour coded according to their major phylogenetic groupings representative of their ancestral glacial refugia (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.

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?

A suite of traits (behavioural, morphological, physiological) representing local adaptation have been found to reliably differentiate limnetic and benthic Lake Whitefish (COSEWIC 2009b). However, no single adaptive trait is diagnostic when differentiating the species pairs among lakes. Because of this, in lakes where the species pairs are purported to exist but phenotype-environment associations have not been assessed, or genetic differentiation between limnetics and benthics remains unknown, DU status should be deferred until these data can be provided.

4. The PDU represents a major range disjunction?

Lake Whitefish are the most broadly distributed freshwater fish in Canada (Figure 2). Consequently, there are no populations separated widely by naturally unoccupied areas to warrant DU delineation from major range disjunctions.

5. The PDU inhabits a different National Freshwater Biogeographic Zone?

National Freshwater Biogeographic Zones represent different eco-geographic regions within Canada (NFBZ, COSEWIC 2009a). Eleven of the fourteen aquatic ecoregions are relevant to Lake Whitefish populations because they depict previously described phylogeographic groupings related to glacial refugia zones (Figure 2). The number of biogeographic zones captured by a phylogeographic grouping indirectly reflects the relative postglacial distribution of Lake Whitefish from a particular glacial refugium. For example, the Mississippian Glacial Race is distributed among 73% of the recognized biogeographic zones, the largest number of zones compared to other phylogeographic DUs. The Atlantic DU, on the other hand, is found in only one biogeographic zone, Lac Témiscouata in the Maritime NFBZ (Figure 2).

RECOMMENDATIONS

Thirty-two DUs at an appropriate scale for the Lake Whitefish (*Coregonus clupeaformis*) are recognized in Canada. This is a large number of DUs for a single species and were strongly supported by more than one criterion of the key. Many of these DUs, however, could be considered low priority for further assessment. For example, with the exception of the Atlantic DU in Lac Témiscouta, several lakes are inhabited by each of the five putative glacial races of Lake Whitefish across Canada. The broad distribution of Lake Whitefish also includes several lakes within each of the 11 NFBZ DUs. Consequently, these DUs (22 to 32) could be considered low priority for individual detailed status assessments.

COSEWIC normally only considers DUs below the species level when justification can be provided. Taxonomic justification exists for putative *Coregonus lavaretus*/*C. pidschian* populations, but more data are needed to resolve the issue. Without additional population genetic data, it is debatable whether a detailed status report could resolve the differences between this putative species and *C. clupeaformis*. Nonetheless, considering that this species would be a new species record within Canada, this DU should be considered as high priority.

The limnetic and benthic species pair DUs should also be considered high priority given their taxonomic distinctness and reproductive isolation as distinct biological species (COSEWIC 2009). Higher priority should be given in cases where both taxonomic distinctness and local adaptation have been demonstrated (Squanga Lake, Little Teslin Lake, Dezadeash Lake, Opeongo Lake, Como Lake, Temiscouata Lake, and East Lake). Altogether, several published research papers have demonstrated that ecological opportunity and divergent natural selection within these 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 the seven Canadian Lake Whitefish populations meeting these guidelines should be considered higher priority DUs, while the remaining provisional DU populations (Caniapiscau Lake, Manicouagan V, and Lac Outardes II) require more information (Figure 1). In some cases there is evidence that species pairs may be at an increased risk for extinction (e.g., extinction of the limnetic species in Squanga Lake following the addition of invasive cisco species). Such species pairs with an increased risk of extinction should be given higher priority.

CONCLUSIONS

The special report of DUs at an appropriate scale for the Lake Whitefish (*Coregonus clupeaformis*) in Canada provided a synthesis of the current 32 DUs for this species in Canada, providing relevant information for the SSC to prioritize candidate DUs for further assessment. 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 exhibited 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*. Ecological speciation of seven Canadian Lake Whitefish species pairs also meet the guidelines for DU delineation. Lake Whitefish populations across Canada were also 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. Adoption of NFBZ DUs that encompass both the major phylogeographic groupings and the species pairs may facilitate conservation scenarios while addressing regional situations. Ultimately, adopting appropriate DUs from this special report will be essential 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.

LITERATURE CITED

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.

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. 105: 87 – 90.

COSEWIC. 2009a. Operations and Procedures Manual. Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca)

COSEWIC. 2009b. Guidelines Designatable units at an appropriate scale for the Lake Whitefish (Coregonus clupeaformis). Available on request from the COSEWIC Secretariat (COSEWIC/COSEPAC@ec.gc.ca)

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.

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.

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.

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., 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.

Mandrak, N. 2003. Aquatic ecoregions 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)

McPhail, J.D., and Lindsey, C.C. 1970. Freshwater Fishes of Northwestern Canada and Alaska. Fisheries Research Board of Canada, Ottawa.

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.

Scott, W.B., and Crossman, E.J. 1973. Freshwater Fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Ottawa 184. 966 pages.

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).