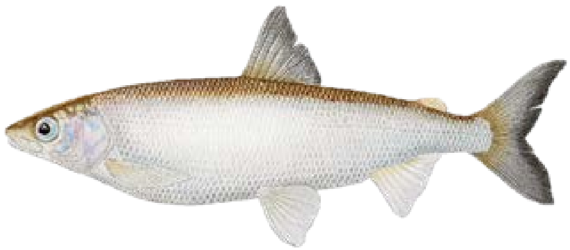
ADVICE ON THE TAXONOMIC VALIDITY AND DESIGNATABLE UNITS OF SHORTJAW CISCO (*Coregonus zenithicus*) POPULATIONS IN CANADA



*Shortjaw Cisco (*Coregonus zenithicus*)*
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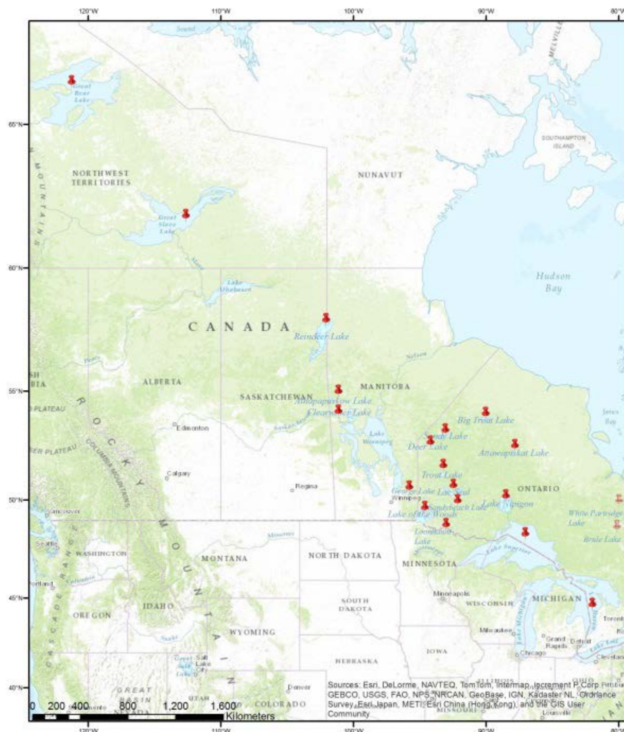

Figure 1. Current distribution of putative Shortjaw Cisco in Canada (modified from Murray 2006).

Context:

*Shortjaw Cisco (*Coregonus zenithicus*) was first assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in April 1987. It was designated as Threatened. The status was re-examined and confirmed in May 2003. Shortjaw Cisco is currently listed as Threatened on Schedule 2 of the* Species at Risk Act *(SARA) (Schedule 1 provisions do not apply). COSEWIC will be re-assessing Shortjaw Cisco as part of its 10 year re-assessment cycle. Fisheries and Oceans Canada (DFO) is required to provide COSEWIC with the best and most current information available on the species to ensure an accurate and complete assessment. This information is peer reviewed at a pre-COSEWIC assessment meeting. In addition to peer reviewing scientific data and analyses, a secondary objective of this assessment meeting was to provide science advice on the taxonomic validity of Shortjaw Cisco outside of the Laurentian Great Lakes and, if valid, the designatable units (DUs) that should be recognized within Canada. These issues have been the subject of ongoing debate in the scientific literature and their resolution will aid in the accurate assessment of the species by COSEWIC.*

This Science Advisory Report is from the October 30-31, 2012 pre-COSEWIC assessment for Shortjaw Cisco. Additional publications from this meeting will be posted on the Fisheries and Oceans Canada (DFO) Science Advisory Schedule *as they become available.*

SUMMARY

- A morphological taxonomic approach does not generally work for new world ciscoes throughout their range; however, for the Great Lakes and Lake Nipigon, it has historical validity.
- The risk of diversity loss following the standard taxonomic approach is very high.
- A species-flock approach will likely result in more complete and representative delineation of DUs, thus facilitating more accurate conservation assessments.
- Shortjaw Cisco is only one of the nominate new world ciscoes to which this advice is applicable – the advice and approach applies generally in situations where multiple cisco forms occur and appear to have been derived through sympatric evolutionary processes.
- Application of the approach is required on a waterbody-specific basis.
- A weight-of-evidence approach including as many aspects of cisco biology as possible is recommended (e.g., morphology, ecology, biology or life history, genetics).
- Based on present knowledge, the application of this approach to new world cisco diversity explicitly results in 15 designatable units; more are likely as evidence accrues.
- Investigation of the applicability of the species-flock approach to similar situations in other taxonomic groups may extend its general utility (e.g., sticklebacks, whitefishes).
- This approach may facilitate the application of ecosystem-based management and analyses of threats to cisco biodiversity (detailed analyses of threats was not conducted as part of this analysis).

BACKGROUND

In April 1987, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated Shortjaw Cisco (*Coregonus zenithicus*) as Threatened. The status was re-examined and confirmed in May 2003. Shortjaw Cisco was listed as Threatened on Schedule 2 of the *Species at Risk Act* (SARA) when the Act came into effect in June 2003. Schedules 2 and 3 of the SARA are reserved for species that were assessed as at risk by COSEWIC before the SARA was enacted. These species must be re-assessed under the new criteria of the Act before they can be added to Schedule 1, and thus receive legal protection, or be removed from the list.

In June 2006, the Governor General in Council referred the assessment for Shortjaw Cisco back to COSEWIC for further information and consideration.

As part of its 10 year review cycle, COSEWIC will be re-assessing Shortjaw Cisco. To ensure an accurate and complete assessment, DFO is tasked with providing COSEWIC with the best and most current information on the species. A pre-COSEWIC Assessment meeting is held by DFO Science to peer-review this information. The pre-COSEWIC Assessment for Shortjaw Cisco was held October 30-31, 2012 in Burlington, ON.

Typically, products of a pre-COSEWIC assessment are Canadian Science Advisory Secretariat (CSAS) Research Documents and Proceedings summarizing key points of discussion at the meeting. In the case of Shortjaw Cisco, however, a second objective of the meeting (in addition to the peer review) was to provide Science Advice on the taxonomic validity of Shortjaw Cisco outside of the Laurentian Great Lakes and, if deemed to be valid, the designatable units (DUs) that should be recognized within Canada. These intertwined issues have been the subject of ongoing debate in the scientific literature. The resolution of these issues will aid in the accuracy of the COSEWIC assessment.

Species Description, Identification and Distribution

The Shortjaw Cisco is a member of the salmonid subfamily, Coregoninae. Its body is elliptical in shape and is covered in large, smooth scales. Colouration is generally silver, with a tan or olive back and white underbelly. The lower jaw is typically even with or shorter than the upper jaw and the mouth is small and toothless (Eddy and Underhill 1978; Becker 1983). Standard lengths vary across its range from less than 150 mm (e.g., George Lake, MB) up to approximately 400 mm (e.g., Lake Nipigon, ON). Larger fish weigh up to 300 g. Gill-raker number is one of the most important diagnostic characters used to identify this species. Shortjaw Cisco generally have less than 40 gill rakers on the first branchial arch, while most other cisco species have more than 40 (Todd 2003). The gill rakers of Shortjaw Cisco also tend to be shorter in length than those of most other cisco species (Becker 1983).

Shortjaw Cisco is widely distributed throughout central Canada (Fig. 1), but are best known from the Laurentian Great Lakes. The species was first described by Jordan and Evermann (1909) from a specimen captured in deep water off Isle Royale, Lake Superior. Their current range extends from Ontario to Great Slave Lake in the Northwest Territories (Clarke 1973; Houston 1988; Scott and Crossman 1973; Todd and Steinhilber 2002; Etnier and Skelton 2003; Murray and Reist 2003). Putative Shortjaw Cisco have recently been identified in Great Bear Lake, Northwest Territories (Howland et al. 2013), thus, their range may extend further north than previously believed.

Designatable Units

COSEWIC defines designatable units (DUs) as: *"discrete and evolutionarily significant units of the taxonomic species, where "significant" means that the unit is important to the evolutionary legacy of the species as a whole and if lost would likely not be replaced through natural dispersion"* (e.g., subspecies, discrete and evolutionarily significant populations or groups of populations). The following section highlights the difficulties in defining DUs for Shortjaw Cisco and the related ciscoes of central Canada.

Cisco Systematics

The following is a brief summary cisco systematics included here as background information. Cisco taxonomy, particularly in North America, is unresolved. Evidence points to the existence of two or three clades within the cisco group – old and new world ciscoes with some authors recognizing two clades within the new world ciscoes (e.g., Smith and Todd 1984). The new/old-world designation refers to the origin of the lineage.

Old world ciscoes include all Eurasian forms, namely (according to Kottelat and Freyhof (2007)), *C. albula* (Baltic Cisco), *C. fontanae* (Stechlin Cisco), *C. kiletz* (Kiletz), *C. ladogae* (Ripus), *C. lucinensis* (Quietschbüker), *C. trybomi* (Spring Spawning Cisco), *C. vandesius* (Vendace), *C. vessicus* (Beloye Cisco), *C. sardinella* (Least Cisco), *C. autumnalis* (Arctic Cisco) (secondary dispersal to North America) and *C. laurettae* (Bering Cisco) (close alliance to *C. autumnalis*). In this view, Beringia (as a source area) is considered old world (Chereshnev 1979; Lindsey and McPhail 1986; Politov et al. 2004).

New world ciscoes include the Great Lakes species (including inland occurrences; see below). Seven species are currently recognized in the Laurentian Great Lakes and Lake Nipigon: *C. artedi* (Cisco), *C. johannae* (Deepwater Cisco), *C. hoyi* (Bloater), *C. kiyi* (Kiyi), *C. nigripinnis* (Blackfin Cisco), *C. reighardi* (Shortnose Cisco), and *C. zenithicus* (Shortjaw Cisco). The cisco species diversity of inland lakes is not as high and usually includes: *C. artedi*, *C. nigripinnis*, and putative *C. zenithicus*. Scott and Crossman (1973), however, treated *C. nigripinnis* from inland lakes as a probable form of *C. artedi*. *C. nigripinnis cyanopterus* from lakes Superior and Nipigon has been synonymized with *C. zenithicus* (Todd et al. 1981). Additionally, *C. nipigon* (not currently recognized by the American Fisheries Society) occurs within the Great Lakes and Lake Nipigon and in inland lakes of North America. *C. nipigon* was described by Koelz (1929) but was later synonymized with *C. artedi* by Scott and Crossman (1973) and Smith and Todd (1984, 1992). Etnier and Skelton (2003) subsequently removed *C. nipigon* from synonymy and argued that it is in fact a valid species based on meristic and morphometric characteristics. The American Fisheries Society did not receive this publication until after Nelson et al. (2004) had gone to press, thus it was not reviewed nor recognized. *C. alpenae* was also recognized by Koelz (1929) but is now considered a junior synonym of *C. zenithicus* in lakes Huron, Erie and Michigan (Todd et al. 1981). *C. reighardi* and *C. johannae* are thought to be extinct and *C. kiyi* has been extirpated in lakes Ontario, Huron and Michigan.

Diversity in some groups of fishes presents taxonomic problems for their assessment through mechanisms such as COSEWIC. Generally two inter-related issues occur. First, differentiating the diversity present at particular sites may present problems with various methods being relevant – e.g., morphological, biological, ecological and genetic criteria have all been used to distinguish forms (taxa) of cisco both within and among sites. Related to this is the alignment of the observed taxa to a particular rank in a taxonomic hierarchy. Second, the assignment of the diverse forms to particular nominate taxa (usually species) requires either demonstration or assumption of lineage homology. That is, for freshwater fish populations which are more-or-less isolated from each other by intervening land barriers, concordance of differentiating or key characters among sites is usually taken as evidence of conspecificity. Character variation and/or congruence driven by convergent evolution may thus result in erroneous homologies being established. Superimposed upon this situation are the unique circumstances of particular water bodies where some fishes occur. For new world ciscoes these appear to include post-glacial lakes of varying sizes having complex habitats, variable durations since deglaciation and colonization by fishes, and often low levels of diversity of other fishes. Resolution of these issues for new world ciscoes and the appropriate delineation of designatable units are essential to the conservation of the underlying diversity.

Identification of the Great Lakes species, particularly inland putative Shortjaw Cisco, is difficult due to the high levels of ecological and morphological variation exhibited by this group and the convergence of characters used to distinguish species (Turgeon and Bernatchez 2003; Murray and Reist 2003). Diagnostic characters do not exist for these species and identification keys are not available. Furthermore, genetic analyses have been unable resolve this issue (Bodaly et al. 1991; Bernatchez et al. 1991; Lockwood et al. 1993; Sajdak and Phillips 1997; Reed et al. 1998; Turgeon et al. 1999; Steinhilber et al. 2002; Turgeon and Bernatchez 2003). This has led to the validity of some species, including Shortjaw Cisco, being questioned (Steinhilber and Rhude 2001; Turgeon and Bernatchez 2003). This uncertainty has been dealt with in different ways in the scientific literature. Bailey and Smith (1981) and Turgeon and Bernatchez (2001 a,b, 2003) recommended that all of the Great Lakes species (see above) be recognized as *C. artedi* (*sensu lato*) or the *C. artedi* complex. Etnier and Skelton (2003) argue that this approach fails to recognize the diversity present in this group of fishes and does not account for the occurrence of multiple morphologically distinct forms in inland lakes. Smith and Todd (1984) put forth an incipient species-flock approach for the Great Lakes ciscoes. They proposed two colonizations of the Great Lakes following the last glaciation, with *C. artedi* and *C. zenithicus* as the original colonists (based upon their distribution outside of the Great Lakes) and the other species derived post-glacially. They recognized two monophyletic assemblages: the *artedi – nipigon* group and its possible sister group *hoyi* and *kiyi*, and the *zenithicus – alpenae – johannae – reighardi – nigripinnis* group.

ASSESSMENT

The lack of fit or correspondence between taxonomy, morphology, ecology and genetics (see Table 1) among lakes indicates a general problem regarding the definition of designatable units in both Shortjaw Cisco and related ciscoes that co-occur throughout central Canada. Clearly, for these ciscoes standard taxonomic approaches are incapable of 1) clearly differentiating species-level taxa, and 2) establishing homologous species (or taxa) at multiple locations across the range. Accordingly, we recommend an approach to delineating designable units in ciscoes based upon the concept of a species-flock. The term species-flock has been defined in several ways, including: a) *“a high level of endemicity amongst its constituent species, their close phyletic relationship [monophyletic], and their geographical circumscription”* (Greenwood 1984); or b) *“an assemblage of a disproportionately high number, relative to surrounding areas, of closely related species which apparently evolved rapidly within a narrowly circumscribed area to which all the member species are endemic”* (recent monophyly is not a requirement of this definition) (Ribbink 1984); or c) *“a monophyletic group of species living in one lake or originally derived from one lake”* (Smith and Todd 1984).

It is apparent that a single, accepted definition of the term ‘species-flock’ is not available in the literature (see Mayr 1984; Greenwood 1984). However, commonalities among the definitions include the following criteria: a) endemic to a geographically circumscribed area; b) recent monophyly; and c) a large number of species (Greenwood 1984). Mayr (1984) noted that “there is no need to define this term of convenience too rigidly”. In the same volume, Ribbink (1984) argued that recent monophyly in the cladistic sense is not a general criterion of a species flock since species flocks are not taxonomic categories as defined by Nelson (1971). Schön and Martens (2004) summarize recent proposed changes to criteria a) and c) above – namely, a large number of species is no longer a requirement and the ancestral species need not be endemic to the lake. Furthermore, they note that difficulties in applying the criterion of endemicity in general have emerged (e.g., there are instances of species nested within ancient lake flocks that are non-lacustrine – they do not, or potentially no longer, occur in the lake). As used herein, the ciscoes fit within the current, broader definition of species-flock, particularly when the argument of Ribbink (1984) is considered. Within a location, we consider all of the Great Lakes and inland lakes new world ciscoes as members of these flocks. Additionally, some aspects of cisco diversity (e.g., a divergent single form present in a system) should be included in the above considerations.

Conceptually, these represent species under one of the many concepts available (e.g., approximately 25, Mayden 2002). Regardless, together taxonomic differences, ecological differences, associated trophic specializations and perhaps habitat specializations all form the basis for differences among co-occurring taxa. Varying degrees of differentiation (see Appendix) among taxa that clearly are closely related constitute the basis for a species-flock. By definition, a species-flock is location specific and thus different from others occurring elsewhere. Species-flocks in different locations may be analogous (i.e., parallelisms derived ultimately from different ancestral lineages) or homologous (i.e., same ancestral lineage).

Each component (i.e., taxon) of a cisco species-flock represents part of the overall biological diversity of that flock. Furthermore, putative Shortjaw Cisco appear to be more closely related to sympatric ciscoes than to allopatric putative Shortjaw Cisco taxa (Turgeon and Bourret 2013), thus the species-flock in each lake is likely functionally endemic (see Drew and Kaufman 2013) and represents a designatable unit with potentially unique genetic diversity. According to the COSEWIC Freshwater Fishes Subcommittee designatable units key, each cisco species-flock meets the following criterion: "The PDU [putative designatable unit] has a distinctive and rare trait or traits (behaviour, life history, physiology, morphology) that represents local adaptation and identifies the PDU as not ecologically interchangeable with other known PDUs within the species, and as an irreplaceable component of Canada's biodiversity". As stated by Bernatchez (1995): "*The goal of conservation biology is to preserve genetic integrity and evolutionary processes*". Accordingly, we feel that the best way to do this in the case of Great Lakes and inland lakes ciscoes is to use a species-flock approach to define designatable units.

Designatable Units

We agreed on an increasing weight of evidence or hierarchy of evidence as a means of assessing criteria for designatable units as follows: biological parameters (e.g., growth trajectories, size/maturity), morphology (inherited traits), ecology (e.g., stable isotopes, trophic ecology), habitat (e.g., depth associations, nature of habitat/life history (lacustrine, riverine), reproductive isolation), and genetic evidence (e.g., allozymes, DNA microsatellites, RFLPs, DNA sequences).

Based on existing knowledge, applying the species-flock criteria to new world cisco diversity results in the following designatable units relevant to C. zenithicus: White Partridge Lake, ON (low gillraker form and a dwarf pelagic form with a broad/overlapping range of gill raker counts); Trout Lake, ON (Cisco, Shortjaw Cisco); Brule Lake, ON (low gillraker form); Lake Huron, ON (Bloater, Shortjaw Cisco); Lake Superior, ON (Bloater, Kiyi, Cisco, Shortjaw Cisco); Lake Nipigon, ON (Bloater, Blackfin Cisco, Cisco, Shortjaw Cisco); Lac Seul, ON (Shortjaw Cisco, two high gillraker forms); Sandybeach Lake, ON (Cisco, Shortjaw Cisco); Loonhaunt Lake, ON (high gillraker form, putative Shortjaw Cisco); Lake of the Woods, ON (Cisco, Shortjaw Cisco); George Lake, MB (Cisco, putative Shortjaw Cisco); Lake Athapapuskow, MB (Cisco, Shortjaw Cisco); Reindeer Lake, MB (Cisco, Shortjaw Cisco); Great Slave Lake, NWT (Cisco, "Bigeye Cisco", putative Shortjaw Cisco, river-spawning form); and Great Bear Lake, NWT (shallow-water form, deep-water form). Shortjaw Cisco-like forms have been identified in other lakes in central and western Canada, but their current status is uncertain (see Murray and Reist 2003), thus they were not included here. Table 1 summarizes current evidence for each designatable unit.

The well-documented occurrence of multiple new world cisco forms within a circumscribed location (typically a lake) and the conclusions drawn regarding the taxonomic level of the constituent forms (i.e., are, or are functionally equivalent to, species) provide the basis for identification of that situation as a designatable unit meeting the criterion of a species-flock of ciscoes. Species-flocks are location-specific, likely represent unique local evolutionary histories, are likely primarily the result of 'in situ' diversification processes (i.e., sympatric, peripatric or parapatric phenomena), and are likely driven to a large extent by habitat considerations specific to the location (e.g., unique glacial history, habitat diversity such as wide depth ranges or multiple embayments, low diversity of other fishes). Accordingly, the species-flock as a designatable unit cannot be separated from the location within which the flock evolved. Thus, both the biological outcomes (i.e., the flock) and the habitat in which it occurs are essential coupled components of this type of diversity. Habitat-driven assortative mating is presumed to underlie the maintenance of differentiation. Designatable units under this concept are both location-specific and taxonomically unique. In this fashion, the local habitat is an essential facet of the designatable unit. The outcomes from allopatric differentiation (i.e., taxa distinct at a species level) could be included in the species-flock, particularly if their origin is not well-documented.

Table 1. Designatable unit criteria met in the hierarchy of evidence for cisco species flocks relevant to C. zenithicus in Canada.

Designatable Unit	Biology	Morphology	Ecology	Habitat	Genetics	Support for DU
Ontario						
White Partridge Lake	Yes	Yes	Yes	Yes	Yes (some)	Yes
Trout Lake	Yes	Yes	In progress	Yes	Yes (strong)	Yes
Brule Lake (new record)	-	-	-	-	No	Uncertain
Lake Huron	-	Yes	-	Yes	-	Yes
Lake Superior	Yes	Yes	Yes	Yes	Yes (weak)	Yes
Lake Nipigon	Yes	Yes	Yes	Yes	Yes (strong)	Yes
Lac Seul	In progress	Yes	In progress	-	-	Uncertain
Sandybeach Lake	-	Yes	-	Yes	-	Uncertain
Loonhaunt Lake	-	Yes?	-	-	-	Uncertain
Lake of the Woods	In progress	Yes	In progress	Yes	Yes (strong)	Yes?
Manitoba						
George Lake	-	Yes	-	Yes	-	Uncertain
Lake Athapapuskow	-	Yes	-	Yes	Yes (strong)	Yes?
Reindeer Lake	-	Yes	-	-	-	Uncertain
Northwest Territories						
Great Slave Lake	Yes	Yes	Yes	Yes	No	Uncertain
Great Bear Lake	Yes	Yes	Yes	Yes	Yes (strong)	Yes

The species-flock concept advanced above must be evidence-based. That is, the simple co-occurrence of two cisco ‘species’ or forms does not necessarily imply a species-flock. For example, presence of a cisco form that utilizes riverine habitats and is ecologically differentiated from that using lacustrine habitats in the same basin may simply be life history variation, thus not merit identification as a species-flock. Presence of the above plus differentiated cisco forms co-occurring in a lake, however, would likely qualify as a putative species-flock.

Finally, as indicated within central North America, the concept advanced above is restricted to the new world group of ciscoes that had their origin from glacial refugia south of the Pleistocene ice sheets. Ciscoes of Beringian origin are of old world affinities and are excluded despite the fact that some may co-occur with new world ciscoes.

Levels of differentiation among members of species-flocks may be relatively weak, are likely maintained due to assortative mating associated with, among other factors, integrity of habitats. Factors that threaten habitat integrity, in turn, threaten the species-flock diversity. An over-arching factor, hybridization among forms, represents an additional threat. Not only does hybridization obscure taxonomic boundaries making identifications difficult, it destroys lineage integrity and thus seriously undermines diversity at this level.

Sources of Uncertainty

- Incomplete evidence to support both the designation of the DUs and synonymizing forms amongst locations
- Conflicting evidence
- Differential weightings placed upon various lines of evidence by taxonomic experts
- Variation in methods used to collect and analyse the data
- Incomplete analysis throughout the range
- Varying timelines among locations over which differentiation has occurred, thus varying degrees of difference among co-occurring taxa
- Unexplored or unknown parallel situations
- Situations where pre-existing diversity has been reduced or altered through anthropogenic factors
- Incomplete understanding of the evolutionary processes specific to this group (e.g., divergent vs. reticulate evolution)

Assumptions

- Gillraker number, a key character in differentiating cisco taxa, is assumed to be generally heritable and non-labile past a certain age/size
- Assumed that for the described DUs that we have defined most of the forms present
- Assumed that diversity in form reflects underlying diversity in function, thus is ecologically (and perhaps evolutionarily) relevant
- Aspects of the diversity present in the ecosystem (e.g., habitat, basins) are somehow correlated with the resulting diversity (ecological, functional)

CONCLUSIONS AND ADVICE

Shortjaw Cisco, *Coregonus zenithicus* is taxonomically valid in the Great Lakes and Lake Nipigon as originally described by Jordan and Evermann (1909) and re-affirmed by Koelz (1929), however, recent morphological, biochemical and biogeographic evaluations question this validity (Bailey and Smith 1981; Smith and Todd 1984; Turgeon and Bernatchez 2001 a,b, 2003 among others).

C. alpenae from lakes Erie, Michigan, and Huron, and C. nigripinnis cyanopterus from lakes Superior and Nipigon were later synonymized with the Shortjaw Cisco (Todd and Smith 1980; Todd et al. 1981).

The above taxonomy is primarily morphologically based; however, subsequent ecological and genetic studies have demonstrated that it is insufficient to address the diversity within and among ciscoes (*Coregonus* spp.).

Application of these approaches outside of the Great Lakes has further demonstrated this insufficiency; specifically, morphological differences in some situations do not correspond with expected ecologies and genetics, leading to inconsistencies of taxonomic identification (and putative synonymization) among lakes.

Moreover, within the Great Lakes, application of a morphologically based approach also does not consistently reflect evolutionary relationships; this applies to situations outside the Great Lakes as well.

Accordingly, a new approach to delineating taxa (e.g., nominate taxa, morphotypes, ecotypes) within ciscoes and designatable units is required. The extant ciscoes for which these issues apply include: *C. artedi* (Cisco), *C. hoyi* (Bloater), *C. kiyi* (Kiyi), *C. nigripinnis* (Blackfin Cisco), *C. nipigon* and *C. zenitihicus* (Shortjaw Cisco) from type localities (Laurentian Great Lakes) and putative *C. zenithicus* from areas outside the Laurentian Great Lakes. The above taxa represent the new world ciscoes; this new approach is not suggested for old world ciscoes (i.e., *C. autumnalis* and *C. laurettae*).

Moreover, it appears that multiple forms of ciscoes within a location as well as characteristics of those locations themselves are situations that support the evolution, presence and maintenance of cisco diversity.

In conclusion, a species-flock approach is viewed as appropriate for the evaluation of the conservation status of this unique freshwater fauna of Canada. For example, the Lake Nipigon cisco flock includes: Cisco, Shortjaw Cisco, Blackfin Cisco and Bloater and the Lake Superior cisco flock includes: Cisco, Shortjaw Cisco, Kiyi and Bloater. These examples fit the following range of definitions of a species flock: a) "a high level of endemicity amongst its constituent species, their close phyletic relationship [monophyletic], and their geographical circumscription" (Greenwood 1984); or b) "an assemblage of a disproportionately high number, relative to surrounding areas, of closely related species which apparently evolved rapidly within a narrowly circumscribed area to which all the member species are endemic" (recent monophyly is not a requirement of this definition as flocks are not taxonomic categories (Nelson 1971 in Ribbink 1984)) (Ribbink 1984); or c) "a monophyletic group of species living in one lake or originally derived from one lake" (Smith and Todd 1984).

Where species-flocks occur or where more than a single form of these ciscoes is present in a location, we consider the combination of cisco forms and the unique circumstances of that location to represent a putative designatable unit. This approach is also applicable to other nominate cisco taxa (e.g., *C. nigripinnis*, *C. nipigon*).

The consequence of this is that the following designatable units are defined relevant to previously identified locations that include *C. zenithicus*: White Partridge Lake, ON (two forms), Trout Lake, ON (two forms), Brule Lake, ON (one form), Lake Huron, ON (three forms); Lake Superior, ON (four forms), Lake Nipigon, ON (four forms), Lac Seul, ON (three forms), Sandybeach Lake, ON (two forms), Loonhaunt Lake, ON (two forms), Lake of the Woods, ON (two forms), George Lake, MB (two forms), Lake Athapapuskow, MB (two forms), Reindeer Lake, MB (two forms), Great Slave Lake, NWT (four forms), and Great Bear Lake, NWT (two forms). Only one of the putative ciscoes in each lake represents nominate Shortjaw Cisco.

Other situations where divergent or unusual ciscoes occur (e.g., even when only one form is present) need to be carefully evaluated under this approach for status as a designatable unit to ensure key diversity is assessed.

SOURCES OF INFORMATION

This Science Advisory Report is from the October 30-31, 2012 pre-COSEWIC assessment for Shortjaw Cisco. Additional publications from this meeting will be posted on the Fisheries and Oceans Canada (DFO) Science Advisory Schedule as they become available.

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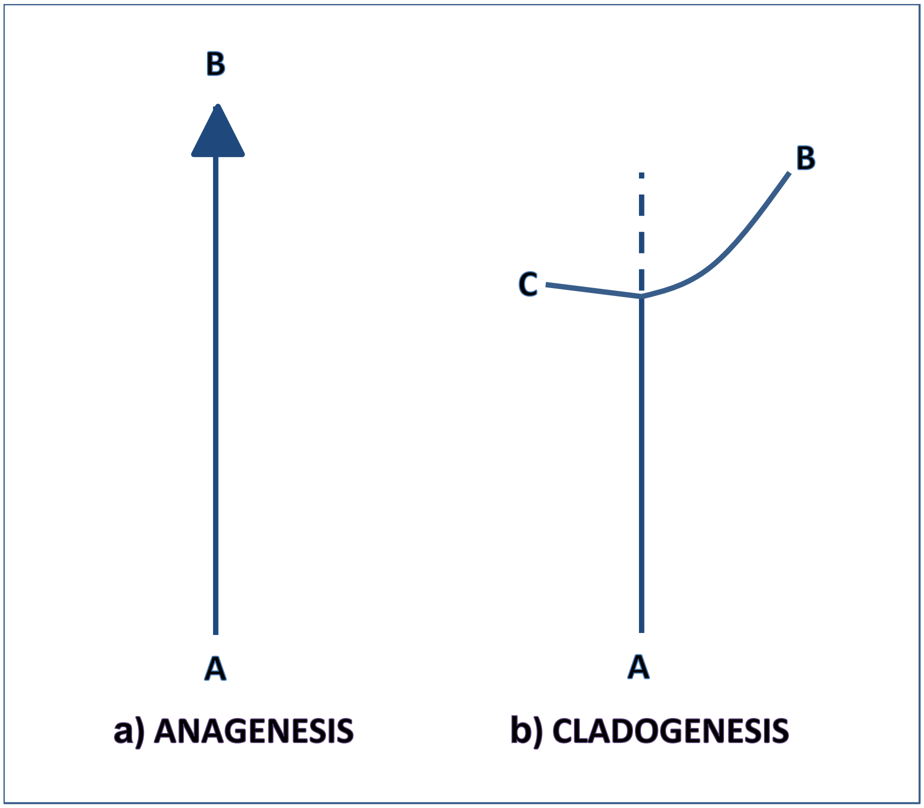
APPENDIX: MODES OF EVOLUTIONARY DIFFERENTIATION

Two modes of evolutionary differentiation have traditionally been recognized:

ANAGENETIC – Unidirectional change in a single, non-branching lineage, involving one species at a single point in time (App. Fig. 1a; McNamara 2006). Anagenesis is assumed to include founder effects due to a small number of colonizers, genetic/phenotypic drift resulting from the evolution of small sets of founding populations (colonizers), and differentiation of character values due to local selection and subsequent adaptation.

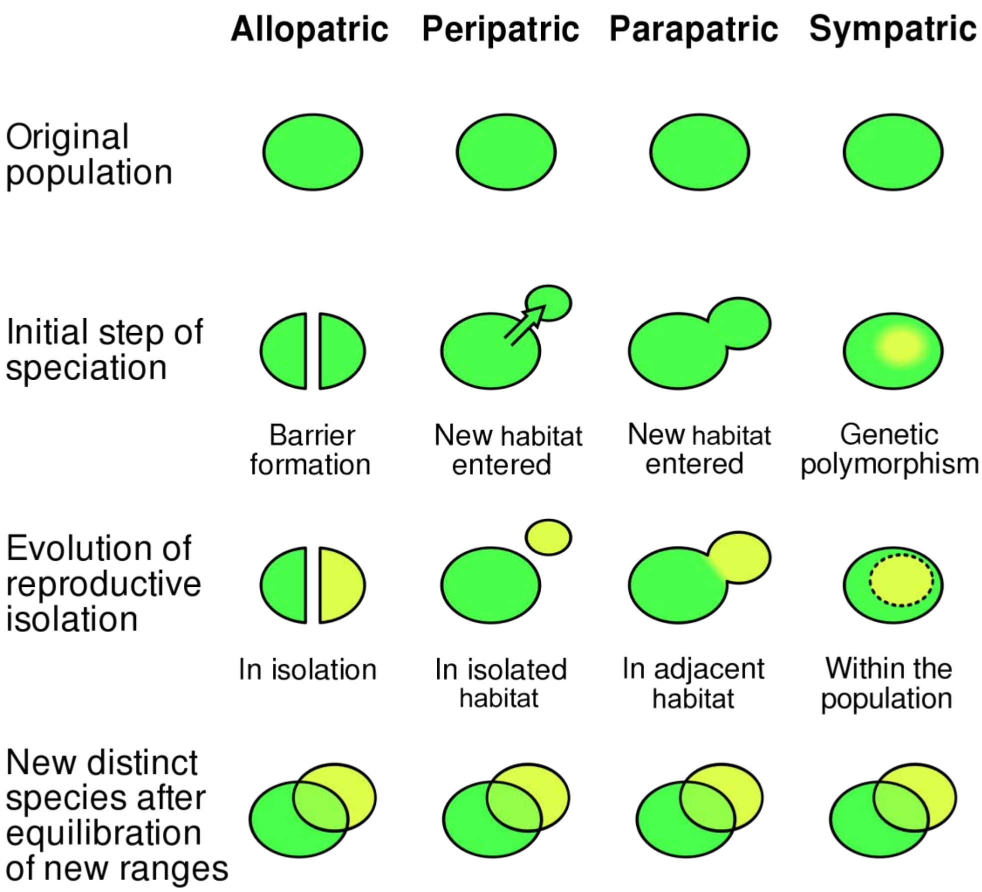
CLADOGENETIC – Directional branching (speciation) events involving multiple species that are evolving simultaneously (App. Fig. 1b; McNamara 2006).



Appendix Figure 1. Basic patterns of evolutionary differentiation.

Cladogenetic speciation has a geographic component, thus several 'types' or modes of cladogenetic speciation have been defined (see Mayr 1963; Futuyma 1986; Ridley 1993; Losos and Glor 2003; McNamara 2006; Bird et al. 2012 among others) (App. Fig. 2):

i. Strict Allopatric – Speciation via geographically separated populations.
ii. Strict Sympatric (ecological) – Speciation that occurs in panmictic populations.
iii. Parapatric (conditional allopatric) – The new species forms from a population adjacent to the ancestral species' geographic range.
iv. Peripatric (conditional sympatric) – The new species forms from a small isolated population at the edge of the ancestral population's geographical range.



Appendix Figure 2. Modes of cladogenetic speciation. Adapted from figure created by Ilmari Karonen and used under Creative Commons Attribution-Share Alike 3.0 Unported license.

Anagenesis and cladogenesis may occur simultaneously and to differing combinations among locations. Both processes promote heterogeneity, whereas hybridization, introgression, genetic swamping and local genetic forcings such as panmixis are countervailing forces that promote homogeneity (e.g., see Allendorf et al. 2001).

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