Identifying intra-specific freshwater fish elements for tracking and ranking in BC
- Proposed Approach -
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Background:

The freshwater fish fauna of BC is considered relatively depauperate at the species level (i.e.<70 species identified) - a reflection of the province's recent glacial history. Considerable variability, however, is apparent within these species. This intra-specific variation remains unrecognized taxonomically for the most part. To date, much of the provincial tracking and ranking (via the Conservation Data Centre) has been maintained only at the species level, with intra-specific fish *elements*[1] (term used by CDC) being added over time in a sometimes inconsistent manner. There has been some criticism from various sources (academic and other) about how these elements are identified (or not). The concern is that important irreplaceable biodiversity that is not formally recognized in discrete taxonomic units may not get properly recognized for protection purposes. This is not merely an issue of incomplete taxonomic studies. In some cases, potential elements for tracking may be based on ecological adaptations that do not have a discrete phylogenetic basis and would therefore never be considered a taxonomic unit. In contrast, some of the intra-specific groups that have been identified and ranked separately may not represent appropriate elements.

It has been argued that such variation at the intra-specific level exists across taxonomic groups; why should freshwater fish be any different? McPhail (2007) argues that freshwater fish are different from many other groups, and this difference is even more apparent across the highly diverse environments associated with BC's complex glacial and geological history. Freshwater fish have limited dispersal abilities; they are immediately limited by the fact that they need connected waterbodies through which to move (McPhail 2007). Dispersal between major watersheds is even more difficult given they are usually only connected via the ocean. In addition, two key elements conducive to rapid evolution, geographic isolation and novel ecological conditions, are particularly abundant for freshwater fishes given BC's glacial history (McPhail and Carveth 1992). Thus, freshwater fish readily form divergent populations (McPhail 2007); depending on the degree and length of time since separation (pre-glacial, post-glacial) as well as local adaptive pressures, divergence can result in differences considered irreplaceable.

Since its development in 2007, the Conservation Framework has become a key driver for the prioritization of conservation activities within the Ecosystems Branch of the Ministry of Environment. The Conservation Framework is based on the ranking of elements provided by the BC Conservation Data Centre. At the national level, the Wildlife Species identified for status designation by COSEWIC often originate from the elements provided by the CDC. Therefore, it is essential that these elements or units are identified at the appropriate level to ensure that intra-specific variation is appropriately represented, and thus recognized for protection purposes.

[1] A species or ecological community. The term "species" is used to include all entities at the taxonomic level of species, including interspecific hybrids, as well as all subspecies and plant varieties. Ecological communities are based primarily on Ministry of Forests vegetation classification and the International Classification of Ecological Communities.

The following sections highlight the key constituents of intra-specific diversity that should be considered and outline the steps to identify elements appropriate for provincial conservation tracking and ranking. Wood and Gross (2008) argue that such an approach should describe diversity at the level of Elemental Conservation Unit (ECU or demographically isolated populations whose probability of extinction over the time scale of interest (e.g.100 years) is not substantially affected by natural immigration from other populations). Data are generally too sparse currently to do this for most species in BC. In addition, it may not be practical or appropriate to apply this concept for status assignment at the provincial level, or for other levels of biological organization (e.g., assemblages of populations into distinct evolutionary lineages). However, the approach described here is consistent with what would be necessary to identify conservation units like ECUs.

Key constituents of intra-specific diversity:

The following key constituents of intra-specific diversity (adapted, in part, from Taylor 2006 and COSEWIC 2009) should be considered in CDC tracking and ranking exercises for freshwater fish. They are listed in order of significance from most compelling to least compelling criteria for identifying intra-specific elements:

1. Biological Species – Where two populations within the same formally described taxon occur in reproductive sympatry (mating in the same time and place) but remain reproductively isolated (the two populations remain as distinct gene pools despite potential or actual genetic exchange), they are two distinct biological species. In such cases, it is the reproductive sympatry that is of greatest significance, not the existence of each separate entity. They should be identified as separate elements for tracking and ranking purposes (e.g. Paxton Lake limnetic stickleback, Paxton Lake benthic stickleback). In contrast, species that have evolved different spawning ecotypes that spawn in same place but at different times, or vice versa, (e.g. stream and lake spawning kokanee) do not meet the reproductive sympatry criterion, and as such, would not be recognized as separate elements under this criterion.

2. Formally Described Sub-Species - Formal recognition means that a taxonomic entity below the identified species level has been described in the published literature. While some sub-species are now being questioned or even refuted using modern molecular techniques, they should be tracked and ranked separately until re-classification has been formally undertaken. There are only a two such sub-species identified for freshwater fish in BC currently (i.e. coastal and westslope subspecies of cutthroat trout).

3. Evolutionary Irreplaceability – Deep divergence within a species is associated with pre-glacial processes and results in major phylogenetic groups. Because these groups diverged before the onset of the last glaciation (i.e. ~75,000 years ago), they undoubtedly have accumulated genetic differences that are now at a magnitude considered irreplaceable (at least within a single human life span).

   (i) ***Direct genetic evidence of deep divergence***[i] - Such groups can be identified directly using certain conservative neutral DNA markers (e.g. mtDNA) to estimate time (on a molecular clock) since divergence (e.g. 1% genetic divergence ~ 500,000 years of

separation). The distribution of major phylogenetic groups reflects BC's biogeography, particularly with respect to glacial refugia and post-glacial dispersal routes into the province (e.g. interior and coastal Bull Trout). The identification of major lineages using molecular data is the most appropriate way to identify these groups; however, other types of information may also signal the existence of these groups. For example, fish distribution that is congruent with other floral or faunal species representing different glacial refugia and major range disjunction may be indicative of long-time divergence.

Direct genetic evidence may not always be available. Other indicators that may reflect long-time evolutionary divergence include:

(ii) ***Geographically disjunct populations***[ii] – Natural disjunctions in distribution mean that movement between populations has likely been severely limited for some extended length of time and may reflect geological and glacial history of the province. Under this scenario, populations have been isolated from each other and had the opportunity to evolve independently.

(iii) ***Populations occurring in different eco-geographic regions*** (see Mandrak 2004, also attached Fig. 1) – these regions correspond to major differences in climate and relief, and have significant effects on the aquatic environment. These regions reflect the major geological and glacial events of the province (and the country). As such, occupation of different regions undoubtedly reflects historic separation, and groups continue to diverge independently. Under different regimes, adaptive traits will also diverge (e.g. Brassy Minnow from Western Arctic and Pacific aquatic ecozones).

A final case, which may be more contemporary in nature (i.e. post-glacial) but likely reflects original, post-glacial dispersal routes:

(iv) ***Limited, widespread populations with differing threats and/or limiting factors*** – In some wide ranging species, population sub-structuring may be fairly limited (i.e. species represented by <10 discrete populations) with each population distributed across a relatively large area. The loss of one such population would represent a significant gap in spatial distribution of the species, at least temporarily. Where such populations are demographically independent and exposed to different threats or limiting factors, they may be identified as discrete elements (e.g. White Sturgeon populations).

4. Ecological Irreplaceability[iii] - Adaptive variation reflects a population's evolutionary response to local environmental conditions (i.e. selective pressure). If selection is maintained over generations, the genetically based adaptive trait is proliferated within the population. Adaptive traits may be the result of an event or series of events that may or may not be repeatable within a reasonable time frame (i.e. human life span). These ecotypes may be recognized where they are considered irreplaceable (i.e. unlikely to be re-colonized or replaced intentionally by another population).

For the purposes of CDC tracking and ranking, the ecological irreplaceability criterion must be further supported by the existence of at least one of the following factors:

(i) ***Rarity of ecotype*** –The ecotype will only be recognized as a distinct element for CDC purposes if the distinct adaptive trait is uncommon in BC (e.g. <10 populations). Note that rarity would be defined on the basis of the known distribution of traits in the species and could be modified in the presence of new information (from Taylor 2006). E.g. Cultus Lake Pygmy Sculpin, Vancouver Lamprey, Queen Charlotte Unarmoured Stickleback, Large-bodied piscivorous rainbow trout.

OR

(ii) ***Presence of a shared, existing/imminent threat*** – The ecotype will be recognized as a distinct unit/element for CDC purposes where it may be present in a number of populations (i.e. considered common) but a shared existing/imminent threat is simultaneously affecting these population such that the risk of extinction is equivalent to the risk to a single population. E.g. summer-run interior steelhead populations which appear to be in decline simultaneously owing to altered ocean conditions.

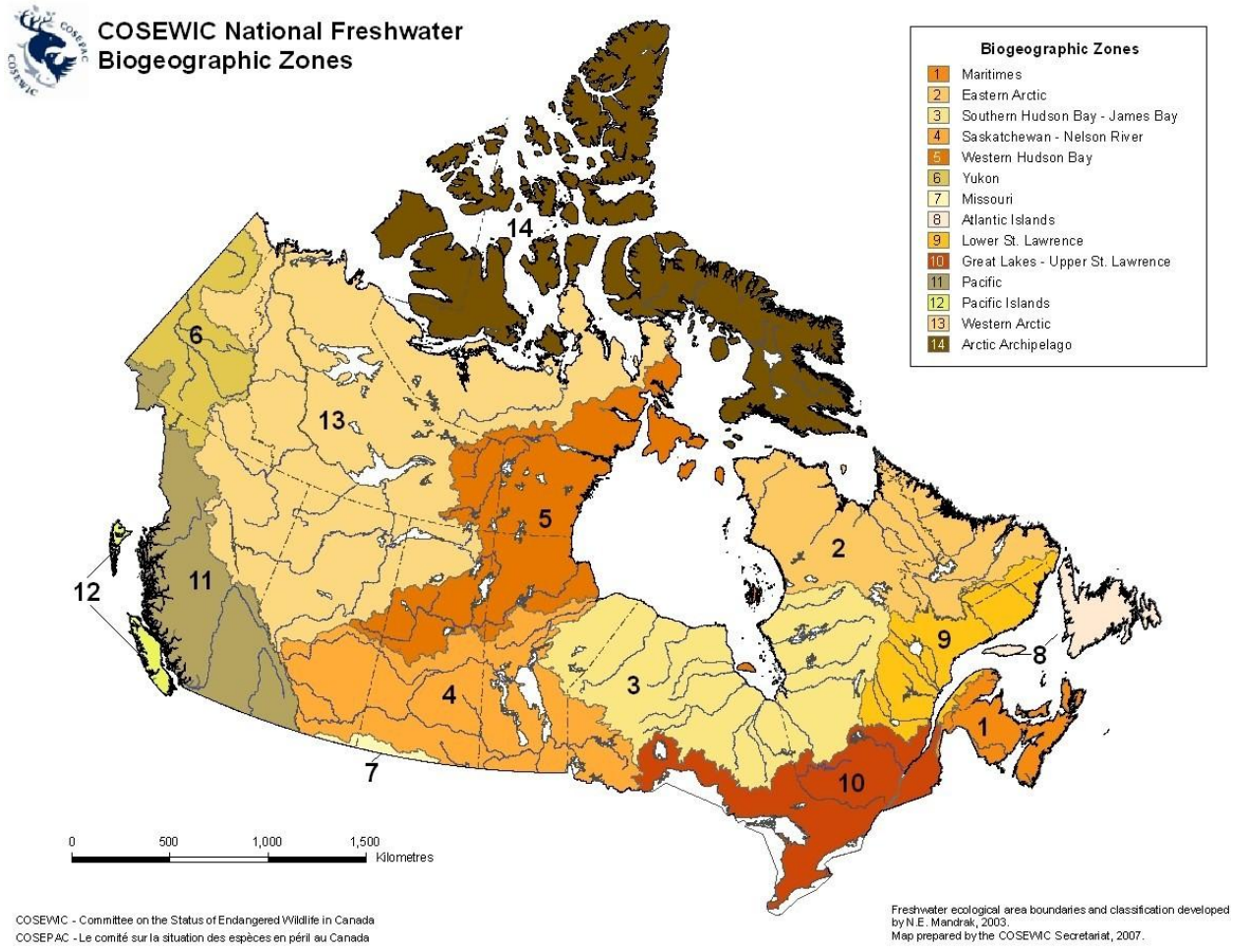

Figure 1. Based on Mandrak (2004). Note that four zones occur in BC: Pacific Islands, Pacific, Western Arctic and Yukon.

Steps to identify units for conservation:

The following key outlines the steps to identify units for conservation purposes (tracking and ranking by CDC). The key and accompanying notes incorporate most elements of a key developed to identify putative Designatable Units (DU) for freshwater fishes being assessed by COSEWIC (Taylor 2006). The above constituents are captured in this key.

Clearly, many fish species in BC have not yet been evaluated in terms of intra-specific diversity. Given that CDC ranking can be revised regularly, a species can be re-assessed as more information becomes available. Where there is good reason to suspect that the species should be further subdivided into intraspecific units, and that doing so could result in such units being at different status levels compared with tracking only at the taxonomic species level, the species should be identified as a priority for inventory and/or research within the Conservation Framework.

Key to identify (ID) CDC Elements for freshwater fish (based on Taylor 2006).

Criterion	Decision
1a. The putative element is a distinct taxonomic entity or qualifies as a distinct biological species.	**ID element**
l b. The putative element is not a distinct taxonomic entity or biological species.	**Go to 2**
2a. The putative element represents a major phylogenetic grouping separate from the other groupings within the taxon in question[i].	**ID element**
2b. The putative element does not belong to a major phylogenetic grouping within the taxon in question.	**Go to 3**
3a. The putative element represents a major range disjunction[ii].	**ID element**
3b. The putative element does not represent a major range disjunction.	**Go to 4**
4a. The putative element occurs in a separate aquatic eco-geographic region compared to other elements.	**ID element**
4b. The putative element does not inhabit a different aquatic eco-geographic region.	**Go to 5**
5a. The putative element is one of only a few (i.e.<10) discrete, demographically independent elements (or populations), representing a wide-ranging species, with differing threats.	**ID element**
5b. The putative element does not meet the above criteria (in 5a) for a wide-ranging species.	**Go to 6**
6a. The putative element has a distinctive, genetically-based adaptive trait or suite of traits (behaviour, life history, physiology, morphology) that represents local adaptation and identifies the element as not ecologically interchangeable with other known elements within the species[iii]. In addition, it is considered rare OR is simultaneously at risk across its BC range due to a shared threat.	**ID element**
6b. The putative element is not distinguished by such traits; the element is considered ecologically interchangeable with other elements OR it is not considered ecologically interchangeable BUT is not rare or at simultaneous risk across its BC range.	**Do not ID element**

Important points regarding use of the key (from Taylor 2006):

1. The key works from the most significant criterion (1) to the least significant (6). Criteria 1-2 reflect largely pre-glacial (long time frame) processes and 3-6 post-glacial processes. Fulfilling any of the criteria would be sufficient to identify as a distinct element, but the more a putative element fulfills, the better.

2. The key is designed to be used in a "nested" fashion. For instance, if elements are recognized after couplet 1 (say there are two accepted subspecies), the user then proceeds to "run" each of these elements through the rest of the key to assess whether or not elements may exist at a finer scale within each of the subspecies.

3. The key may also be used in a broader sense when trying to identify elements within a complex of populations evaluated for element status at one time. The key may then take the form of an ordered series of questions to ask when summarizing and evaluating data on genetic, ecology, distribution, etc for a set of populations. For instance, in this kind of situation the first step would be to ask: "Does the species as a whole contain accepted subspecies"? If the answer is "yes", then each of the subspecies is recognized as a separate element initially and the remaining questions (major phylogenetic groups present? Distinctive traits?, range disjunctions?, etc.) are asked for each of these subspecies. If the answer is "no", the complex as a whole is run through the rest of the questions on phylogenetic groupings, distinctive traits, range disjunctions, etc.).

4. This scheme is meant to capture the major divisions within named taxa (i.e., those just below the species level). They would typically apply to collections of populations, but could apply in some cases to single populations (e.g., Cultus Lake Pygmy Sculpin).

References:

COSEWIC. 2009. Guidelines for Recognizing Designatable Units Below the Species Level.

McPhail, J.D. 2007. The freshwater fishes of British Columbia. The University of Alberta Press, Edmonton, AB.

McPhail, J.D. and R. Carveth. 1992. A foundation for conservation: the nature and origin of the freshwater fish fauna of British Columbia. Produced for the BC Ministry of Environment.

Mandrak, N. 2004. Aquatic ecoregions of Canada, *in* COSEWIC (2005). Guidelines for recognizing designatable units below the species level. Available at http://www.cosewic.gc.ca/eng/sct2/sct2_5_e.cfm . Fourteen aquatic ecoregions were defined: Maritimes, Eastern Arctic, Southern Hudson Bay-James Bay, Saskatchewan-Nelson, Western Hudson Bay, Yukon, Missouri, Atlantic Islands, Eastern St. Lawrence, Great Lakes-Western St. Lawrence, Pacific, Pacific Islands, Western Arctic, Arctic Archipelago.

Taylor, E. 2006. How to identify putative designatable units (PDUs) for COSEWIC. Adopted by COSEWIC Freshwater Fishes Scientific Subcommittee.

Wood, C. And M. Gross. 2008. Elemental conservation units: communicating extinction risk without dictating targets for protection. Conservation Biology. 22:36-47.

Endnotes (Taylor 2006):

[i] As evidenced by the possession of diagnostic alleles or haplotypes, and/or by forming a distinct assemblage in a phylogenetic (tree) analysis with some measure of statistical support (e.g. at least 75% bootstrap support, significant branch lengths, significant monophyly as determined by maximum-likelihood analyses). Such support at more than one genetic locus is highly desirable. Phylogenetic analysis should be conducted using marker loci that are appropriate for resolving long-term (pre-glacial) evolutionary events (e.g., mtDNA or nDNA sequence variants). More rapidly evolving loci such as microsatellites (which might resolve distinctive groups that have evolved over rapid time frames should not be used as criteria for monophyly unless they are corroborated by other more slowly-evolving loci or by biogeographic evidence (e.g., significant genetic groupings that overlap with geographic areas thought to have served as glacial refugia).

[ii] Major range disjunction meaning two or more groups of populations separated "widely" by naturally unoccupied areas. The definition of "widely" cannot really be quantified, but it would generally mean an area at least as large as the area actually occupied, but across which natural dispersal (although possible) is not observed or expected. These disjunctions are meant to reflect evolutionarily significant events such as those caused by historical effects like glaciation or sea level changes, mountain building. The best thing to do would be to compare any proposed disjunctions to examples of what we already accept as significant.

[iii] The criterion "not ecologically interchangeable" (sensu Crandall et al. 2000; *Trends Ecol. Evol*. **15**: 290-295) refers to cases where no single trait distinguishes the putative element or unit, but there is good evidence that a particular suite of adaptations make it very unlikely that the unit could be replaced by recolonization or deliberate introductions from another population.