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FRAMEWORK FOR CHARACTERIZING CONSERVATION UNITS OF PACIFIC SALMON (*ONCORHYNCHUS* SPP.) FOR IMPLEMENTING THE WILD SALMON POLICY
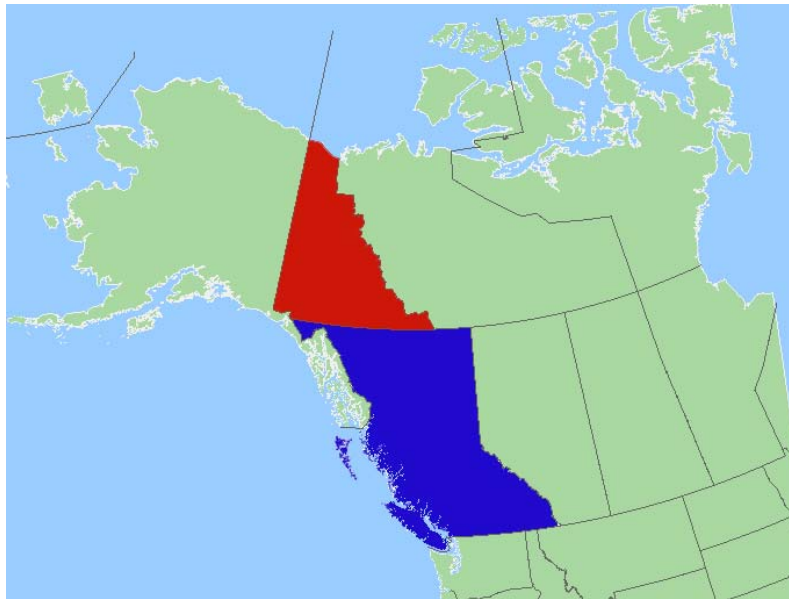

Figure 1:The Pacific-Yukon Region of Western Canada consists of the Yukon Territory (red) and the province of British Columbia (blue). This document pertains to those portions of the Region inhabited by anadromous Pacific Salmon.

Context

   Pacific salmon (genus Oncorhynchus) are the most ecologically, morphologically and behaviorally diverse vertebrate species in Canada, with many thousands of more or less distinctive "populations". To conserve their biodiversity and to manage the species for the benefit of all Canadians the Canadian Department of Fisheries and Oceans (DFO) adopted and is now implementing Canada's Policy for the Conservation of Wild Salmon Policy (the WSP) (DFO 2005). Implementation of the WSP consists of six strategies, the first of which stipulates the standardized monitoring of wild salmon status. Standardized monitoring begins with the identification of species-specific Conservation Units or CUs. The CUs serve two roles under the WSP. First, each CU is, in some sense, a significant element of biodiversity that the WSP seeks to conserve and manage. Second, each CU is a unit for reporting on the success (or failure) of actions taken under the WSP to conserve wild Pacific salmon. Subsequent steps in the Policy's implementation, including the characterizing of the biological, habitat and ecological status of each CU are contingent on providing a consistent, objective, defensible and operational definition of the CU that is both practicable and will insure that the important elements of salmon biodiversity can be conserved and managed.

   Any scheme to compartmentalize biodiversity in Pacific salmon will be, at best, an approximation. In addition to all of the usual difficulties caused by limited and incomplete information, the highly dynamic nature of the interactions between salmon and their diverse habitats means that their diversity is continually evolving. Only 10000 years ago there were no salmon in western Canada at all because the entire region was glaciated but now virtually all accessible habitats are full. Humans, with their alterations to habitat on all scales and their often intense predation, are creating conditions that can only serve to accelerate adaptive change in salmon. Consequently, the characterizations of diversity in

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salmon that we present are imperfect and will be subject to change as new information becomes available and as our interpretations of that information are refined. For current information about the WSP, including the current lists of Conservation Units and their statuses as well of details of the processes in place to review and modify the lists of Conservation Units, the interested reader is referred to the DFO, Pacific Region's web portal, http://www.pac.dfo-mpo.gc.ca/pages/default_e.htm.

SUMMARY

- The first step in the implementation of Canada's Policy for Conservation of Wild Pacific Salmon (the Wild Salmon Policy or WSP) is the identification of units for their conservation.

- The WSP defines these units, called Conservation Units or CUs, as "a group of wild salmon sufficiently isolated from other groups that, if extirpated, is very unlikely to recolonize naturally within an acceptable timeframe". This definition embodies the concepts of reproductive isolation, adaptive variation and ecological exchangeability that underlie commonly used units for the conservation of species diversity.

- The approach of Waples et al. was modified to characterize diversity in Pacific salmon along three major axes: ecology, life history, and molecular genetics, and then to compartmentalize that diversity into Conservation Units. The three descriptive axes are used to map local adaptation in a variety of ways. The maps were then examined and combined to locate and describe the Conservation Units.

- The first stage in the description of the Conservation Units is based solely on ecology. The ecotypologies used included a characterization of the near-shore marine environment in addition to one for fresh water. The second stage of the description involves the use of life history, molecular genetics, and further ecological characterizations to group and partition the first stage units into the final Conservation Units. The result was Conservation Units that are described through the joint application of all three axes.

- There is a high degree of concordance between ecotypic, biological (life history) and genetic characterizations of intraspecific diversity. Molecular genetics was essential in areas of high genetic diversity but once identified, ecotypology appeared capable of mapping the genetic diversity. Similarly, there were instances where diversity in life histories (age structure, juvenile ecology) was mapped through ecological descriptors. The high levels of concordance between the three axes strongly suggest that the Conservation Units describe real and presumably adaptive diversity.

- The described method is data intensive and we anticipate that the CUs identified will be regularly modified as new information becomes available and our interpretations of it improve.

- One general conclusion from this work is that Pacific salmon in Canada are very diverse. This diversity is reflected in the estimated numbers of CUs by species in Western Canada (exclusive of the Yukon and Mackenzie Rivers and the Arctic Coast): pink salmon – 32, chum salmon – 39, coho salmon – 43, chinook salmon – 68 and sockeye salmon – 238.

- In addition to the pragmatic advantages of a method that uses all available information to describe intraspecific diversity, an ecotypic approach has benefits stemming from characterizations of salmon habitat in its broadest sense. Importantly, the method supports the intent of the WSP to use CUs for the conservation of both pattern and process.

INTRODUCTION

Canada's Policy for Conservation of Wild Pacific Salmon (the WSP) was released in 2005 following six years of discussion, consultation, review, and revision (DFO 2005). The WSP is one of several policies whose provenance was the New Directions discussion paper (DFO 1998). The goal of the WSP is to "restore and maintain healthy and diverse salmon populations and their habitats for the benefit and enjoyment of the people of Canada in perpetuity".

Concerns about the loss of biodiversity through extinctions of species have been with us for decades and Canada, along with many other countries, acknowledged the importance of diversity by ratifying the 1992 United Nations Convention on Biological Diversity (United Nations 1992). Canada subsequently adopted a federal law, the Species at Risk Act or SARA (Canada 2002). SARA substantially broadened the concept of species, i.e., those biological entities that could be afforded protection under the Act, by defining the term "wildlife species" to include not only species and subspecies but also races, varieties and distinct populations.

Perhaps the most phenomenal characteristic of Pacific salmon is their ability to return or "home" to their natal river, even after spending several years in the Pacific Ocean thousands of kilometers away. This homing ability is so refined that in some circumstances adults return to their natal nest site. Complex traits such as homing arise because they confer a survival advantage. Fish that spawn close to their natal redds tend to produce more offspring that survive to reproduce than those individuals that spawn distantly from their natal redds. Many of the biological traits of Pacific salmon that vary from one population to the next, such as where and when to spawn, egg size and number, body size and shape, whether fry should migrate upstream or downstream after emerging from the nest, etc., have been shown to be site-specific. Since a particular set of traits or phenotype confers a survival advantage in a particular place but not necessarily in other places, mechanisms that link a phenotype to the places where it survives well have evolved. That evolution has occurred in a vast geography that has both pattern, due to geology, latitude, and climate, and tremendous heterogeneity at the scales on which individual salmon interact with their environment. The results are levels of intraspecific diversity unparalleled in any other vertebrate species in Canada.

The Wild Salmon Policy formalizes concern for the phenomenal intraspecific diversity of Pacific salmon. The WSP introduced the biological concept of the "Conservation Unit" or CU and described how the diversity of wild Pacific salmon would be safeguarded by protecting CUs. CUs are conceptually defined as mutually interchangeable groups of wild salmon with similar adaptations that are reproductively coupled. Under the WSP CUs have the dual roles of firstly being, in some sense, fundamental units of biodiversity and secondly, of being the accounting units for documenting progress in achieving the policy goals of the WSP.

The initial steps in protecting biological diversity and also the primary roles of scientific research, are to identify the diversity and then take inventory of the units of diversity that require conservation (Wood 2001). Consequently, the first of six strategies in the WSP concerns the identification of the units and determining their conservation status. The purposes of the paper were first to describe the method that was developed to identify the CUs of the five species of Pacific salmon under federal jurisdiction and second to apply the method to identify and describe the CUs. This advisory deals only with the method.

ANALYSIS

The Wild Salmon Policy (WSP) defines the Conservation Unit (CU) as the "groups of wild salmon living in an area sufficiently isolated from other groups that, if extirpated, are very unlikely to be recolonized within an acceptable time frame". All else equal, the time required for recolonization following an extirpation would vary directly with the degree of similarity between the colonizing fish and those extirpated, i.e., the extent of "preadaptation". If what is an "acceptable" period of time is interpreted as an ecological rather than an evolutionary time frame, then the definition of the CU can be couched in terms of ecological exchangeability, a concept introduced by Crandall et al. (2000). Experience has demonstrated that for natural recolonization to occur in short periods requires a very high degree of similarity, certainly a higher degree than implied by current definitions of either the Evolutionarily Significant Unit of the American Endangered Species Act or the Designatable Unit of the Canadian Species at Risk Act. Importantly, a variety of tools is available to estimate the ecological exchangeability of groups of organisms (Table 1).

Table 1. The tools used to describe diversity in Pacific salmon and to gauge ecological exchangeability are summarized in this table.

Approach	Details
1. Experimental	• unidirectional or reciprocal transplants to demonstrate persistence in a novel habitat; • extensive history of attempted transplants has shown limited exchangeability in all species; • direct & powerful test of exchangeability but expensive and time-consuming and dangerous in advance of extirpation.
2. Descriptive	• comparison of phenotype or observable traits such as morphology, behaviors and life-histories; • includes quantitative genetics • indirect but powerful test of exchangeability; • requires that the variations described be genetic (i.e., heritable) and adaptive; • open to argument that something important to exchangeability has been missed.
3. Genetical	• uses molecular genetics techniques and mathematical models to gauge extent of reproductive isolation between populations (reproductive isolation is required for local adaptation to persist); • indirect and weak test of exchangeability
4. Ecological	• comparison of the adaptive landscape, i.e., similarity of the habitats and presumably the selective forces to which fish are locally adapted; • indirect and weak test of exchangeability largely because of scale mismatches (habitat is quantified at scales different scale from those that fish-habitat interact occur on); • can be easily applied over a large area and when information about the fish is lacking or patchy.

Waples et al. (2001) characterized diversity in Pacific salmon in the American Pacific Northwest along three major axes: life history, biochemical genetics and ecology and biochemical genetics, corresponding to approaches 2 through 4 of Table 1. Our approach built upon a similar characterization of diversity to compartmentalize that diversity into units for conservation. From our perspective, the axes of Waples et al. (2001) were akin to tool sets that allowed us to map local adaptation, which is what we actually want to conserve, in a variety of ways. We then examined and combined the maps to locate and describe the units of conservation. Waples et al. (2001) have demonstrated that the three tool sets provide very similar results for Pacific salmon at least at the geographic scales that both they and we are considering. That is

important because each tool has both strengths and weaknesses and often data limits the application of at least one of the tools in a particular area. Those shortcomings can be overcome with a toolbox outfitted with interchangeable and complimentary tools.

All of the factors we used to identify CUs are proxies for assessing local adaptation. Ecotypology, characterizing the adaptive environment, is the most indirect of the proxies. Life-history and adaptive traits such as spawn timing are fairly direct measures of adaptation but do not directly determine that the characteristics are inherited (although others have demonstrated numerous times that they are!) Genetic distinctiveness is an indirect measure of reproductive isolation, both a requirement and an indication that local adaptation is present. The intent is to identify groups of spawning sites where the fish are adaptively similar and hence are likely to be ecologically interchangeable. This method does not lead to proof that salmon within a CU are, in fact, interchangeable. Such proof can only come from experimental exchanges of fish and confirmation that transplanted fish can produce persistent and wild populations without human support or with only minimal and short-term human assistance.
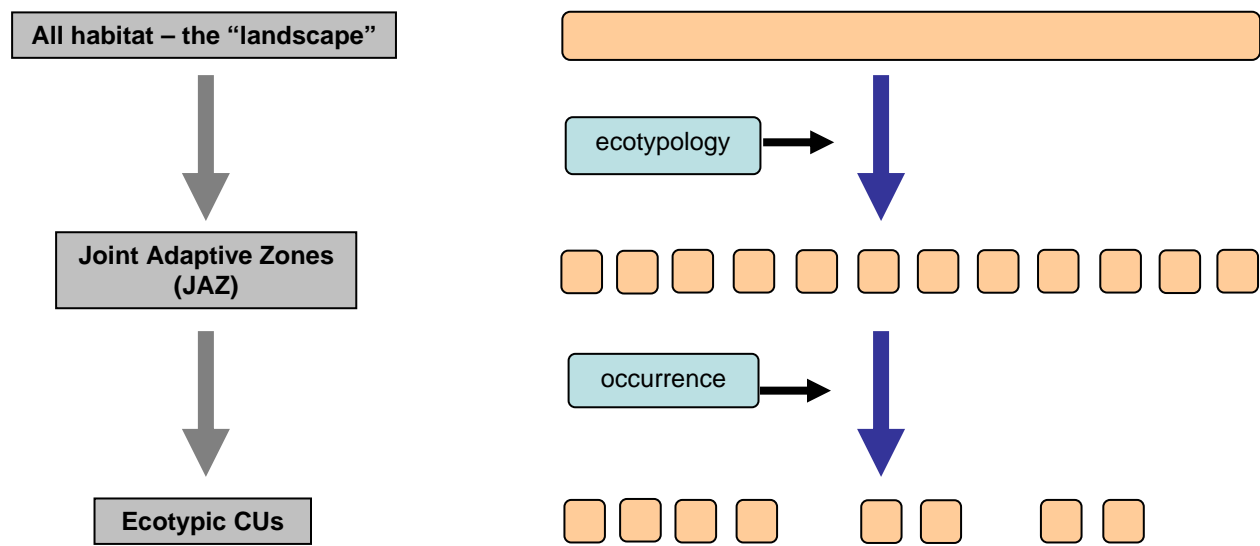

Figure 1. The identification of Conservation Units begins by using ecotypology (classification of aquatic ecosystems) to describe Joint Adaptive Zones (JAZ) within British Columbia. JAZ without a particular species present are then excluded. The JAZ where a species occurs become the ecotypic Conservation Units for that species. In the absence of any additional information, the ecotypic CUs would become the Conservation Units for the species.
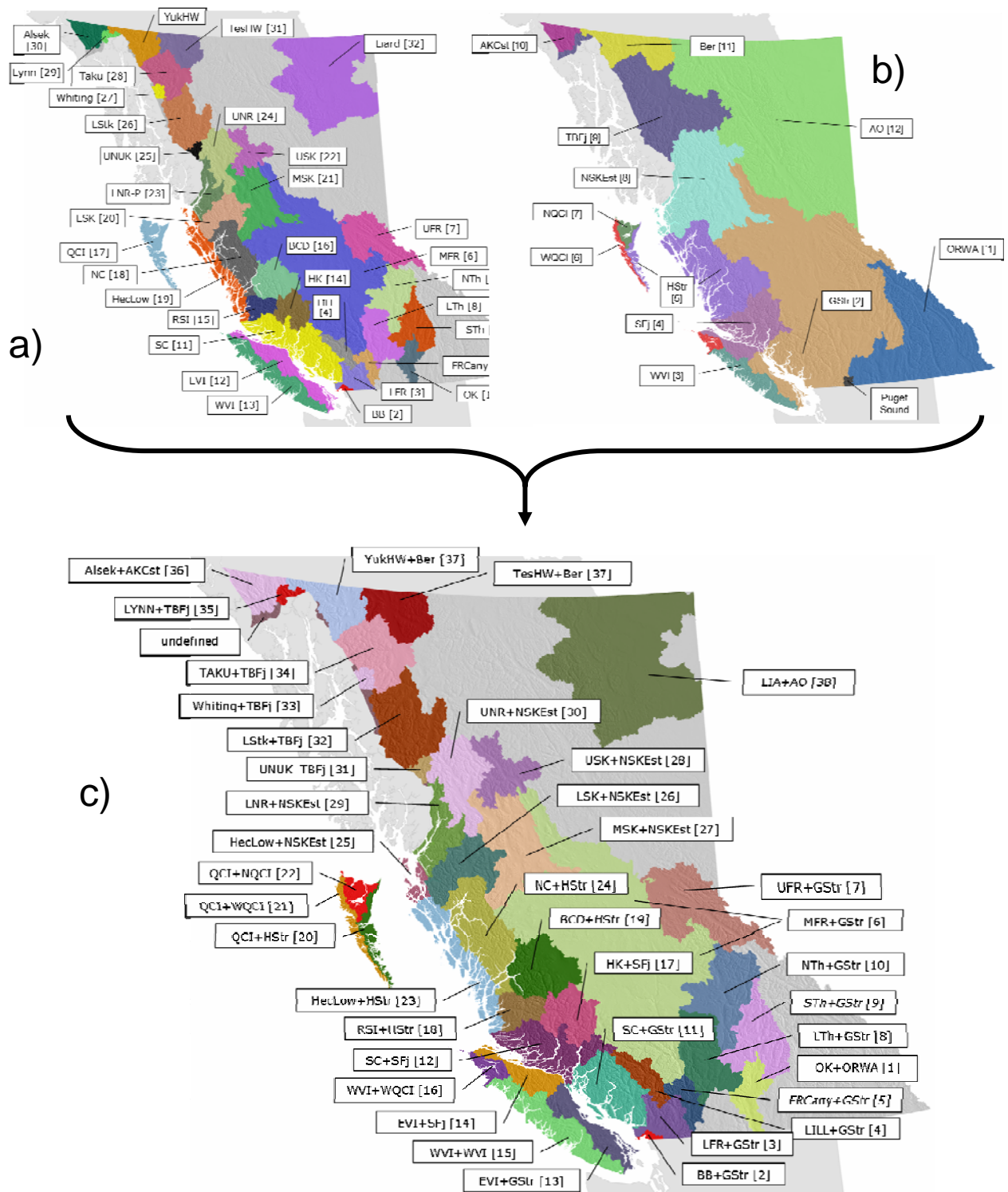
Figure 2. The ecotypic zones for Pacific salmon in British Columbia. a) The 32 Freshwater Adaptive Zones are combined with the b) 12 Marine Adaptive Zones to describe c) the 38 Joint Adaptive Zones. Additional zones will be identified in the Yukon Territory.

The first two steps in the method involve ecotypology and species occurrence (diagrammed in Figure 1). We first used ecotypology to subdivide British Columbia into ecologically homogeneous zones. The typology is focused on fluvial freshwater habitats (rivers not lakes) (Freshwater Adaptive Zones, Figure 2a) and near-shore and estuarine habitats (Marine Adaptive Zones, Figure 2b). The zoogeography of freshwater fishes is also incorporated into the Freshwater Adaptive Zones. The Freshwater and Marine Adaptive Zones are combined into 38 Joint Adaptive Zones or JAZ in British Columbia (Figure 2c). Each JAZ where a species is known to occur or where it probably occurs is called an Ecotypic-CU. In the absence of any other information about the species, each Ecotypic-CU would become a CU. Not all of the species occur in all of the 38 JAZ. Consequently, the sets of ecotypic-CUs are species specific.

Other than presence, identification of the ecotypic-CUs does not require any information about salmon. That information is applied when the salmon with each ecotypic CU are examined in detail using a variety of factors for assessing the nature and extent of local adaptations and ecological exchangeability (Figure 3). The intent is to identify groups of spawning sites where the fish are adaptively similar and hence are likely to be ecologically interchangeable. Life history traits and phenotypic traits such as spawn timing are usually reliable indicators of adaptation. Clusters of adaptations are sometimes described as life history variants, races or types. The biochemical genetics approach seeks to identify populations that are either sufficiently isolated reproductively from other populations for local adaptations to persist or are behaving genetically as if such local adaptations do exist. In the detailed examination of fish within the ecotypic CUs, ecology and habitat are examined at a finer spatial scale than that used to describe the JAZ. The intent, to identify "ecological adaptive zones", remains the same.
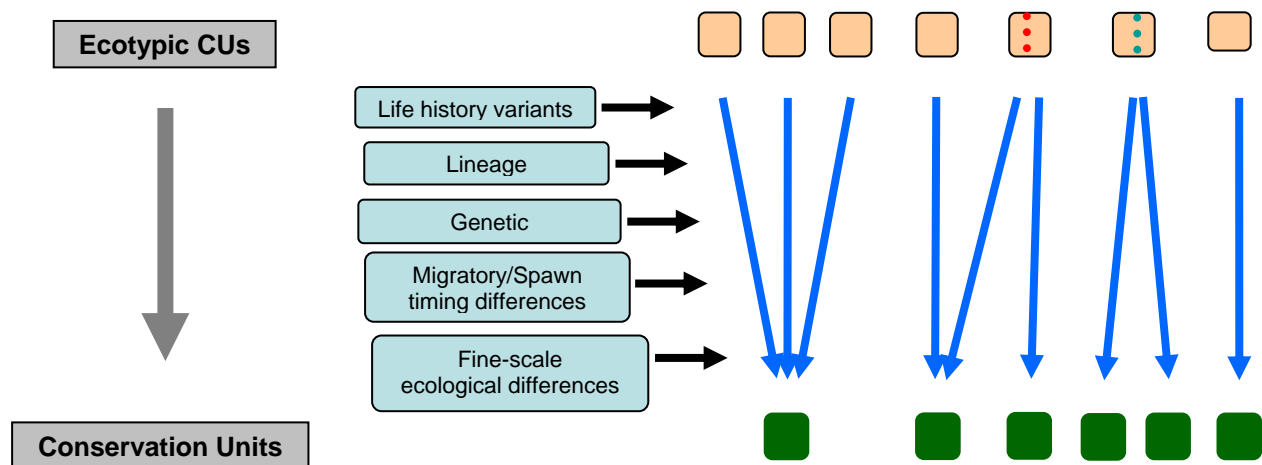

Figure 3. The Conservation Units of a species were identified by using site-specific information about lineage (recolonization following glaciation), life-history variants, molecular genetics (reproductive isolation), migratory and spawning time variations and fine-scale ecology. Ecotypic CUs could be combined, split, split and recombined or left unaltered. The intent was to find CUs that were internally homogeneous and externally different from neighboring CUs on as many axes as possible. Life-history variation, timing differences and molecular genetics were the most used descriptors of CUs. In all species but pink salmon, CUs were identified by splitting ecotypic-CUs more frequently than by other alterations. In pink salmon ecotypic-CUs were often combined more often than they were split.

Within the Pacific salmon some forms of intraspecific variation in life history, such as whether your young rear in a lake, a river or the ocean, aren't so much local adaptation as they are high-

level strategies for survival. Such distinctive variants could readily be recognized as races or even subspecies. Diversity of this sort is found in pink, sockeye and chinook salmon.

Even-year and odd-year pink are completely reproductively isolated because of their fixed two-year life cycle, and are properly considered temporal races. Sockeye salmon have three distinctive life-history variants. In the most familiar form, juvenile sockeye rear for one or more years in freshwater lakes before entering the ocean. In the river- or ocean-type variants, the juveniles rear in riverine habitats rather than lakes. River-type sockeye are thought to be a colonizing form that gives rise to the lake-type form. There is little evidence of facultative switching between forms and we treated them separately in describing CUs. Kokanee, the third form of sockeye salmon is not anadromous and completes its life cycle in freshwater lakes. As an obligate freshwater fish kokanee fall under provincial jurisdiction and are not covered by the Wild Salmon Policy. Our method of identifying CUs could be readily applied to kokanee although a typology of lakes would be required. There are two distinctive life-history types in chinook salmon that are characterized by how long juveniles rear in freshwater, although there are numerous other differences in their life histories. Juveniles of the ocean-type variant leave their natal streams at some point during their first summer. Juveniles of the stream-type variant remain in freshwater for at least one year. In some locations, notably the Columbia River, the ocean-type and stream-type forms of chinook salmon have all the attributes of distinct species. In Canada, the ocean-type predominates in coastal streams in the south, both types are found in streams on the northern coast and the stream-type predominates in the interior zones of the large rivers. However, there are numerous exceptions. When both types are present in the same river they usually have different spawning sites, migration and spawning times, and age structures.

For sockeye and pink salmon, we partitioned the sites within each ecotypic CU into the two major life-history types found in each of those species before proceeding with further analysis. The lake- and river/ocean-types of sockeye are not nearly so isolated as the two temporal races in pink salmon but our characterization of the diversity within the two sockeye types is quite different. Consequently, partitioning them at this point in the analysis facilitated their different treatment. At this point in the analysis, we also considered separating chinook salmon into its two major life history types, ocean- and stream-types. We decided not to make such a split in part because many populations in Canada are mixtures of the two types and because those situations where the two types are distinctive were fully captured in the subsequent analysis.

Each of the ecotypic CUs for the now seven "species" was examined for phenotypic, genetic and ecological evidence that might warrant their modification. First, the ecotypic classification was compared to a biochemical genetic classification. This comparison was used to detect instances where the ecotypic classification subsumed significant genetic diversity, in which case the ecotypic CU might be partitioned. Conversely, the ecotypic classification might have separated populations where there was no evidence of reproductive isolation, in which case two or more ecotypic CUs could be merged. The ecotype-genetic comparison was also used to examine whether the ecotypic CUs adequately separated major lineages and whether the ecotypic boundaries matched the genetic groupings. In a few instances, ecotypic CUs were partitioned to separate major lineages. Otherwise, partitioning of the ecotypic CUs required additional evidence that the resultant CUs were distinctive and were required to describe local adaptation. Merging ecotypic CUs was never based solely on genetic evidence but required evidence of a high degree of similarity on all compared factors.

That evidence came from an examination of life history differences, differences in migration and spawning dates, and other ecological (habitat) differences. For example, spawning times within ecotypic CUs were often bimodally distributed (i.e., there were two distinct periods of spawning).

In such situations, the spawning period could often be related to habitat-dependent temperature differences (e.g. whether the site was in a headwater stream or below a large lake). In some locations, the predominant age of the spawners was related to the "size" of the spawning streams. Since older salmon are nearly always larger, fish spawning in small headwater streams were consistently younger in some areas. In most cases where differences in spawning/migration timing and age structure were consistently observed within an ecotypic CU, we partitioned that ecotypic CU into two or more CUs.

In many instances, multiple factors were used to refine the ecotypic CUs. In particular, the genetic classification often revealed structure within an ecotypic CU (i.e., geographic patterns of relatedness) that were insufficient by themselves to identify CUs but which suggested comparisons of timing, life history and habitat that were sufficient to recognize CUs. This was particularly true in chinook salmon, where CUs were usually identified through multiple factors.

Lake-type sockeye were treated somewhat differently from the other species. There is a considerable body of genetic, behavioral and empirical evidence that sockeye are highly adapted to their nursery lake. For example, nearly all transplants of sockeye between lakes have failed, sometimes despite decades of attempts. This distinctiveness was readily confirmed in the large lakes that support large runs of sockeye and where considerable information was available. However, most of the sockeye lakes in British Columbia (at least half of the approximately 250 lakes) support small runs for which there is little information. To protect the potential diversity that might exist, we treated each nursery lake (or groups of small lakes) as separate CUs. The sockeye of large lakes (>50 ha) were combined into single CUs only when multiple lines of evidence indicated no differences between the fish and their habitats. In several instances, multiple CUs were recognized within single nursery lakes, usually in association with spawning locations and times.

CONCLUSION

In a species group as fantastically diverse, as adaptable and as rapidly evolving as *Oncorhynchus*, we think it very unlikely that any one characterization of diversity could ever be accepted for all purposes to which it might be put. We had two objectives in describing an approach to describe Conservation Units for Pacific salmon in Canada. First, we wanted to establish at what level in the biological continuum of diversity the WSP is focusing conservation efforts for Pacific salmon. We concluded that that level appears to lie below the wildlife species of SARA or the ESU of the American ESA. In other words, a CU is not equivalent to a Designatable Unit (DU) of COSEWIC or to an ESU of the American ESA as applied to Pacific salmon. However, Conservation Units are based on the same kinds of criteria as are DUs (Green 2005) and we have used much of the same information. Consequently, CUs will always be nested within a DU. We think that characterizing the CU in this way fully supports the first priority of conservation under the WSP: to safeguard genetic diversity. Defining the CU at a higher level in the continuum would not fully support the objectives of the WSP because the loss of a closed population (i.e., a DU) is not reversible within a reasonable time (Waples et al. 2001). Viewed from the reverse perspective, the loss of a CU might not appreciably increase the risk of extinction for the DU and so would not necessarily result in invocation of SARA protections.

The methodology that we propose for use in characterizing CUs is closely modeled on the approach of Waples (2001). Compared to Waples we emphasize ecotypology more than molecular genetics but we use both approaches in a complimentary way. In most cases, there was a high level of concordance between the ecotypic characterizations of diversity and the patterns in genetic diversity. The only major disagreements came in areas where there were

there were high levels of genetic diversity. In many of those situations, however, additional environmental typology appeared useful in mapping much the apparent genetic diversity. This was particularly the case for coho. The power of molecular techniques to detect diversity at a fine spatial scale and once recognized, the ability to explain the patterns through ecological patterns, suggests that both approaches are detecting real and likely adaptive diversity.

One important benefit of an ecotypic approach is that it characterizes the habitats, environments, and ecosystems where diversity exists and on which the processes that maintain diversity rely. By doing so, the intent of the WSP to use Conservation Units as more than collections of representative populations but as the basis for comprehensive habitat and ecosystem-based management is made apparent and operational.

One general conclusion from this work is that Pacific salmon in Canada are very diverse. This is reflected in the estimated numbers of CUs by species shown in the following table:

species	number of CUs
pink-odd	19
pink-even	13
chum	39[†]
coho	43
chinook	68[†]
sockeye-river	24
sockeye-lake	214

† Additional CUs will be described in the Yukon River and possibly in the Mackenzie River.

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