A Review of Metrics of Distribution with Application to Conservation Units under Canada's Wild Salmon Policy

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A REVIEW OF METRICS OF DISTRIBUTION WITH APPLICATION TO CONSERVATION UNITS UNDER CANADA'S WILD SALMON POLICY

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ABSTRACT

Peacock, S.J., and Holt, C.A. 2010. A review of metrics of distribution with application to Conservation Units under Canada's Wild Salmon Policy. Can. Tech. Rep. Fish. Aquat. Sci. 2888: xii + 36 p.

Metrics describing the distribution of individuals among groups and across the landscape can provide information on the resilience of a population that may not be apparent from abundance information alone. The distribution of spawners has therefore been recommended as an indicator of the biological status of Conservation Units (CUs) under Canada's Wild Pacific Salmon. The objectives of this report were to review metrics of distribution from the scientific and management and compare those to metrics previously proposed for assessing status of CUs. Only a subset of metrics were relevant for assessing status of CUs, but others may be useful for other biological and management settings.

RÉSUMÉ

Peacock, S.J., and Holt, C.A. 2010. A review of metrics of distribution with application to Conservation Units under Canada's Wild Salmon Policy. Can. Tech. Rep. Fish. Aquat. Sci. 2888: xii + 36 p.

Les paramètres décrivant la distribution des individus parmi les groupes et à l'échelle du paysage peuvent fournir de l'information sur la résilience d'une population qui peut ne pas être évidente d'après l'information sur l'abondance à elle seule. La distribution des reproducteurs a par conséquent été recommandée comme un indicateur de la situation biologique des unités de conservation (UC) aux termes de la Politique du Canada concernant le saumon sauvage. Les objectifs de ce rapport sont de passer en revue les paramètres de distribution du point de vue scientifique et de la gestion et de les comparer aux paramètre déjà proposés pour l'évaluation de la situation des UC. Un seul sous-ensemble de paramètres se prêtait à l'évaluation de la situation des UC, mais d'autres sous-ensembles pourraient être utiles dans d'autres contextes biologiques ou de gestion.

GLOSSARY

Adaptive capacity: the ability of salmon to adapt under stress to changing environmental conditions without sacrificing the provision of ecosystem and socio-economic services. Adaptive capacity stems from genetic diversity, and contributes to resilience.

Conservation Unit (CU): a group of wild salmon sufficiently isolated from other groups that, if lost, is very unlikely to recolonize naturally within an acceptable time frame (e.g., a human lifetime or a specified number of salmon generations)(Figure 1).

COSEWIC: Committee on the Status of Endangered Wildlife in Canada.

Counting location: a spawning group that has been monitored.

Designatable Unit (DU): discrete and evolutionarily significant units of the taxonomic species used by COSEWIC when assessing threatened or endangered status, 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 (COSEWIC 2006).

Diversity: variation or differences among groups within a unit (e.g., population, species, CU).

Distribution: the allocation of fish or characteristic of fish among different groupings (e.g., spawners among spawning groups). See also frequency distribution and spatial distribution.

Evolutionary Significant Unit (ESU): the minimum unit that must be conserved under the US Endangered Species Act, described as a population that is reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species (Waples 1991).

Frequency distribution: a tabulation of the number of times a certain value (or range of values in the continuous case) appears in a sample.

Genetic diversity: sum of the combinations of genes (and alleles within genes) among individuals within a unit (e.g., spatial unit, Conservation Unit).

IUCN: International Union for Conservation of Nature.

Metapopulation: any assemblage of discrete local populations with migration among them (Schtickzelle and Quinn 2007)(Figure 1).

nuSEDS: the DFO **S**almon **E**scapement **D**atabase **S**ystem.

Occupied habitat: habitat that is used by spawning adult salmon. Note, the converse, "unoccupied" habitat, may be used by other life history stages (e.g., juvenile and migrating adult and juvenile salmon) but these stages are not considered in this report.

Phenotypic diversity: diversity in observable traits or characteristics, including morphology and behaviour (e.g., life-history tactics).

Population: a group of interbreeding salmon that is sufficiently isolated from other populations so that there will likely be persistent adaptations to the local habitat (Irvine and Fraser 2008)(Figure 1).

Spatial unit: a generic geographic area that supports multiple spawning groups (e.g., the area occupied by a CU or an ESU).

Resilience: the amount of disturbance from environmental and other stressors that a system can absorb and still remain within the same state or domain of attraction (Elmqvist et al. 2003).

Response Diversity: traditionally defined as the range of reactions to environmental change among species contributing to the same ecosystem function (Elmqvist et al. 2003), we apply the term to the range of reactions to environmental change among spawning groups within the same spatial unit (e.g., Conservation Unit).

Shannon-Weiner Diversity Index (H'): a metric of diversity among groups of individuals within a population that quantifies the uncertainty that one individual picked at random from an infinite population will be from a particular group (DeJong 1975).

Simpson Diversity Index (D): a measure of diversity that describes the probability that two individuals chosen at random and independently from the population will belong to the same group (Simpson 1949).

Spatial distribution: the geographic arrangement of individuals or groups of individuals on the landscape.

Spawning group: a group of spawning salmon in a particular stream reach that is semi-isolated from other spawning groups (Figure 1).

Strategy 1 (WSP): the first of four strategies outlined in the WSP with the goal of standardizing monitoring of wild salmon status through identifying Conservation Units, developing criteria and benchmarks of biological status and continued monitoring and assessment of the biological status of CUs.

Strategy 2 (WSP): the second of four strategies outlined in the WSP with goal of assessing habitat status of CUs through documenting habitat characteristics, selecting indicators for habitat assessment and developing benchmarks, continued monitoring and establishing linkages to develop an integrated data system for watershed management.

WSP: Canada's Policy for Conservation of Wild Pacific Salmon (DFO 2005).

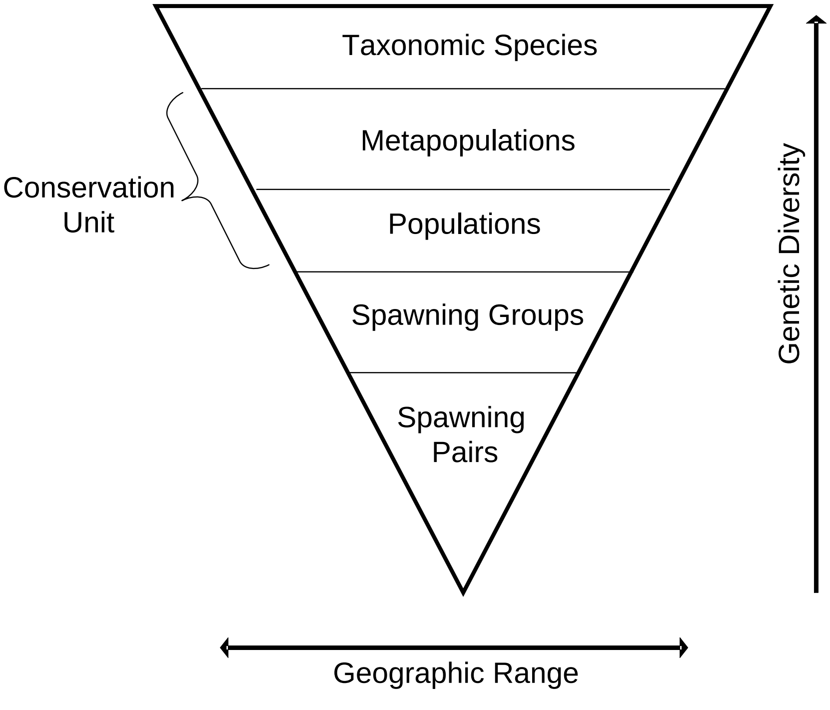

Figure 1. Schematic illustrating the relationship among the various terms defining the levels of genetic and geographic structure within a species of Pacific salmon (adapted from Riddell 1993).

EXECUTIVE SUMMARY

Metrics describing the distribution of individuals among groups and across the landscape can provide information on the resilience of a population that abundance metrics cannot, and the distribution of spawners has therefore been recommended as a status indicator for Canada's Wild Pacific Salmon (WSP). The WSP, released in 2005, placed a new focus on safeguarding the natural diversity of wild salmon. One of the first action steps towards the goal of preserving healthy and diverse salmon populations was developing metrics for the abundance and distribution of spawners to assess the biological status of Conservation Units (CUs). The objectives of this report were to present a variety of metrics of distribution from the literature and to compare those to the metrics proposed by Holt et al. (2009) for assessing status of CUs for the WSP. We surveyed the literature on metrics of distribution from a wide variety of ecological and management contexts. Although only a subset of those metrics were relevant for assessing status of CUs, we provided the complete review to demonstrate the breadth of available metrics that may have future applications to other biological and management settings.

Metrics of Distribution

In accordance with Holt et al. (2009), we identified four categories of metrics to characterize the distribution of salmon spawners within a specified region or management unit ("spatial unit"). In Section 1 of this report, we describe metrics of distribution for generic spatial units, and then apply them to two example CUs in Section 2. Metrics in the first category assess the distribution of spawners among counting locations[1] and distinguish spatial units in which spawners concentrate in a few key locations from those in which spawners are widely distributed across many locations. The ability of spawning salmon to home to their natal stream suggests that local adaptations to spawning locations may arise and a wider distribution of spawners across counting locations has greater phenotypic diversity than a spatial unit with only a single spawning location. Distribution among counting locations can be quantified by metrics such as the number of highest escapement counting locations comprising some specified percentage of total escapement (e.g., 10 highest escapement locations comprising 80% of total escapement) and the area-under-the-curve (AUC) of cumulative escapement over counting locations ranked by escapement.. These metrics focus on the highest escapement counting locations in a spatial unit, while the number of counting locations with zero spawners gives insight into changes in occupancy of low escapement counting locations and possible range contractions. If percent occupancy is low and spawners are concentrated in a smaller area, the spatial unit may be at risk of extinction from a local catastrophic event. Empirical relationships show that the proportion of spawning locations occupied increases exponentially with spawner abundance until a maximum (asymptotic) occupancy is reached (and conversely very few are occupied when population abundances are low). Previous assessments have used this relationship to set target occupancy levels (i.e., levels above which increased numbers of fish will not result in wider distribution across more locations). Shifts in distribution can be detected by trends in these metrics over time. For example, increases in the AUC reflect the concentration of spawners in fewer counting locations, and a contraction in distribution.

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[1] The distinction between counting locations and spawning groups is important (see GLOSSARY) since many of the metrics discussed can only provide insight into the distribution among counting locations, not necessarily representing the distribution among all spawning groups.

Salmon that are distributed over diverse habitat types may differ in genotype and phenotype (i.e., differences in habitat may affect how genotypes are expressed) and genetic and phenotypic diversity may increase resilience of a spatial unit and reduce probability of loss from a single event of environmental driver. Substantial losses of spawners from specific habitat types may indicate a loss of diversity associated with those spawning groups.

The spatial distribution of counting locations within a spatial unit was the third category of metrics investigated. Previous studies have used such metrics to assess whether spawning groups are distributed widely enough to avoid extirpation from a single catastrophic event but close enough to allow recolonization by straying should a group be lost. A variety of GIS tools and spatial statistics have been developed to assess spatial arrangements.

The final category of metrics was the variations in temporal patterns of abundances among counting locations. Metrics in this category differ from the first three in that they explicitly provide information on trends over time in abundances and examine the frequency distribution of those trends among counting locations, instead of providing a direct measure of spawning distribution. Large variability or multiple modes in the frequency distribution of time trends may indicate that spawners are exposed to different environmental signals at different counting locations, spawners at different counting locations are responding in different ways to a common environmental signal ("response diversity"), or both phenomena are occurring.

Application to Conservation Units (CUs) for the Wild Salmon Policy (WSP)

A preliminary description of metrics of distribution for application to the WSP was described by Holt et al. (2009). For the distribution of spawners among counting locations, we have recommended all but two of the metrics proposed by Holt et al. (2009) and included a new metric on occupancy (Table 2). Metrics in categories 2 and 3 were not elaborated upon in Holt et al. (2009). In this report, we describe metrics for the distribution of spawners across habitat types, spatial distribution, and variations in time trends in greater detail, although our conclusions are very much the same to those of Holt et al. (2009). Habitat metrics overlap with Strategy 2 of the WSP, habitat diversity within CUs may not be important for long-term persistence, and monitoring fine-scale features of habitat may be logistically difficult. Metrics in category 3, spatial distribution, are difficult to quantify given that the only data available is at counting locations and the choice of those locations is not random or spatially balanced. In category 4, we have included the metric examining the frequency distribution of time trends proposed by Holt et al. (2009), and propose to expand that metric to include a qualitative analysis of multi-modality in time trends.

The quality of escapement data available for evaluating the status of CUs may limit application of these metrics of distribution. We recommend a quantitative analysis of the sensitivity and specificity of selected metrics for detecting changes in distribution. Further, we suggest that these metrics be evaluated for their sensitivity to gaps in escapement data. Verifying the reliability of these metrics for detecting change, especially given inconsistent escapement data, is an important step towards accurately assessing the distribution of spawners. As well as the metrics used, the monitoring design for selecting which spawning groups are enumerated each year may influence our ability to detect actual changes in distribution. On the west coast of Canada, the pattern of monitoring salmon spawners is aimed at detecting trends in abundance, not distribution. Implementing a consistent pattern of monitoring that is evaluated *a priori* for its power to detect changes in distribution as well as abundance may greatly increase our ability to accurately assess distribution by eliminating the “shifting baseline” resulting from discontinued monitoring of low abundance counting locations. Although it will not be possible to monitor all spawning groups or CUs, the trade-offs between accuracy and costs of monitoring must be made explicit.

1. INTRODUCTION

Metrics assessing distribution are now commonly used as status indicators for salmon, and the motivation behind this review was the eventual application of such metrics under Canada’s Policy for conservation of wild Pacific Salmon (WSP). The aim of Strategy 1 of the WSP is to assess the status of Conservation Units (CUs) for each species of Pacific salmon (DFO 2005). A CU is “a group of wild salmon sufficiently isolated from other groups that, if extirpated, is very unlikely to recolonize naturally within an acceptable timeframe” (DFO 2005, page 10), and is defined based on unique ecological and/or life-history traits and molecular genetics (Holtby and Ciruna 2007). It has long been recognized that diversity exists among spawners from different counting locations and current debate has centered on the level of diversity necessary to ensure the health and viability of a species and how to measure that diversity (Riddell 1993; Holtby and Ciruna 2007; Irvine and Fraser 2008). Four classes of indicators have been proposed to assess the status of CUs (Holt et al. 2009), the distribution of spawners across a CU being one class that provides a measure of resilience within the CU.

In general, protecting and conserving multiple spawning groups can reduce extinction risk by enhancing the resilience of salmon populations, and hence fisheries (Healey 2009). Resilience is the natural capacity to absorb disturbance and reorganize under environmental and other stressors. This characteristic of salmon populations has enabled them to persist despite pressures from fisheries and habitat loss over the past century (Healey 2009). More specifically, the resilience of salmon populations within a spatial unit may be influenced by at least two aspects of distribution: (1) the distribution of spawners among groups, affecting genetic and phenotypic diversity, and (2) the spatial distribution, or geographic arrangement, of spawning locations on the landscape.

First, the ability of salmon to return to their natal streams to spawn allows genetic differences among streams to develop over time. In some cases, this homing ability is so refined that salmon return to their natal incubation sites (Quinn et al. 1999). Genetic differences among spawning groups conserves the overall genetic diversity of the species, which provides the ingredients for salmon species to adapt to future environmental change. Genetic diversity also influences phenotypic diversity (Narum et al. 2008), including variation in life-history traits like age at return. Phenotypic diversity may increase resilience and reduces the risk of extinction by reducing the probability that any one disturbance will affect all phenotypes and life-history types.

In addition to the composition of spatial units, the configuration of spawning groups within spatial units may also be important to resilience. The spatial distribution of spawning groups can affect how susceptible the spatial unit is to extinction from a single catastrophic event and how likely spawning groups are to recolonize after extirpation (Ruckelshaus et al. 2004). If spawners are clustered in a single stream or nearby tributaries, they may all be vulnerable to extinction from one anthropogenic or natural disaster such as a toxic spill or major flood. However, if spawners are too dispersed, colonization of unused habitat is unlikely since straying rates tend to decrease with distance from natal streams (Quinn 1993).

The WSP (DFO 2005) explicitly aims to protect within-species genetic and phenotypic diversity by conserving not only the overall population, but also individual CUs. However, diversity also exists within CUs, and that fine-scale diversity may be important for maintaining resilience of the CU and/or larger spatial aggregations.

Metrics of distribution have been developed by numerous management agencies and assessment bodies. The metrics chosen by each agency to assess distribution depend on the goal of the assessment (e.g., to assess biological criteria such as risk of extinction or population viability over the long term) and vary widely. In the following report, we review metrics from the scientific literature and previous management experience in Canada and the US. Based on this review and in accordance with Holt et al. (2009), we have identified four categories of metrics under distribution: (1) distribution of spawners among counting locations, (2) distribution of spawners over available habitat, (3) spatial distribution, and (4) variations in temporal trends of abundance among counting locations. We apply metrics, where possible, to two example CUs identified in the WSP, South Thompson coho and Takla/Trembleur Early Stuart lake-type sockeye. Monitoring of counting locations within CUs is sparse in most cases (Price et al. 2008), and so only a subset of the metrics introduced were applied. We compare the list of metrics derived from the literature to those suggested by Holt et al. (2009) for the WSP, and discuss the limitations and challenges in applying those metrics. We conclude with recommendations for future research.

2. METRICS OF DISTRIBUTION

2.1. Distribution of spawners among counting locations

Metrics in this category describe how spawners are distributed among multiple counting locations, i.e., concentrated into a small number of locations or dispersed over a large number. Information on distribution of spawners among counting locations within a spatial unit may lead to different conclusions about biological status than those based solely on total escapement. For example, if small spawning groups are lost from a region but a large spawning group remains highly productive, total escapement for the spatial unit may increase despite a reduction in the number of spawning groups. This loss will result in an overall contraction in distribution and a possible loss of genetic and/or phenotypic diversity.

The Committee on the Status of Endangered Wildlife in Canada, COSEWIC, developed criteria for assessing risk of extinction (COSEWIC 2006) that includes a metric of distribution, the number of extant locations of spawners (i.e. counting locations with abundances >0). Specifically, a Designatable Unit (DU, see Glossary) known to exist in ≤ 5 (≤ 10) locations with either declines or extreme fluctuations in extent/area of occurrence, number of locations, or abundance is considered endangered (threatened). For example, Cultus Lake sockeye salmon exist at only one location with declining area and habitat quality, and were categorised as endangered by COSEWIC (2003).

A slight variation on that metric that has been used to assess population viability is the number of counting locations of a particular abundance. The Interior Columbia Basin Technical Recovery Team (TRT) chose the number of major spawning areas containing sufficient habitat to support >500 spawners based on physical characteristics including stream width, gradient, and valley width (Cooney et al. 2007, p. 16, 54). They hypothesized that multiple large spawning areas protect against catastrophic loss, analogous to the risk reduction associated with multiple viable populations within an Evolutionary Significant Unit (ESU, see Glossary). The total area of a major spawning area varied according to species requirements (e.g., 100,000 m^2 for chinook, and 250,000 m^2 for steelhead). Likewise, Holt et al. (2009) proposed the mean number of counting locations within a CU with abundances >100 fish over a generation as a metric of distribution for the WSP.

Similarly, Ford et al. (2001) report the number of streams within the Wenatchee River Basin (Columbia River) contributing to >5% total spawning abundance of Chinook salmon. A goal of at least three streams contributing to that percentage was based on historical distributions in the watershed. For assessing status of CUs for the WSP, Holt et al. (2009) present the proportion of spawners in each counting location and report the number of counting locations that make up a specified percentage (e.g., 80%) of the total abundance (Figure 2).

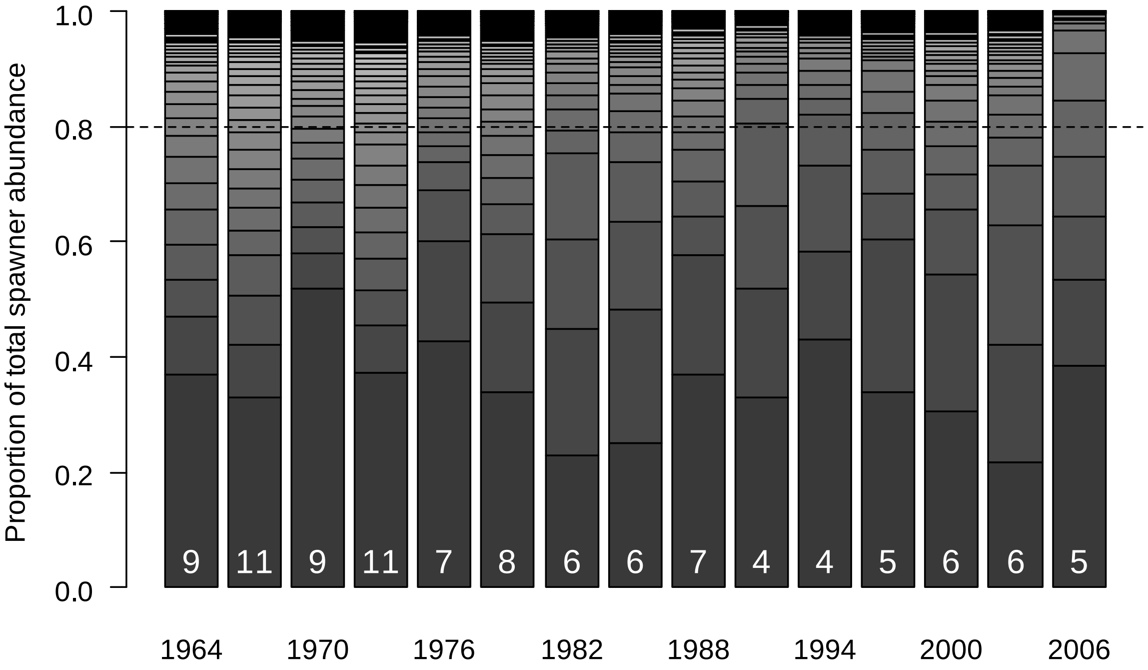


Figure 2. Proportion of the total spawner abundance at each counting location for an example CU averaged over generation, ranked from highest proportion (bottom) to lowest (top). White numbers inside the bars are the number of counting locations making up 80% of total abundance.

Instead of measuring the distribution of spawners across counting locations, some metrics have evaluated the converse, the distribution unoccupied counting locations. For example, to examine trends in habitat occupancy of in the Thomson River/Upper Fraser River coho, Irvine et al. (1999) looked at the proportion of counting locations with zero fish.

In addition to metrics of occupied and unoccupied locations, targets in occupancy (i.e., targets in the number of counting locations occupied by spawners) have also been identified, and these targets have accounted for density-dependent processes. Empirical studies by the Oregon Department of Fish and Wildlife (2007) show that the percentage of spawning locations occupied increases exponentially with spawner abundance and asymptotes at maximum occupancy. They set an occupancy target at the occupancy predicted by the exponential curve fit to historical data on occupancy rates and the total number of spawners in the spatial unit. The reported metric was the number of years out of the past 12 that the observed percent occupancy was greater than or equal to the target occupancy. Metrics examining occupancy are sensitive to variability in very small populations in marginal habitats that are only occasionally occupied. In many cases, these ephemeral populations do not represent important genotypic, phenotypic, and life-history diversity, or contribute to the overall status, and therefore metrics sensitive to variability in these small populations may be inappropriate measures of diversity. Alternatively, those small populations may contain diversity important for resilience and long-term persistence of the CU.

Metrics described so far have either considered the number of locations occupied/unoccupied by spawners or their distribution among locations, but not both. At least three metrics capture both dimensions: the Shannon-Weiner diversity score, Simpson diversity index, and the area under the curve of the cumulative plot of abundances over counting locations.

The Shannon-Weiner diversity score, H', is used widely in ecology to assess biodiversity at a variety of taxonomic levels and was applied by Isaak and Thurow (2006) to measure the distribution of chinook redds on the Middle Fork Salmon River, Idaho:

$$H' = \sum_{i=1}^{k} p_i \log(p_i) \qquad (1)$$

where k is the total number of stream segments where spawners are found (i.e., counting locations) and p_i is the proportion of redds (or spawning pairs) counted in stream segment i. Higher scores indicate greater evenness of spawners over streams; lower scores represent greater dispersion. To assess whether observed distributions were more clustered than what would be expected by chance, observed indices ($H'_{observed}$) were compared to a null distribution of indices from redds randomly allocated to stream segments (H'_{random}). For Chinook salmon in the Middle Fork Salmon River, Isaak and Thurow (2006) found $H'_{observed}$ was less than expected from random distributions ($p <$ 0.001).

The Simpson index (D) also provides information on the distribution among groups, and can be interpreted as the probability that two individuals chosen at random are from the same group (e.g., counting location):

$$D = 1 - \sum_i \left(\frac{n_i}{N} \right)^2 \qquad (2)$$

where N is the total escapement and n_i is the number of individuals in counting location i. High values of D indicate an evenly distributed population. Relative to the Shannon-Weiner diversity score, the Simpson Index puts more weight on the number of spawning groups (richness) rather than how evenly escapement is distributed among those groups (eveness) (DeJong 1975). Although used in at least one assessment (Sands et al. 2007), the Simpson's index has been criticized by DeJong (1975) for being too sensitive to the abundance of the two or three most abundant groups, with relatively little weight given to the contribution from smaller groups. In other words, in contrast to metrics of percent occupancy or total number of counting locations, this metric is not sensitive to counting locations with low abundance. Therefore, this metric may be appropriate when counting locations with small abundances are considered marginal, but not if those smaller counting locations contribute significantly to overall diversity within the CU.

The third metric is derived from cumulative abundance curves, which describe the cumulative proportion of total spawners at each counting location ranked from most abundance to least abundant. The area under the curve (AUC) quantifies the concentration of spawner abundances among counting locations, where both axes are scaled between zero and one (Walters and Cahoon

1985). If each counting location contributes equally to the total escapement (i.e., an even distribution), the cumulative escapement will increase in equal increments with each additional counting location, resulting in a diagonal line intersecting the points (0,0) and (1,1) and an AUC close to 0.5 (Figure 3, dashed line). Alternatively, when spawners are concentrated into one or two dominant counting locations, the cumulative escapement will increase steeply with the first few counting locations and then asymptote, resulting in an AUC closer to 1 (Figure 3, solid line). AUC has the advantage over the previous two metrics of being visually intuitive and easy to interpret (Isaak and Thurow 2006). Accordingly, Holt et al. (2009) proposed AUC as a metric to assess distribution of spawners among counting locations within CUs.

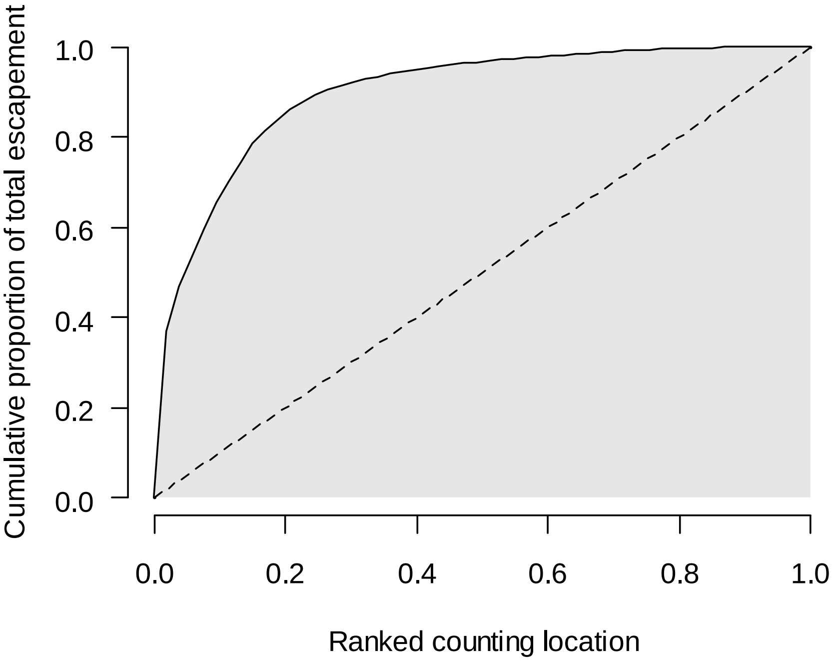


Figure 3. The curve of cumulative proportion of total spawner abundances over counting location (as a proportion of total counting locations) ranked from most abundant to least abundance. The area-under-the-curve (AUC) is a proposed metric of distribution. The dashed line is at an AUC = 0.5 representing a spatial unit in which all counting locations contribute equally to total escapement, and the solid line has an AUC = 0.91 (grey area), representing a less even distribution of spawners among counting locations.

2.2. Distribution of spawners over habitat

Spawner distribution over habitat refers to the quantity of habitat occupied by or available to spawners and its associated habitat characteristics, and may be related to the resilience of a spatial unit. Increases in the total quantity of accessible habitat may be associated with increased resilience because salmon can respond to changing environmental conditions by exploiting habitat not otherwise occupied. Conserving habitat that is currently unoccupied allows for colonization events under future disturbance regimes. In addition to the extent or proportion of habitat occupied, the diversity of habitats within a spatial unit may reflect phenotypic and/or genetic diversity and therefore contribute to the resilience of the spatial unit (Narum et al. 2008; Healey 2009). In addition, in the event of a catastrophe, habitat diversity may provide viable habitat types for colonization.

Assessing the quality and quantity of salmon habitat for the WSP is described in Strategy 2, and assessing metrics in this category requires collaborate efforts between Strategies 1 and 2 (Appendix

A). Strategy 2 aims to identify habitats necessary for the conservation of wild salmon and assess changes in habitat status of CUs over time using a suite of indicators and associated benchmarks (DFO 2005). Although progress has been made towards providing an inventory of suitable habitat (Stalberg et al. 2009), those assessments have not yet identified the portion of suitable habitat currently and historically used by salmon. By merging data on distribution with information on suitable habitat collected under Strategy 2, it may be possible to track changes in the quantity and diversity of occupied habitat.

2.2.1 Quantity of occupied habitat

The extent of occurrence and area of occupancy of a species or population are used to evaluate risk of extinction by the IUCN (2001) and COSEWIC (2006). For example, an endangered (threatened) listing is triggered by COSEWIC when the area of occupancy of a species <500 km^2 (<2,000 km^2) and extent of occurrence <5,000 km^2 (<20,000 km^2) with a substantial declining trend (although it is recognized these areas may vary among species). The Cultus Lake Sockeye were classified as endangered by COSEWIC in 2003, in part due to dramatic declines in spawner abundance and occupied habitat over the past three generations (only one of six historical spawning locations was occupied).

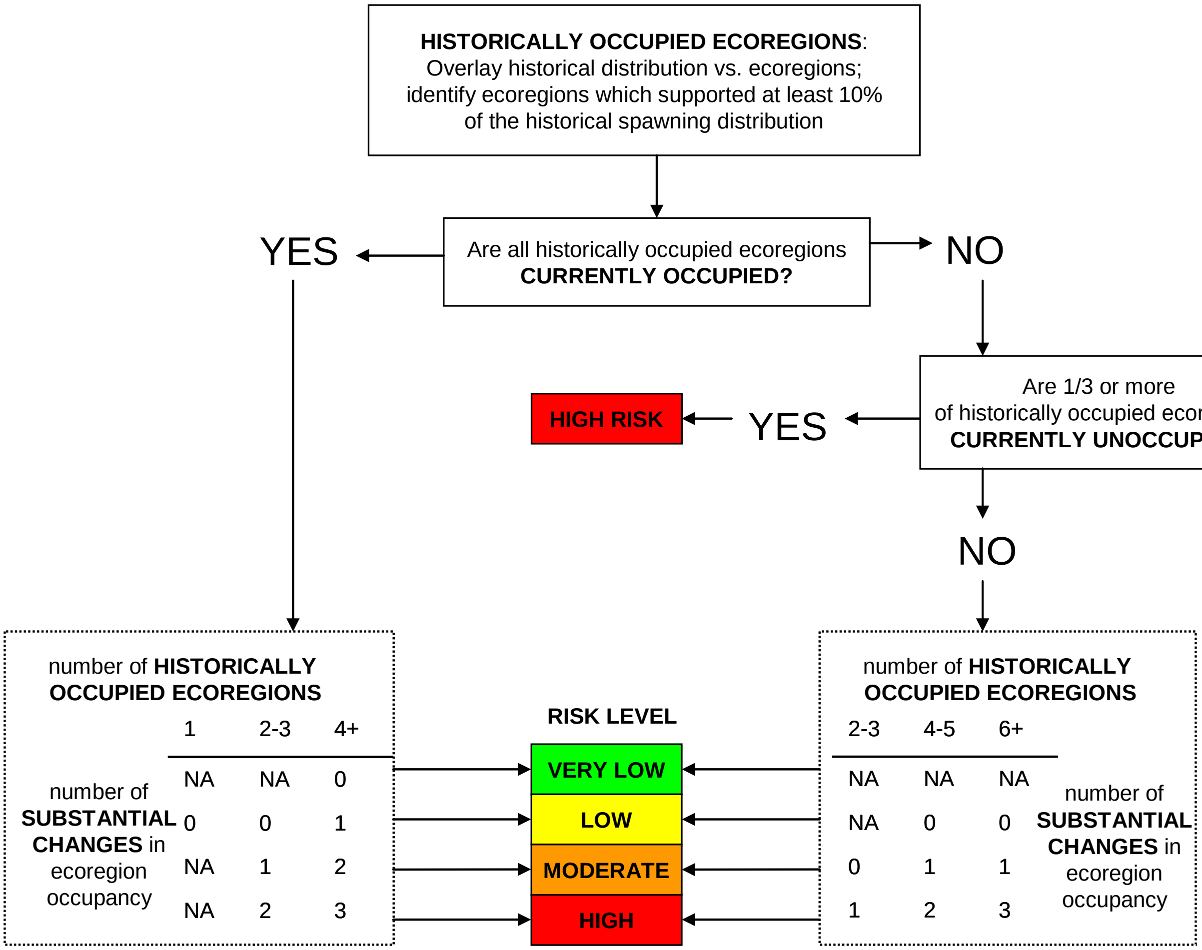
Other metrics of distribution take account of the proportion of historical habitat currently occupied. Unoccupied habitat may be habitat lost due to anthropogenic blockages (e.g., culverts, dams) or natural disasters (e.g., landslides) or habitat that remains available but is not currently used by spawners. In an effort to assess the natural distribution of spawning areas for salmonid species in the Interior Columbia Basin, Cooney et al. (2007) compared current to hypothesized historical spawning range, predicted from species-specific thresholds in stream width, gradient, and valley width. Historical habitat can also be determined from information on the construction of river blockages such as dams and culverts. However, neither approach fully considers habitat quality and therefore likely overestimates suitable habitat (McElhany et al. 2006; Sheer and Steel 2006).

When assessing population viability, Cooney et al.(2007) evaluated the proportion of historical range occupied and the quantity of habitat outside major spawning areas (i.e., in potentially marginal habitat). The authors further identified a benchmark in occupancy of 50% of major historical spawning areas, below which populations were deemed to be at high risk of collapse. Above that benchmark, rates of dispersal, gene flow, and other spatially mediated processes were assumed to be sufficient to maintain genetic and phenotypic variation.

One habitat indicator that has been identified for the WSP under Strategy 2 that is similar to those identified above for other regions, is accessible stream length (Stalberg et al. 2009). This indicator can be combined with information on blockages to determine the proportion of historically accessible habitat that has been lost.

2.2.2 Diversity of occupied habitat

Cooney et al. (2007) captured changes in the diversity of habitat types by examining the change in occupancy across ecoregions (Figure 4), where ecoregions were defined based on climate, soils and geology, vegetation, and land use by Omernik (1987). Cooney et al. (2007) looked for substantial (i.e., biologically significant) changes in spawning distribution over ecoregions, where a "substantial change" was defined as a >67% decrease in the relative distribution of spawning within an ecoregion. Categories of extinction risk (very low, low, moderate, and high) were then determined from the proportion of ecoregions with substantial changes in spawning distribution. Substantial declines in the occupancy of major ecoregions result in high risk of extirpation because the natural pattern of variation is lost.



1	2-3	4+	RISK LEVEL
NA	NA	0	VERY LOW
0	0	1	LOW
NA	1	2	MODERATE
NA	2	3	HIGH

RISK LEVEL	2-3	4-5	6+
VERY LOW	NA	NA	NA
LOW	NA	0	0
MODERATE	0	1	1
HIGH	1	2	3

Figure 4. A flow chart for evaluating the risk of extinction over a 100-year time frame due to changes in spawner distribution over ecoregion types with all other contributing factors unchanged (Cooney et al. 2007).

At a finer spatial scale, McElhany et al. (2006) developed a metric to represent "ecological diversity", *ED*, arising from differences in stream order and elevation among stream reaches (i.e., counting locations) in the Lower Columbia and Willamette ESUs:

$$\Delta ED = \frac{\sum_i (P_{Hi} - P_{Ci})}{n} \qquad (3)$$

where n is the number of stream order (or elevation) categories, P_{Hi} is the proportion of the historical potential range of stream order i (or elevation category i), and P_{Ci} is the proportion of the current potential range of stream order i (or elevation category i). Similarly, Sheer and Steel (2006) calculated the Simpson’s diversity index (equation 2, with n_i as the number of streams of order i and N is the total number of streams) for available habitat and habitat lost due to anthropogenic blockages (e.g., dams). To determine the significance of changes in the diversity of stream order, Sheer and Steel (2006) used paired t-tests on the value of D between habitats that have been lost and those that remain available and suggested that significantly higher diversity among lost habitats would indicate a reduction in habitat diversity. Diversity of other variables important for determining habitat suitable for salmon spawning (e.g., gradient, stream width) could be considered using the same methods.

2.3. Spatial distribution

Spawning groups within a spatial unit can be regarded as a spatially structured metapopulation (Schtickzelle and Quinn 2007) because suitable habitat is discrete, there may be asynchrony between dynamics of local populations (Rogers and Schindler 2008), and migration or dispersal among spawning groups occurs at a decreasing rate with distance from the natal stream (Quinn 1993). The arrangement of suitable spawning habitat (e.g., inter-patch distance and connectivity) plays a central role in metapopulation dynamics, and can affect the risk of extinction in several ways (McElhany et al. 2000; Schtickzelle and Quinn 2007). Spatial structure affects straying among spawning groups (Quinn 1993), a phenomenon which can increase genetic fitness of individuals through interbreeding among spawning groups. Spatial structure may also affect the rate of recolonization of spawning locations following local extirpation. However, when spatial distribution is concentrated into a small region, the spatial unit may be vulnerable to extinction from a single localized catastrophe (McElhany et al. 2006).

Qualitative descriptions of the arrangement of spawning habitat, such as those presented in Table 1, can be combined with quantitative information to yield metrics that capture both the spatial distribution and amount of habitat. For example, Cooney et al. (2007) hypothesized that linearly arranged spawning areas are at higher risk of extinction than spawning areas dispersed in a dendritic structure. They categorized populations into four levels of spatial complexity based on qualitative descriptions (Table 1) and combined this information with the total amount of spawning habitat weighted by population size to characterize the relative within-population complexity of tributary spawning habitats.

Table 1. Population spatial complexity designations from the Interior Columbia Basin Technical Recovery Team (Cooney and McClure 2007).

Category	Description
A	Linear structure, with no more than 2 branches in one major spawning area. Typically small (basic) drainages.
B	Dendritic tributary structure including 2 or more major spawning areas. Typically intermediate or large drainages.
C	Trellis-structured drainage including main stem spawning and multiple branches.
D	Populations with one or more major spawning areas with well-separated minor spawning areas downstream.

One quantitative metric of spatial structure for detecting the likelihood of colonization is the minimum shoreline distance among spawning groups (Cooney et al. 2007; Sands et al. 2007). Sands et al. (2007) measured geographical distances between pairs of spawning locations (the shoreline distance between entry points of streams using the most direct passage over open water). A maximum threshold of 20 km between most counting locations, and 40 km between major counting locations was set as a target spatial distribution. These maximum distances allowed spawners to stray among groups, with less abundant counting locations functioning as stepping stones between major spawning locations (i.e., source populations). In this way, the overall connectivity in the spatial unit was maintained.

In addition to determining the likelihood of colonization, spatial structure can also be important for probability of extirpation from disturbances. McElhany et al. (2006) quantified the spatial distribution of habitat loss from one category of disturbance, anthropogenic blockages, for adult coho salmon. They hypothesized that a single blockage resulting in a substantial loss of habitat (e.g. occurring for highly spatially aggregated groups) was more detrimental to coho than the same total loss incurred by multiple smaller blockages (e.g., occurring for spatially distributed spawning groups). In their assessment, the severity of loss depended on both watershed size and the percent of habitat lost per blockage. Their analysis did not consider habitat quality beyond gradient, and therefore likely overestimated the available habitat actually suitable for spawning salmon.

Although the previous two metrics provide information on the connectivity of habitat, they do not explicitly describe the spatial arrangement of that habitat on the landscape. A third metric, the *SVB* statistic (Sides, Vertices, Boundaries), captures the regularity of the point pattern created by occupied counting locations (Stevens 2006; as applied in Oregon Department of Fish and Wildlife 2007). To calculate the *SVB* metric, polygons are drawn around counting locations that include all area closer to that location than any other. If counting locations are distributed evenly across the landscape, the polygons will be approximately hexagons of equal area. The *SVB* statistic measures the variation in distance between points and the boundaries of the polygons around those points, and considers both size and shape of the polygons, and is then calculated by:

$$SVB = \sum_{s_i \in S} \left(\int_{B(D(s_i))} \left(D(b, s_i) - \bar{d} \right)^2 db \right) / SVB_{NOM} \qquad (4)$$

where,

s_i is counting location i,
$D(s_i)$ is the polygon for point s_i,
$B(D(s_i))$ is the boundary of $D(s_i)$,
$D(b,s_i)$ is the distance from s_i to the point b,
$\bar{d}$ is the radius of a circle with area equal to that of $D(s_{i,})$ divided by number of samples,
SVB_{NOM} is the mean square deviation for a hexagon with area equal to domain area divided by number of samples.

If spacing is clumped and irregular, *SVB* values will be large; if spacing is regular, *SVB* values will be close to one. To test if occupancy is random, the observed *SVB* statistic can be compared to a distribution of *SVB* statistics from locations that are randomly assigned fish (presence/absence). In addition to random distributions, hypotheses about patterns of occupancy related to habitat variables can also be tested by assigning probabilities of occupancy stratified according to those variables (e.g., assigning lower probabilities of occupation at higher stream orders where it is unlikely to find salmon spawning). Statistical significance can be calculated by comparing the observed statistic to the expected distribution (Oregon Department of Fish and Wildlife 2007).

2.4. Variations in temporal patterns of abundance

Variation in time trends among counting locations may arise through two very different processes. First, salmon may be responding to environmental conditions in the same way, but conditions may differ among spawning groups. However, previous studies have found that despite similar climatic conditions within regions, salmon productivity may be asynchronous among spawning groups within the region (Rogers and Schindler 2008). Therefore, variation in time trends may indicate differences in the way that individual spawning groups respond to common environmental stressors (i.e., response diversity). This second process is essential to the resilience of spatial units of salmon (Elmqvist et al. 2003). If spawning groups respond differently to common disturbances (short-term events such as floods or long-term stressors such as climate change), there is a higher probability that at least some groups will persist to recolonize habitat formerly used by extirpated groups compared with the scenario where all groups respond in a similar way to disturbances. In this way, response diversity among spawning groups may increase the overall resilience of a spatial unit.

Isaak and Thurow (2006) applied a repeated measures analysis of variance (ANOVA) of spawner abundances from various stream segments to detect differences in time trends among segments, a measure of response diversity. A strong interaction between stream segment and year indicated that either the segments were subject to local stressors that differed among stream segments (e.g., selective fishing or localized monitoring), or that response of spawners to common stressors varied by stream segment. However, the stronger effect of year on abundance in this study suggested that these streams responded synchronously over time. In some cases, mixed-effects models may be able to detect response diversity, but their statistical power is dramatically reduced by data gaps resulting in incomplete time series (Urquhart and Kincaid 1999).

To assess response diversity for CUs for the WSP, Holt et al. (2009) developed a metric based on the proportion of counting locations with rates of decline over 3 generations or 10 years (whichever was greater) that exceed those associated with COSEWIC threatened status (COSEWIC 2006) (Figure 5). A CU with a high percentage of counting locations showing declines in spawner abundances greater than the COSEWIC threshold would be considered at high risk of extinction. Multi-modality in the frequency distribution of linear rates of change may indicate different disturbances among counting locations or diverging responses to common environmental or anthropogenic disturbances. If the latter is true, this divergence may be evidence of genetic and/or phenotypic diversity within a CU, and may provide the basis for the creation of a new CU. One disadvantage of this metric is that it does not accommodate non-linear trends in abundance over time.

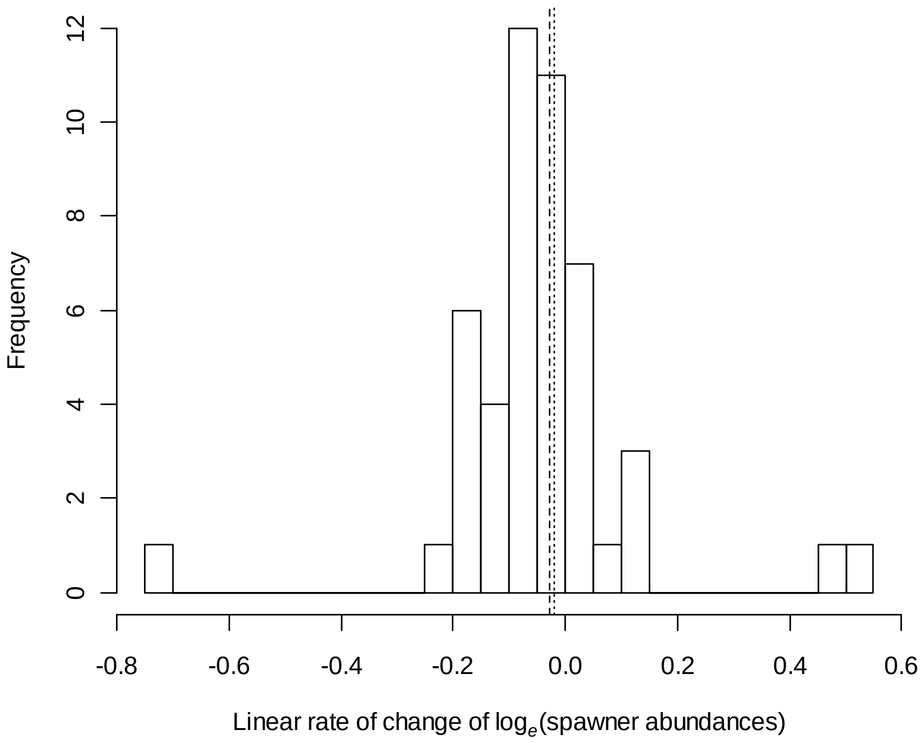


Figure 5. Histogram of linear rates of change of log-transformed spawner abundances over 3 generations (12 years) for 48 counting locations from an example CU. The linear rates of change associated with 20% and 30% declines in abundances over three generations are shown with the dotted and dashed lines, respectively. 58.3 % of counting locations had rates of declines greater than those that required for COSEWIC vulnerable designation.

3. APPLICATION OF METRICS TO CONSERVATION UNITS UNDER CANADA’S WILD SALMON POLICY

3.1 Suggested metrics with application to two example Conservation Units

Not all metrics of distribution we identified from the literature are relevant for assessing the status of Conservation Units (CUs) for Canada’s Wild Salmon Policy (WSP). Many of the metrics of distribution we presented quantify overlapping characteristics of distribution. In addition, some metrics captured information that is not biologically relevant for CUs (e.g., *SVB* statistic of spatial arrangement of counting locations) or require data that is not currently available for CUs (e.g., diversity of eco-regions within CUs). Nonetheless, the metrics described in Table 2 can be applied to most CUs and capture two of the four components of distribution: distribution among counting locations and variations in temporal patterns of abundance.

The distribution among counting locations was best described by three metrics. First, the minimum number of counting locations that contribute 80% to total abundance (Holt et al. 2009) provided information on the distribution of the majority of spawners, and focused on counting locations with higher escapement. For highly concentrated CUs, when ranked from most to least abundant, the top 80% of the total abundance may be comprised of only one or two spawning group(s). To complement this metric, examining trends in percent occupancy captured the loss of spawners in low escapement counting locations. By setting the target occupancy based on the historical relationship between occupancy and total escapement for the CU (Oregon Department of Fish and Wildlife 2007), this metric accounted for changes in distribution resulting from spill-over of spawners in years of high abundance (i.e., the target occupancy increased with increasing spawner abundance). To be consistent with COSEWIC guidelines, we chose to report the number of years out of the past 3 generations (or 10 years, whichever is greater) that meet the occupancy target, rather than out of the past 12 years as done by the Oregon Department of Fish and Wildlife (2007). For CUs for which percent occupancy is independent of spawner abundances (i.e., the exponential model suggested by Oregon Department of Fish and Wildlife (2007) is not appropriate), target occupancy can be derived from the mean percent occupancy for the range in spawner abundances observed. Third, the AUC metric captured both presence/absence and distribution among counting locations, and was intuitive and easily visualized (e.g., Figure C 4). AUC has been used to indicate changes in distribution in previous assessments of salmon (e.g., Walters and Cahoon 1985; Isaak and Thurow 2006) and provides similar information as the other diversity indices.

Most metrics on distribution of spawner across habitats cannot be applied to CUs under Strategy 1. Specifically, metrics on the quantity and diversity of available versus historical habitat (not considering occupancy) fall under Strategy 2 of the WSP, and are not considered here. Metrics describing the diversity of occupied habitat were also not considered for CU status assessment. Although habitat diversity may reflect genetic and phenotypic diversity, and therefore may be associated with resilience of a CU to disturbances, those categories of diversity were accounted for when defining CU boundaries. Holtby and Ciruna (2007) suggest diversity within CUs is relatively small compared with overall diversity among CUs, and therefore may be less biologically relevant for long-term persistence.

To capture the variations in temporal patterns of abundance within CUs, the repeated measures ANOVA suggested by Isaak and Thurow (2006) may not be appropriate because the statistical power to detect diverging responses is highly sensitive gaps in time series (Urquhart et al. 1998) and sampling for CUs is opportunistic and extremely patchy. If monitoring practices change in the future to eliminate gaps in the time series or if systematic sampling designs are adopted (e.g., a rotating panel), this analysis might be more useful. In agreement with Holt et al. (2009), we recommend examining the frequency distribution of linear rates of change in abundances among counting locations within a CU . This distribution may indicate, for example, diverging responses among groups of counting locations (i.e., multi-modality in responses) within a CU.

Metrics on spatial arrangement (e.g., distance between counting locations) may not be relevant to ecological processes due to the non-random monitoring design currently in place (i.e., counting locations are selected by accessibility and are not random or spatially balanced). Futhermore, more complicated metrics on spatial structure (e.g., the *SVB* statistic) were difficult to calculate and interpret given the patchy nature of spawning habitat and the unknown area occupied by enumerated spawners. The absolute distance among counting locations is likely not biologically meaningful for spawners that travel by waterways which are often circuitous.

In the following two sub-sections, we apply metrics of distribution, when possible, in assessing the status of two example CUs: South Thompson coho and Takla/Trembleur Early Stuart lake-type sockeye. The escapement data were obtained from the DFO nuSEDS database[2], last updated December 2009. Although some metrics provide redundant information (i.e., are highly correlated), we present all present all metrics for which data are available and are appropriate for assessing distributional status of CUs (e.g., those described in Table 4, in addition to others that provide similar information).

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Table 2. Suggested metrics of distribution for application to CUs under the WSP (DFO 2005).

Category	Specific metric	Reference	Examples	Caveats
Distribution of spawners among counting locations	Minimum number of spawning groups that comprise 80% of total abundance	(Holt et al. 2009)	Figure C 2, Figure C 7	• Discontinued monitoring of inconsistently occupied streams contribute to "shifting baseline" (Price et al. 2008) • Multiple spawner enumeration techniques have varying degrees of accuracy (Cousens et al. 1982) • Unreliable zero counts means percent occupancy cannot accurately be determined • There may not be sufficient historical data to set target
	Number of years meeting percent occupancy target (based on asymptotic exponential of occupancy over total spawners)	(Oregon Department of Fish and Wildlife 2007)	Figure C 3	
	Area under the curve (AUC) of percent contribution to total abundance from ranked spawning groups (as a proportion of total spawning groups) over group rank	(Walters and Cahoon 1985; Isaak and Thurow 2006; Holt et al. 2009)	Figure C 4, Figure C 8	
Variations in temporal patterns of abundance within CUs	The proportion of spawning groups that exceed linear rates of decline associated with COSEWIC threatened status, and qualitative assessment of the frequency distribution of linear rates of change.	(Holt et al. 2009; Pestal and Cass 2009)	Figure C 5, Figure C 9	• Asynchrony among counting locations may be due to variations in environmental conditions, rather than response diversity • Linear rates of change may not capture long term changes in abundance

3.1.1 South Thompson coho

The Fraser River coho salmon, of which South Thompson coho are a part, were designated as endangered by COSEWIC in 2003 (Irvine 2002). There have been noticeable contractions of distribution (Irvine et al. 1999), and this CU was chosen to evaluate which metrics best capture this change. Relatively consistent and reliable escapement data were available for the past 10 generations (1978-2007), with a total of 47 counting locations for the South Thompson. Abundances were estimated by visual counts on stream walks or helicopter flights, standardized with fence counts at up to 10 locations (e.g., in 1997, counting facilities were operated in Bessette Creek, Bonaparte River, Danforth Creek, Deadman River, Dunn Creek, Huihill Creek, Lemieux Creek, Louis Creek, Mann Creek, and Salmon River (Irvine et al. 1999)). The Eagle River was hatchery enhanced from 1983-1993, and the Salmon River enhanced from 1984 to present (with the exception of 1992) (Irvine et al. 1999).

Data from many of the sites were highly patchy. We selected 26 counting locations with >50% data over the period 1977-2008 (Table B 1). A three-year running geometric mean using the previous and proceeding year or a three-year non-overlapping generation mean was used to account for the variation in return year within each generation.

Distribution of spawners among counting locations

The South Thompson had its highest escapement on record from 1985-1989, after which abundances dropped to a historical low in 1996 (Figure C 1). The number of counting locations contributing to 80% total escapement has declined since the early 1980s, with a high of six in 1983 and a low of three in 1989, 1992, 1998, 2001, and 2004 (Figure C 2). Although this CU consisted of a relatively large number of counting locations (26 selected), an increasing number of those locations had entries of zero spawners in recent years, leading to a decline in percent occupancy. Target occupancy of counting locations was identified from an exponential relationship between occupancy of counting locations and spawner abundances over the past 30 years (Figure C 3). For South Thompson coho, the percent occupancy was greater than the target occupancy for only two of the past ten years (1999 and 2006). Further, these two years that did meet the target had very low total escapement resulting in low target occupancy. It should be noted again, however, that the proportion of habitat occupied in any given year is inaccurate due to uncertainties in zero counts.

The Shannon-Weiner and Simpson's diversity indices showed the lowest diversity in 1998. The observed Shannon-Weiner score (H'_{actual}) was significantly greater than that expected from a random allocation of spawners among counting locations ($p<0.001$), indicating that spawners were not distributed randomly among counting locations. The AUC showed the lowest diversity in 1998 (highest AUC value, Figure C 4) in agreement with the Shannon_weiner and Simpson's indices. Relatively low AUC values from 1983 through 1995 indicated higher diversity during that period. Due to similarity in temporal trends among three diversity indices, reporting a single metric, AUC, may be sufficient.

Variations in temporal patterns of abundance

A linear mixed-effects model with year, counting location, and a year:counting location interaction as factors was fit to log-transformed escapement data from 1963-2007 for only those 20 counting locations with >50% data over this 45-year period (different from the 26 counting locations selected for other metrics). A longer time series was used for this model (45 years instead of 30 as was used for other metrics) to increase power for detecting an interaction effect. The residuals were assumed to have an autoregressive correlation structure at lag-1 or lag-3 years to account for the similar freshwater environment experienced by coho in consecutive years or the three-year life cycle. The lag-3 autoregressive model was a better fit to the data than both the model without an autoregressive term (ΔAIC = 73.797) and the lag-1 autoregressive model (ΔAIC = 56.574) (Burnham and Anderson 2002). The year by counting location interaction was not significant indicating that counting locations responded similarly to environmental changes (i.e., low response diversity). In addition, the year and counting location terms were not significant suggesting that any time trends in coho escapement in the South Thompson were accounted for with the autoregressive correlation structure. It is also possible that this metric was not sensitive to an interaction due to substantial data gaps (across the 20 counting locations used, on average 37.8% of the years were missing data).

The proportion of counting locations that exceeded linear rates of decline associated with COSEWIC threatened status (COSEWIC 2006) over the past 10 years was 34.6% (Figure C 5). When extended to 30 years, that proportion jumped to 57.7% which suggested long-term declines in escapement for the majority of counting locations. The distribution of time trends was approximately normal (Figure C5), and was not multi-modal, suggesting time trends did not differ systematically among counting locations.

Conclusions

The South Thompson CU has seen declines in the distribution of spawners since the early 1990s, and most metrics successfully captured this (Table 3). Although there have been slight improvements in distribution and declines in zero counts since the late 1990s, a drop in monitoring effort in 2007 and declining escapement remain causes for concern.

Table 3. Summary of metrics of distribution for the South Thompson Coho CU. Red indicates that generation was below the 33rd percentile and green indicates that generation was above the 66th percentile for that metric over the entire time period 1980-2007. Data availability and zero counts were not metrics, but refer to the number of counting locations with no available data and records of zero spawners for that generation.

	Generation									
Metric	**80**	**83**	**86**	**89**	**92**	**95**	**98**	**01**	**04**	**07**
Total escapement	🟩	🟨	🟩	🟩	🟨	🟥	🟥	🟨	🟩	🟥
# streams making up 80% escapement	🟩	🟩	🟨	🟥	🟥	🟨	🟥	🟥	🟥	🟨
AUC	🟩	🟩	🟨	🟥	🟨	🟩	🟥	🟥	🟥	🟩
Occupancy target	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟩
Data availability	🟥	🟥	🟩	🟩	🟨	🟥	🟥	🟩	🟨	🟥
Zero counts	🟩	🟩	🟨	🟩	🟨	🟥	🟥	🟨	🟥	🟥

3.2.1 Takla/Trembleur Early Stuart lake-type sockeye

Spawner abundances for Takla/Trembleur Early Stuart (EStu) sockeye were estimated using visual stream surveys, and a fence count at Dust Creek to standardize those estimates to total abundances. Assessment methods have been consistent since 1987 when the fence was introduced, though there have since been refinements to the expansion factor used to standardize visual estimates.

There were 42 counting locations in the Takla/Trembleur EStu CU with data from 1938-2007. Twenty-seven of the counting locations had >50% data from 1966-2008, and only these locations were selected for analysis (Table B 2). Escapement was smoothed with a four-year running geometric mean using the two years prior and one year ahead or the non-overlapping generation mean to account for the variation in return year within each generation and minimize the effect of measurement error in any one year.

Distribution of spawners among spawning groups

Most recent escapement estimates for the Takla/Trembleur EStu sockeye were near historical numbers after a steady decline from high escapement in 1991 (Figure C 6). O’Ne-Ell Creek was by far the dominant counting location from 1975-1987, after which escapement appeared to be spread across more counting locations. The number of counting locations making up 80% of total escapement was at a high of 10 in 1971, and a low of six in 1987 (Figure C 7). After the mid 1980s, this number stabilized around eight counting locations comprising 80% of total escapement. The percent occupancy was 100% (i.e., no counting locations with zero counts) until 2003 when occupancy dropped to 96.3%. The percent occupancy has since declined further to 88.9% for 2005-2007. An occupancy target could not be established using the exponential curve method from the Oregon Department of Fish and Wildlife (2007) because the occupancy over total spawners did not follow an exponential relationship (most occupancy was 100%). The AUC was lowest in 1971, increasing to a high in 1987 and then declining sharply to the late 1990s, and has since increased indicating a recent decline in diversity (Figure C 8). The Shannon-Weiner and Simpson’s diversity scores showed similar trends to the AUC.

Variations in temporal patterns of abundance

A linear mixed-effects model was fit to log-transformed escapement data for the Takla/Trembleur. Similar to the coho example, we fit two models with three factors and either a lag-1 or lag-4 year autocorrelation structure in the residuals. The lag-1 model was not significantly different from the model with no correlation structure (ΔAIC = 1.418). The lag-4 model was a significant improvement on the model with no correlation structure (ΔAIC = 115.393), but had no significant factors.

The past three generations have seen obvious declines in total escapement (Figure C 6), a trend observed across all counting locations. Escapement for all 27 counting locations displayed declines greater than those required for COSEWIC vulnerable designation (30% decline, Figure C 9). This created a concerning picture of status for the Takla/Trembleur sockeye in terms of trends over time despite total abundances near the long-term baseline mean (Figure C 6). When the linear trends over time were extended to 10 generations, only 25.9% of counting locations showed the same slope of declines. Distribution of time trends did not exhibit obvious multiple modes, suggesting time trends did not differ systematically among counting locations.

Conclusions

Escapement for the Takla/Trembleur sockeye has declined since the early 1990s to near historical mean levels. Recent increases in the number of streams with zero fish and declines in diversity indices since 2000 are cause for concern, but overall distribution is fairly stable (Table 4). The entire time series from 1938-2008 shows improving distribution, although this trend may be reflective of increased monitoring from the 1930's to present, which is why we only quantitatively assessed the past 40 years.

Table 4. Summary of metrics of distribution for the Takla/Trembleur lake-type sockeye. Red indicates that generation was below the 33rd percentile and green indicates that generation was above the 66th percentile for that metric over the entire time period 1971-2007. Data availability and zero counts were not metrics, but refer to the number of counting locations with no available data and records of zero spawners for that generation, and for these, green indicates no missing data or zeros, and red and amber were qualitative based on the number of missing values or zeros for that generation.

	Generation									
Metric	71	75	79	83	87	91	95	99	03	07
Total escapement	🟥	🟨	🟨	🟥	🟩	🟩	🟩	🟩	🟨	🟥
# streams making up 80% escapement	🟩	🟥	🟥	🟥	🟥	🟨	🟨	🟩	🟩	🟨
AUC	🟩	🟥	🟨	🟥	🟥	🟨	🟩	🟩	🟨	🟥
occupancy target	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
data availability	🟥	🟨	🟩	🟩	🟩	🟨	🟩	🟩	🟩	🟩
zero counts	🟩	🟩	🟥	🟨	🟩	🟩	🟩	🟩	🟩	🟩

3.2 Limitations

The distribution of spawners was chosen to be an indicator of status under the WSP because it provides information on the connections among spawning groups necessary for long-term persistence of CUs, which cannot be determined simply from abundance metrics. As described in detail earlier in this report, distribution can serve as a proxy measure of genotypic and phenotypic diversity and vulnerability of a CU to local catastrophes. However, this interpretation is limited by at least two factors.

First, distribution of spawners may be more closely linked to overall abundances and/or environmental variables than diversity within a CU. For example, an even distribution may occur in years of high spawner abundance when salmon disperse from optimal habitat towards less favourable or marginal habitat. In this case, the wider distribution does not represent salmon with local adaptations or unique genotypes, but simply spill-over from a fairly homogeneous group of fish. Conversely, a contracted distribution may be the result of low autumn river discharge preventing salmon from entering certain streams, rather than the loss of unique adaptations associated with those spawning groups. At least one metric accounts for density-dependent effects, (e.g., the target percent occupancy that increases with spawner abundance, Figure C 3), but density-dependence may affect other metrics to varying degrees. Regardless of the mechanism, maintaining a wide distribution may reduce the chance of extirpation of the CU from localized catastrophes, even if peripheral groups (i.e., in marginal or "spill-over" habitats) are not genetically diverse.

The second limitation to applying metrics of distribution is poor quality data. Inconsistent monitoring of all counting locations presents a significant challenge for accurately assessing distribution of spawners. In our application of metrics to CUs, we only included counting locations that had escapement estimates for more than 50% of the years in the past 10 generations (slightly less strict than the rule applied by Irvine et al.(1999)). When this rule is applied coast-wide, there are substantial data gaps that result in less than half of the counting locations being included for most CUs across all species (Figure 6). Furthermore, counting locations that do have escapement estimates for more than 50% of the years in the past 10 generations have seen declines in monitoring effort in recent years (Figure 7). Indeed, streams with low abundances are not consistently monitored (Riddell 1993; Price et al. 2008) making occupancy metrics unreliable. Reducing monitoring effort on counting locations with lower escapement or poor status contributes to a ″shifting baseline″ (Pauly 1995), and makes an accurate assessment of the distribution of spawners difficult.

In addition, DFO is challenged by lack of reliable records on unoccupied streams. Proving absence in for any species is difficult, but in DFO's database of spawning escapements, escapements of zeros and blanks have historically been confused. Although this has now been somewhat rectified by specific definitions of escapement codes, questionable zeros still remain in the database. Further, the definition of “none observed” could mean that the stream was checked thoroughly and there were actually no fish or the stream was monitored at an unusual time (i.e., for a different species of salmon) and so there were no observed spawners, but spawners may have been present at a different time during the season.

The quality of spawner data also varies according to the enumeration techniques used to estimate abundances (e.g., foot surveys, aerial counts, photographic enumeration, observation towers, mark-recapture studies and fence counts) which vary across counting locations and CUs (Cousens et al. 1982). The range in techniques and the discrepancy among different observers introduces considerable measurement error in escapement data.

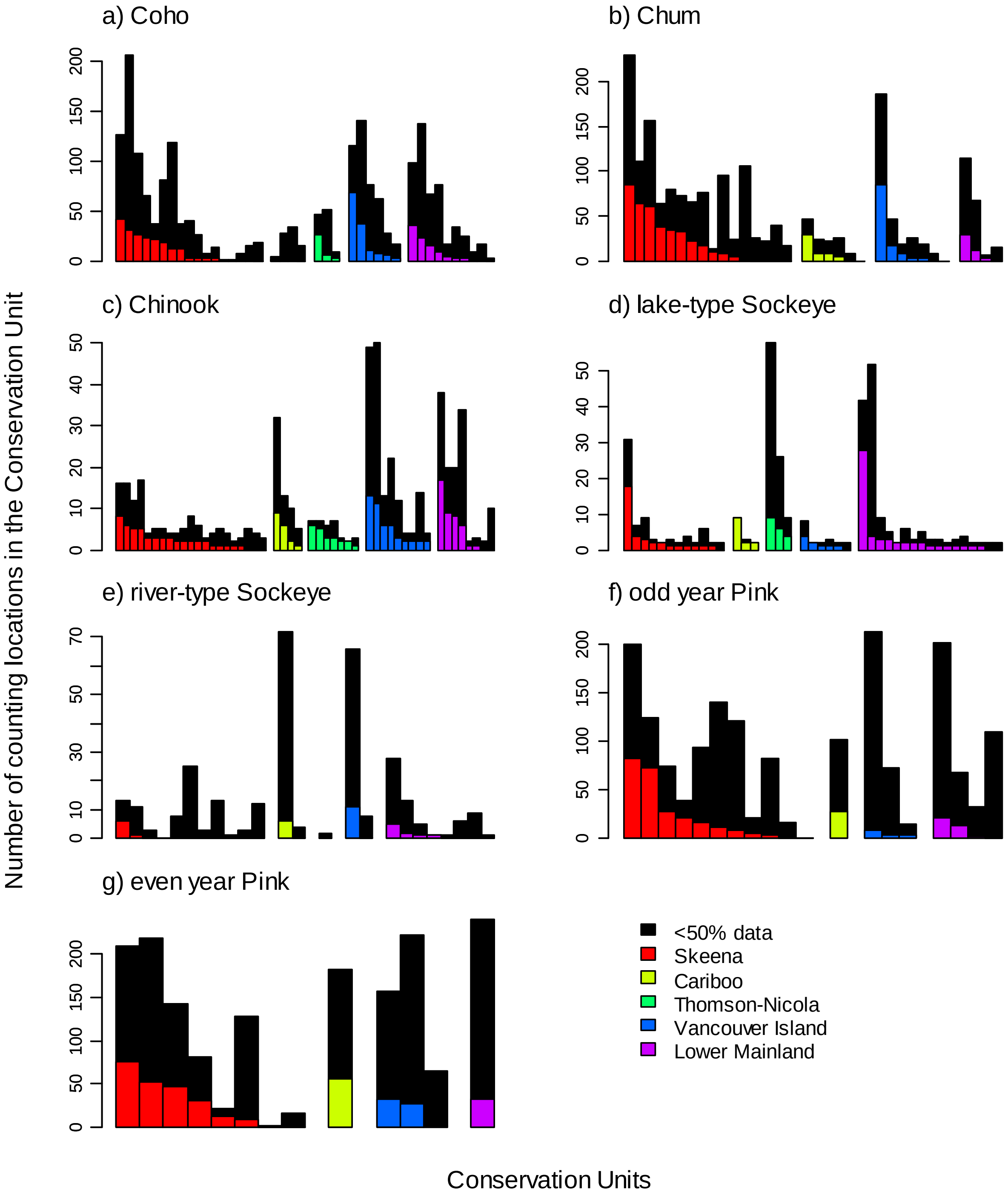

Figure 6. Inconsistent monitoring is a major challenge to implementing metrics of distribution. This figure shows the number of counting locations per Conservation Unit (CU) for each species of Pacific salmon (a-g) under Canada's Wild Salmon Policy. Each bar represents a CU, within which counting locations that have ≤50% data are black and those with >50% data are coloured. The most recent 10 generations were considered for all species except pinks, for which we extended the analysis to 15 generations due to their shorter life-cycle. The CUs are divided along the x-axis into five major freshwater regions (Skeena, Cariboo, Thompson-Nicola, Vancouver Island, and the Lower Mainland). CUs with only one counting location (occurred for lake-type sockeye and chinook) were not included in this figure.

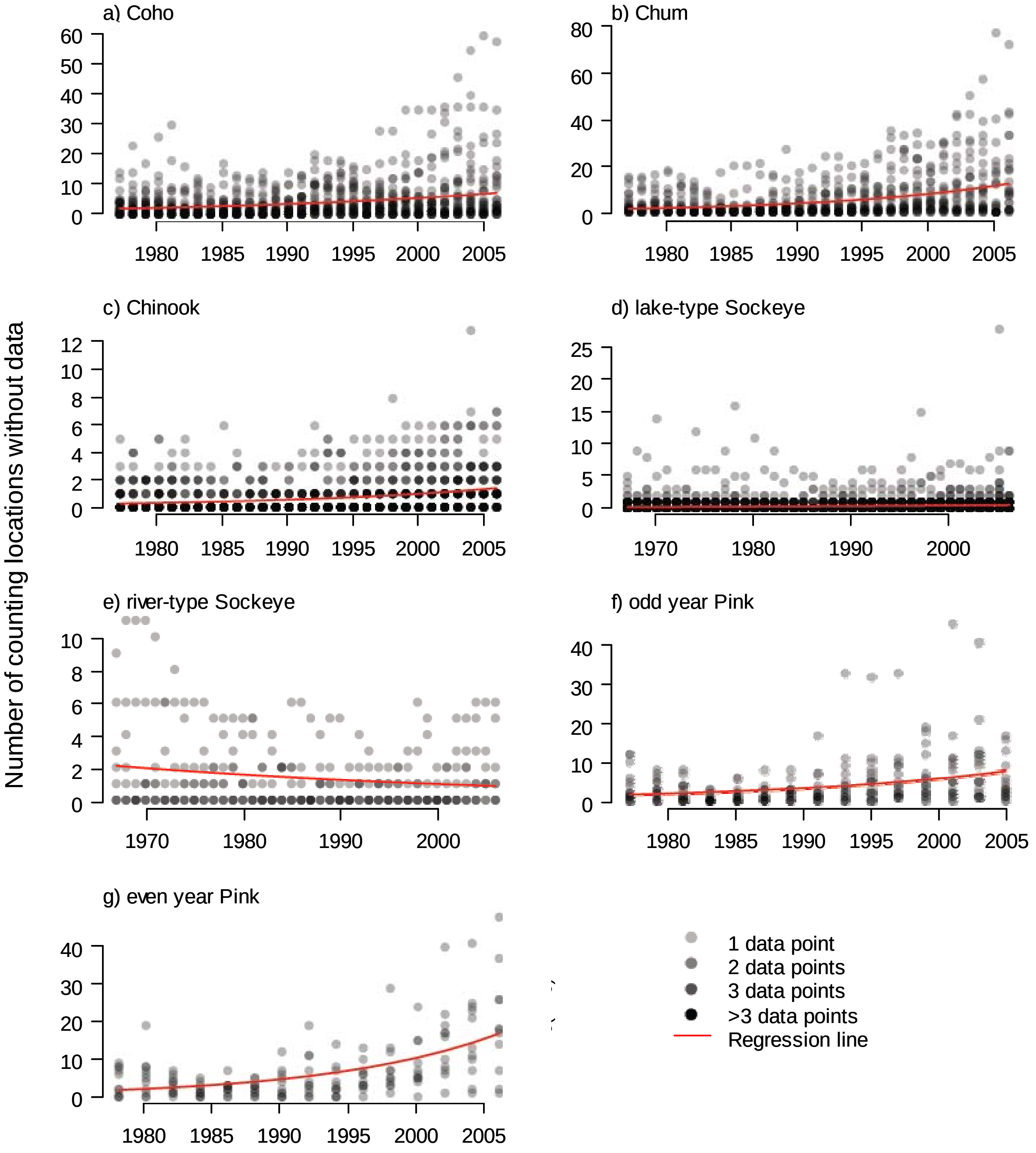

Figure 7. The number of selected counting locations (i.e., those with >50% data over the past 10 generations, or 15 for Pink) that are missing data each year. The red line is a linear regression with quasi-Poisson errors (due to over-dispersed count data) for the number of selected counting locations with no data over time. Statistically significant positive slopes are seen for all species except river-type sockeye, perhaps due to the small number of counting locations with quality data to begin with for this species.

4. FUTURE RESEARCH

We recommend further research in three areas: evaluation of proposed metrics in retrospective and prospective (i.e., forward simulation) analyses, comparison of monitoring designs for assessing distribution, and identification of benchmarks of status. A prospective analysis evaluating the sensitivity of metrics (i.e., the ability to correctly detect changes in distribution when they occur) is currently being undertaken (S. Peacock and C. Holt). Similar sensitivity and analyses have been performed for metrics on rates of change in spawner abundances by E. Porszt (School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6). The relative performance of distributional metrics could then inform their selection for status assessment.

In addition to evaluating metrics against historical sampling patterns, the performance of metrics under different statistically based sampling designs should also be evaluated. The current sampling design for Pacific salmon in B.C. does not consider assessment of distribution. Since it is not possible to monitor all counting locations, streams with lower escapement are often poorly monitored (Price et al. 2008). Alternative monitoring designs, such as sampling a random subset of counting locations or sampling at random from counting locations stratified by escapement level, may provide more accurate assessments of distribution than current designs, and with reduced effort. Additional designs involving rotating panels consist of annual monitoring of certain streams and surveys of others on a rotating basis, so that more counting locations are monitored overall with the same annual effort. Such designs have been effective at detecting trends in spawner abundances (Urquhart et al. 1998; Urquhart and Kincaid 1999), and are currently being evaluated in a forward simulation model to assess status of abundances, trends, and distribution of time trends of Pacific salmon (K. Holt, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6). That analysis is currently being extended to include the metrics of distribution identified here (S. Peacock and C. Holt).

Evaluating the status of CUs requires that quantitative benchmarks on metrics of distribution be set to differentiate CUs that are a conservation concern. Benchmarks may be set relative to historical values of metrics or by population viability analysis that incorporates metapopulation dynamics. COSEWIC guidelines (COSEWIC 2006) set precedence for identifying benchmarks, as one goal of the WSP is to avoid any chance of CUs being considered at risk of extinction by COSEWIC (DFO 2005). A lower benchmark between amber and red zones "will be established at a level of abundance high enough to ensure there is a substantial buffer between it and any level of abundance that could lead to a CU being considered at risk of extinction by COSEWIC" while accounting for uncertainty in data and control of harvest management (DFO 2005, page 17). An upper benchmark between amber and green "will be established to identify whether harvests are greater or less than the level expected to provide, on an average annual basis, the maximum catch for a CU, given existing environmental conditions"(p.18). In accordance with the precautionary approach, we recommend that uncertainty in metrics due to poor quality data also be considered when setting benchmarks on metrics of distribution.

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APPENDIX A: OVERLAP WITH STRATEGY 2

Metrics on the distribution of spawners over available habitat overlap substantially with Strategy 2 of the WSP. Strategy 2 requires an assessment of habitat associated with CUs (DFO 2005). The proposed habitat indicators, metrics and their benchmarks fall into three categories: pressure, status, and quantity (Stalberg et al. 2009). In a draft report of proposed stream, lake, and estuarine habitat indicators, Stalberg et al. (2009)identify the following stream quantity indicators:

1. **Accessible stream length** (km) based on barrier locations. This indicator quantifies the amount of habitat supporting salmon production. Data are available, but require considerable auditing and updating. This is similar to the proportion of historical habitat currently available, or accessible vs. lost stream length.
2. **Key spawning areas** (km) defined as "*those areas of spawning habitat used foremost annually regardless of escapement*". This is similar to the number of major spawning areas, or number of spawning groups contributing >5% to total escapement for the CU which were metrics of distribution proposed in the first category of metrics. Changes in the stream length of key spawning areas over time was suggested to be a trigger for further investigations into potential causes such as compaction, which also overlaps with metrics of distribution.

Some separate lake indicators were proposed that may also overlap with assessing the distribution of spawners (e.g., lake shore spawning area (km)). Cooperation is particularly important for lake-type sockeye since many of the CUs for this species (168/211) have only one counting location, making it impossible to calculate most of the proposed metrics of distribution.

APPENDIX B: SUMMARY OF DATA USED FOR EXAMPLES

Table B 1 . Summary of counting locations in the South Thompson coho CU. nuSEDS data last updated December 2009 were provided by Erik Grundmann (Erik.Grundmann@dfo-mpo.gc.ca, Pacific Biological Station, Nanaimo, BC V9T 6N7). Highlighted counting locations were those with >50% data over the past 10 generations, and were included in our analyses.

Site	nuSEDS data	>50% (1977-2008)	>75% (1977-2008)
Hiuihill Creek	x		
Perry River	x		
Crazy Creek	x		
Shuswap River - Middle	x		
Rienecker Creek	x		
Tsuius Creek	x		
Harbour Creek	x		
Nikwikwaia Creek	x		
Senn Creek	x		
Wright Creek	x		
Palmer Creek	x		
McNomee Creek	x		
Adams River	x		
Adams River - Upper	x	x	x
Sinmax Creek	x	x	x
Momich River	x	x	
Cayenne Creek	x		
Scotch Creek	x	x	x
Onyx Creek	x	x	
Ross Creek	x		
Celista Creek	x		
Seymour River	x	x	
Hunakwa Creek	x	x	x
Anstey River	x		
Eagle River	x	x	x
Owlhead Creek	x		
South Pass Creek	x	x	
Tappen Creek	x	x	x
Salmon River	x	x	x
Bolean Creek	x	x	
Canoe Creek	x	x	x
Shuswap River - Lower	x	x	x
Shuswap River - Middle	x	x	x
Johnson Creek	x	x	
Blurton Creek	x	x	x
Fortune Creek	x		
Trinity Creek	x	x	x
Kingfisher Creek	x	x	x
Danforth Creek	x		
Noisy Creek	x	x	
Wap Creek	x	x	x
Ireland Creek	x	x	x
Bessette Creek	x	x	x
Creighton Creek	x	x	x
Duteau Creek	x	x	x
Nicklen Creek	x	x	x
TOTAL	**47**	**26**	**19**

Table B 2. Summary of counting locations in the Takla/Trembleur (Early Stuart) lake-type sockeye CU. nuSEDS data last updated December 2009 were provided by Erik Grundmann (Erik.Grundmann@dfo-mpo.gc.ca, Pacific Biological Station, Nanaimo, BC V9T 6N7) . Highlighted counting locations were those with >50% data over the past 10 generations, and were included in our analyses.

Site	nuSEDS data	>50% (1966-2008)	>75% (1966-2008)
Takla Lake – Unnamed Creek (North of Blanchette)	x		
Tliti Creek	x		
Tildesley Creek	x		
Middle River-Rossette Bar	x		
Fleming Creek	x	x	x
Paula Creek	x	x	x
Sidney Creek	x	x	x
Kazchek Creek	x		
Van Decar Creek	x	x	x
O'Ne-Ell Creek	x	x	x
Forfar Creek	x	x	x
Gluske Creek	x	x	x
Casimir Creek	x		
Bivouac Creek	x	x	x
Leo Creek	x	x	
Sandpoint Creek	x	x	x
Sakeniche River	x	x	
Mcdougall Creek	x		
Sinta Creek	x		
Dust Creek	x	x	x
Crow Creek	x	x	x
Hooker Creek	x	x	
Point Creek	x	x	
Narrows Creek	x	x	x
25 Mile Creek	x	x	
Shale Creek	x	x	x
Blanchette Creek	x	x	
15 Mile Creek	x	x	x
Maclaing Creek	x	x	
Hudson Bay Creek	x	x	
Frypan Creek	x	x	x
Forsythe Creek	x	x	x
French Creek	x	x	
Ankwill Creek	x	x	x
Bates Creek	x		
Driftwood River	x	x	x
Blackwater Creek	x		
Lion Creek	x		
Porter Creek	x		
Kotsine River	x		
Consolidate Creek	x		
Kastberg Creek	x		
TOTAL	**42**	**27**	**18**

APPENDIX C: FIGURES FOR EXAMPLES

South Thompson coho

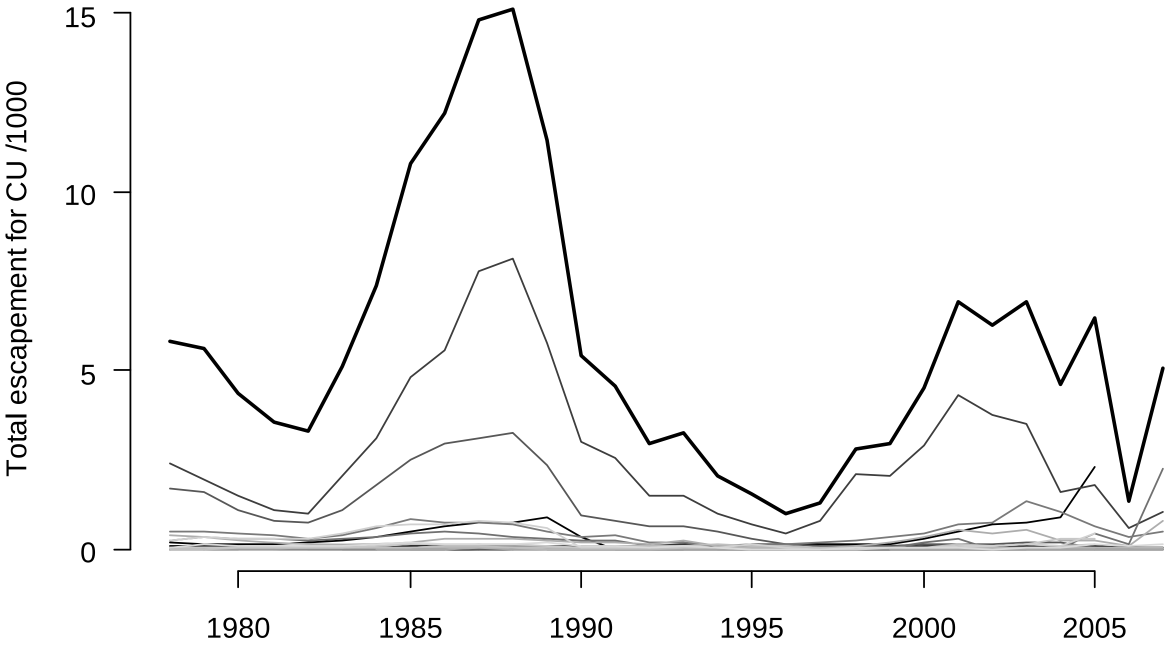

Figure C 1. Total escapement for the South Thompson coho CU from 1977-2007 (thick black line) with contribution from each of the selected counting locations (thin black line). Each reported year is the three-year running geometric mean of that year, the year before and the year after.

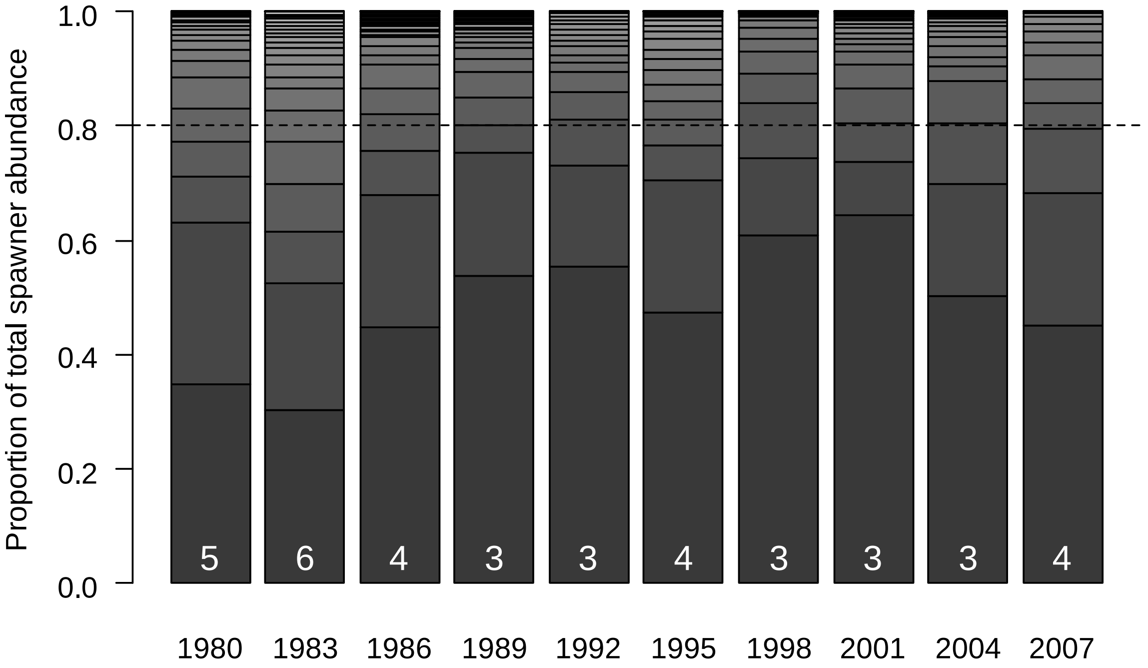

Figure C 2. Mean proportion of the total spawner abundances at each selected counting location for non-overlapping generations, ranked from highest proportion (bottom) to lowest (top) for the South Thompson coho CU. Numbers inside the bars are the number of counting locations that make up 80% of total escapement.

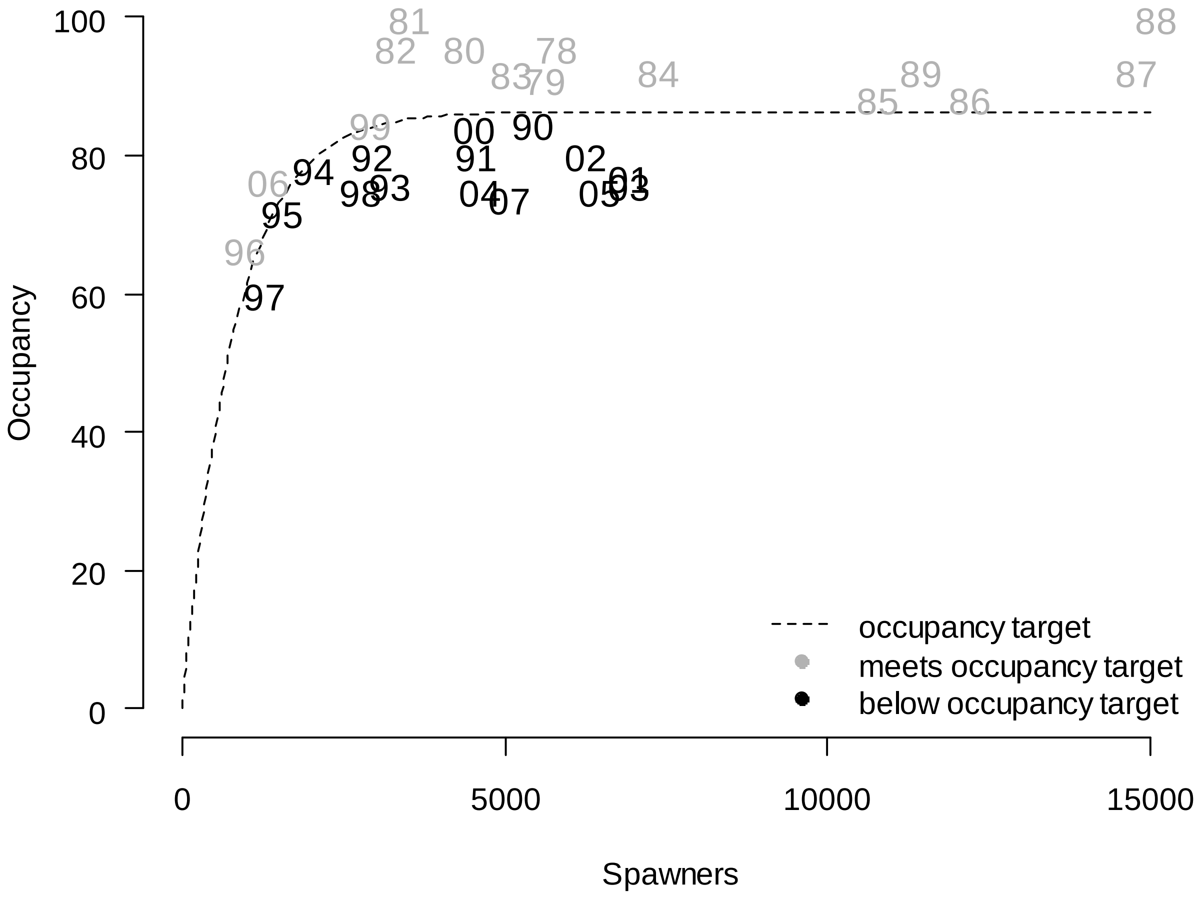

Figure C 3. The occupancy of counting locations over the total number of spawners in South Thompson coho CU for 1978-2007 (n=30). The black line is an asymptotic exponential model fit to the data ($y \sim a(1 - e^{-bx})$), a = 86.32 ± 1.767, $e^b = -6.68 \pm 0.154$, $p < 0.001$). The target occupancy was that predicted by the curve by spawner abundance. Grey numbers are the years that meet the occupancy target and black numbers are the years that fall below the occupancy target. Three of the past 12 years meet the occupancy target, putting the South Thompson below the benchmark set by the Oregon Department of Fish and Wildlife (2007).

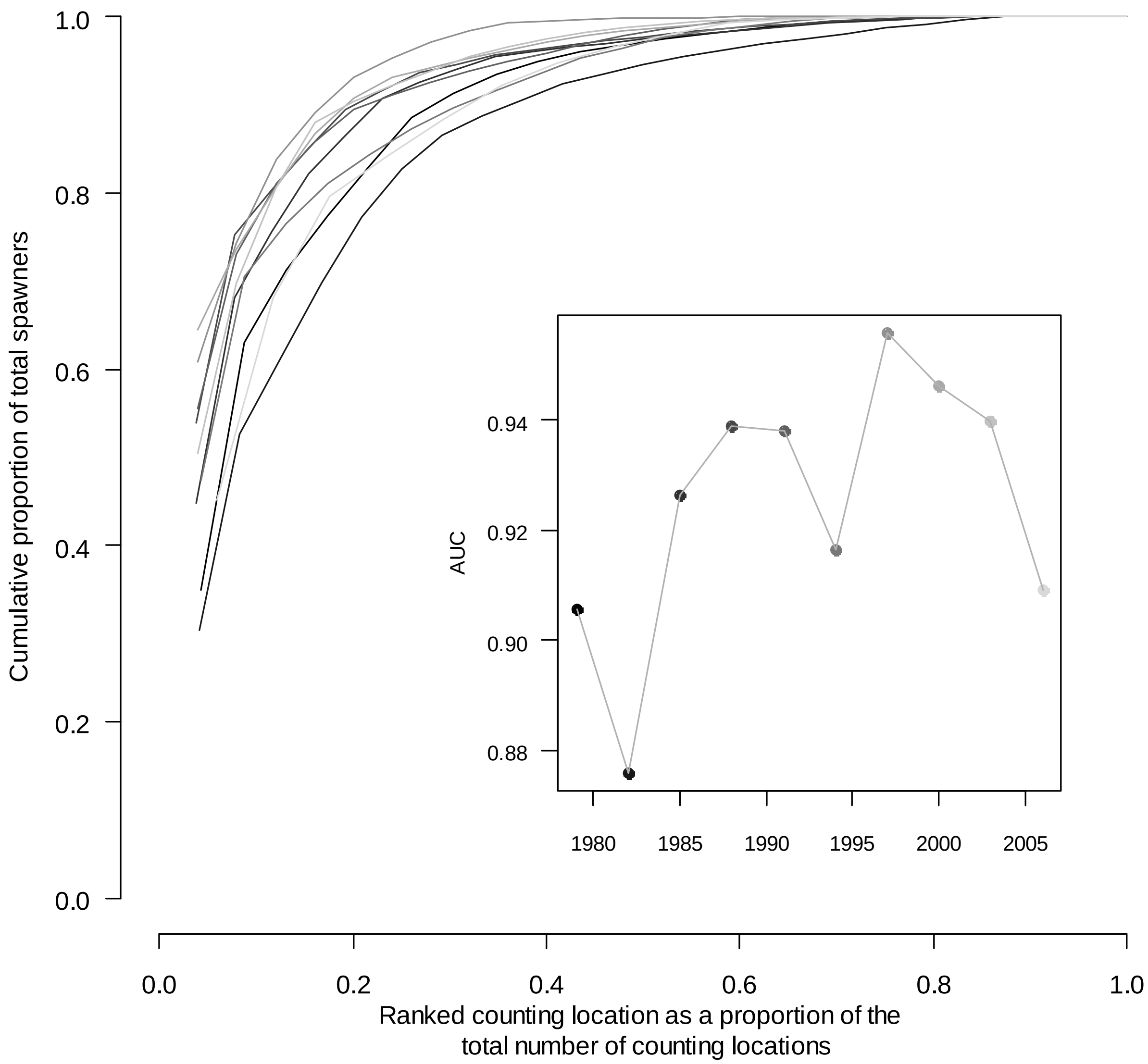

Figure C 4. Cumulative proportion of total spawners from each counting location, ranked in decreasing order of abundance for the ten most recent generations of spawners in the South Thompson coho CU. The inset plot shows the change in area-under-the-curve (AUC) over time. Each curve represents a generation, with the shade matching the corresponding AUC in the inset. The non-overlapping generation mean is used instead of the running mean to make the figure more readable.

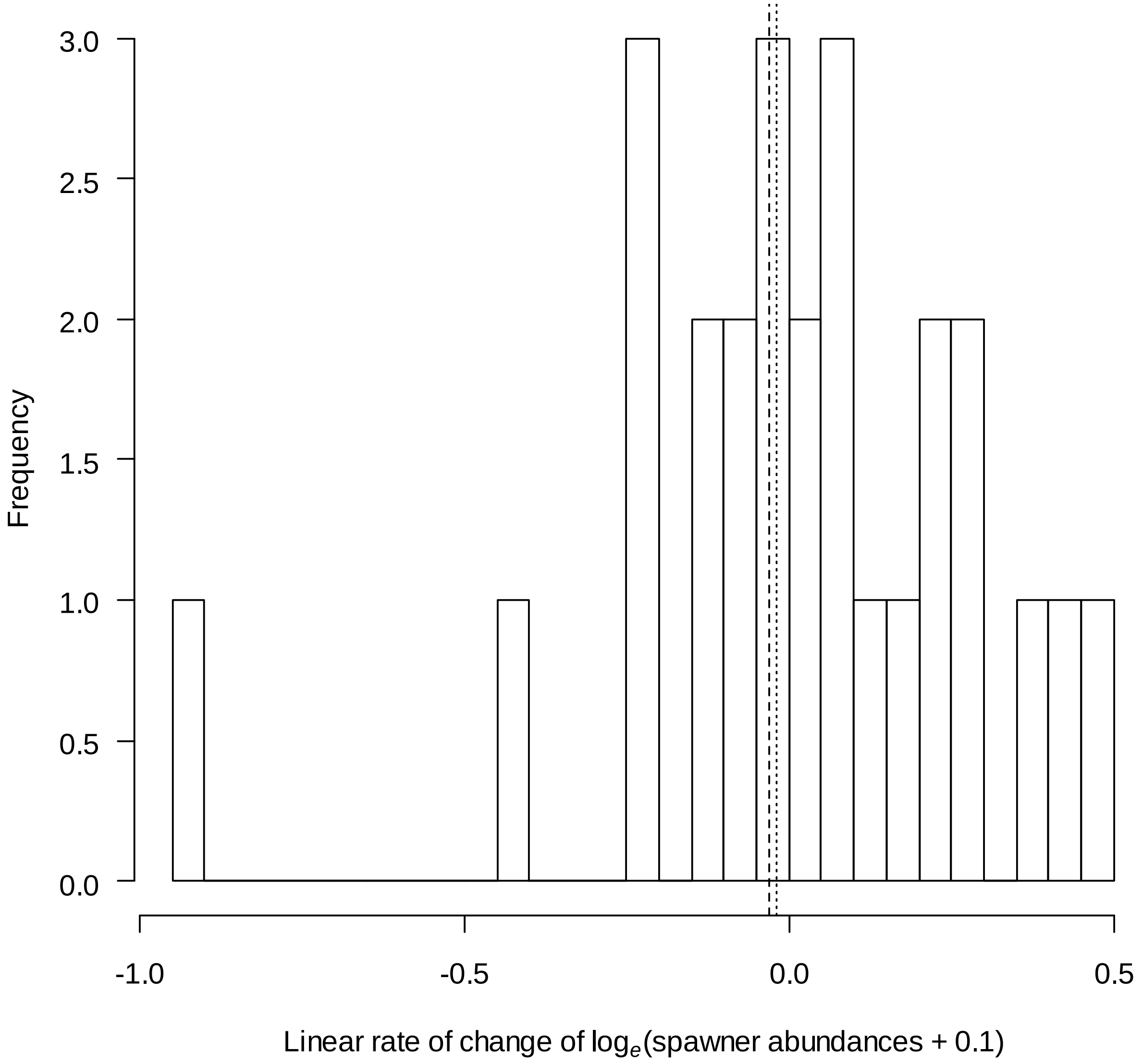

Figure C 5. Histogram of linear rates of change of log-transformed spawner abundances over the past three generations (ten years) for selected counting locations. The linear rate of change associated with 20% and 30% declines in abundances over ten years are shown with the dotted and dashed lines, respectively. 34.6% of counting locations had rates of declines greater than those that required for COSEWIC vulnerable designation. When the time trends analysis was extended to ten generations (30 years), 57.7% of counting locations had rates of declines greater than those that required for COSEWIC vulnerable designation. This is consistent with the recent increases in abundance seen in Figure C 1, but the long term declines. However, extending an analysis of linear rates of change to 30 years is likely not valid since abundance time trends over this period are not linear.

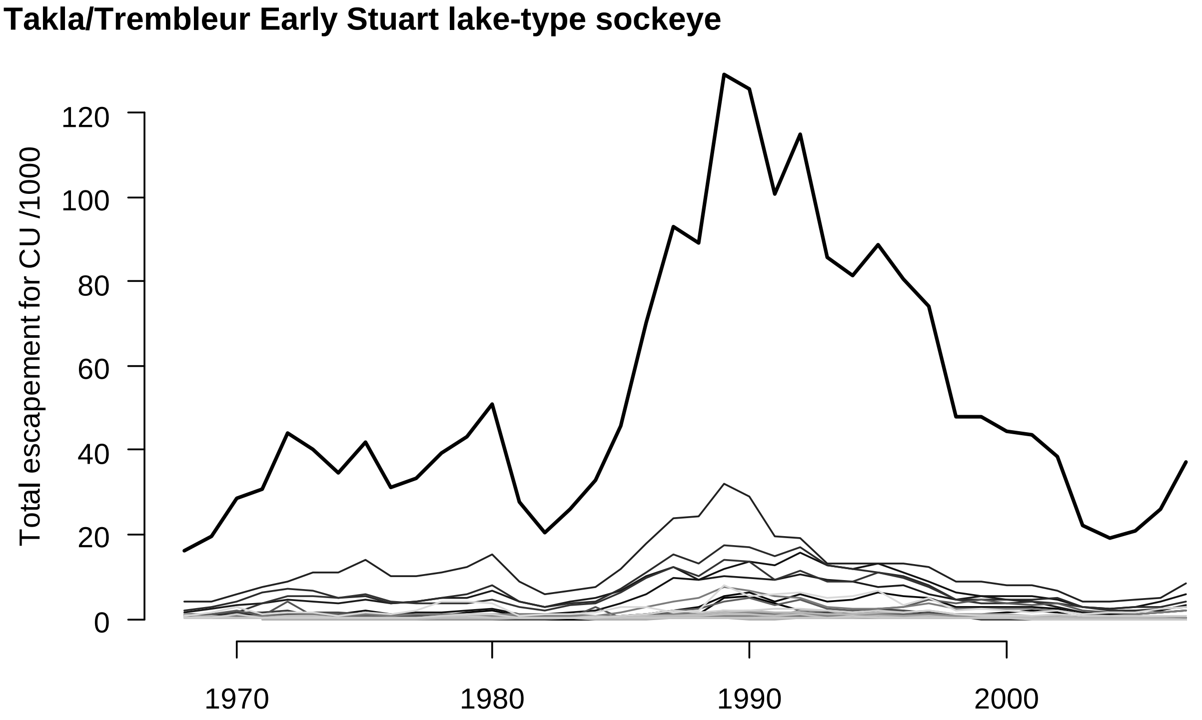

Figure C 6. Total escapement for the Takla/Trembleur EStu sockeye CU from 1967-2007 (thick black line) with contribution from each of the selected counting locations (thin black line). Each reported year is the four-year running geometric mean of that year, the two years before and the year after.

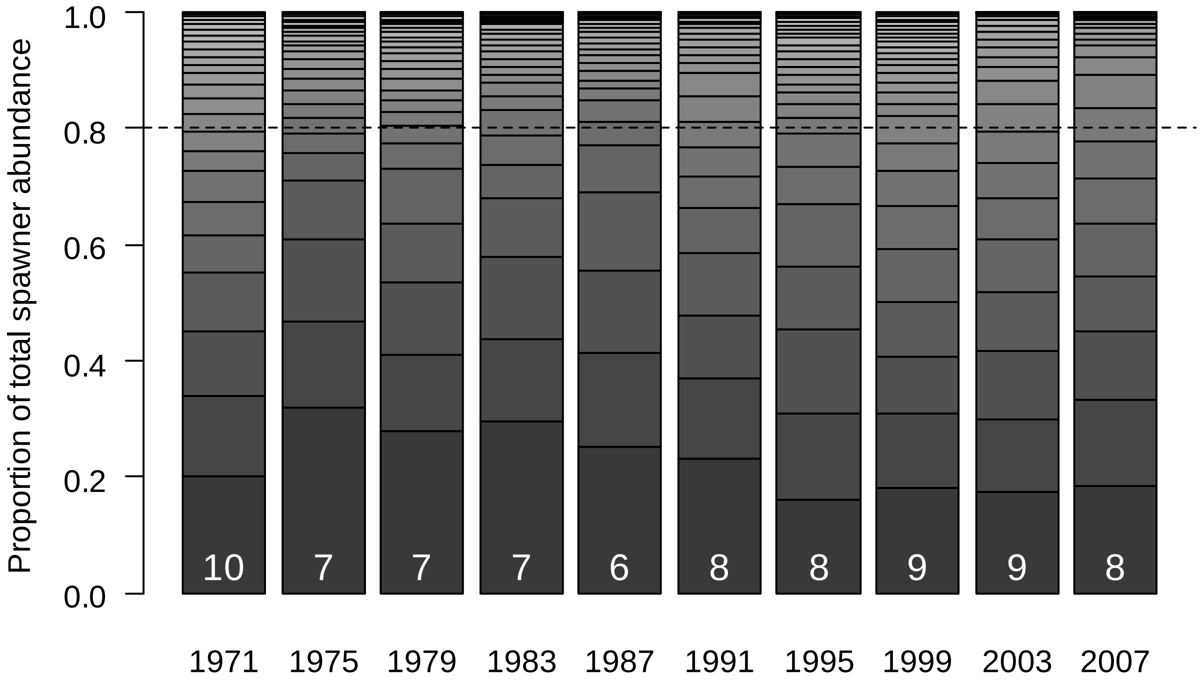

Figure C 7. Mean proportion of the total spawner abundances at each selected counting location for non-overlapping generations, ranked from highest proportion (bottom) to lowest (top) for the Takla/Trembleur EStu sockeye CU. Numbers inside the bars are the number of counting locations that make up 80% of total escapement.

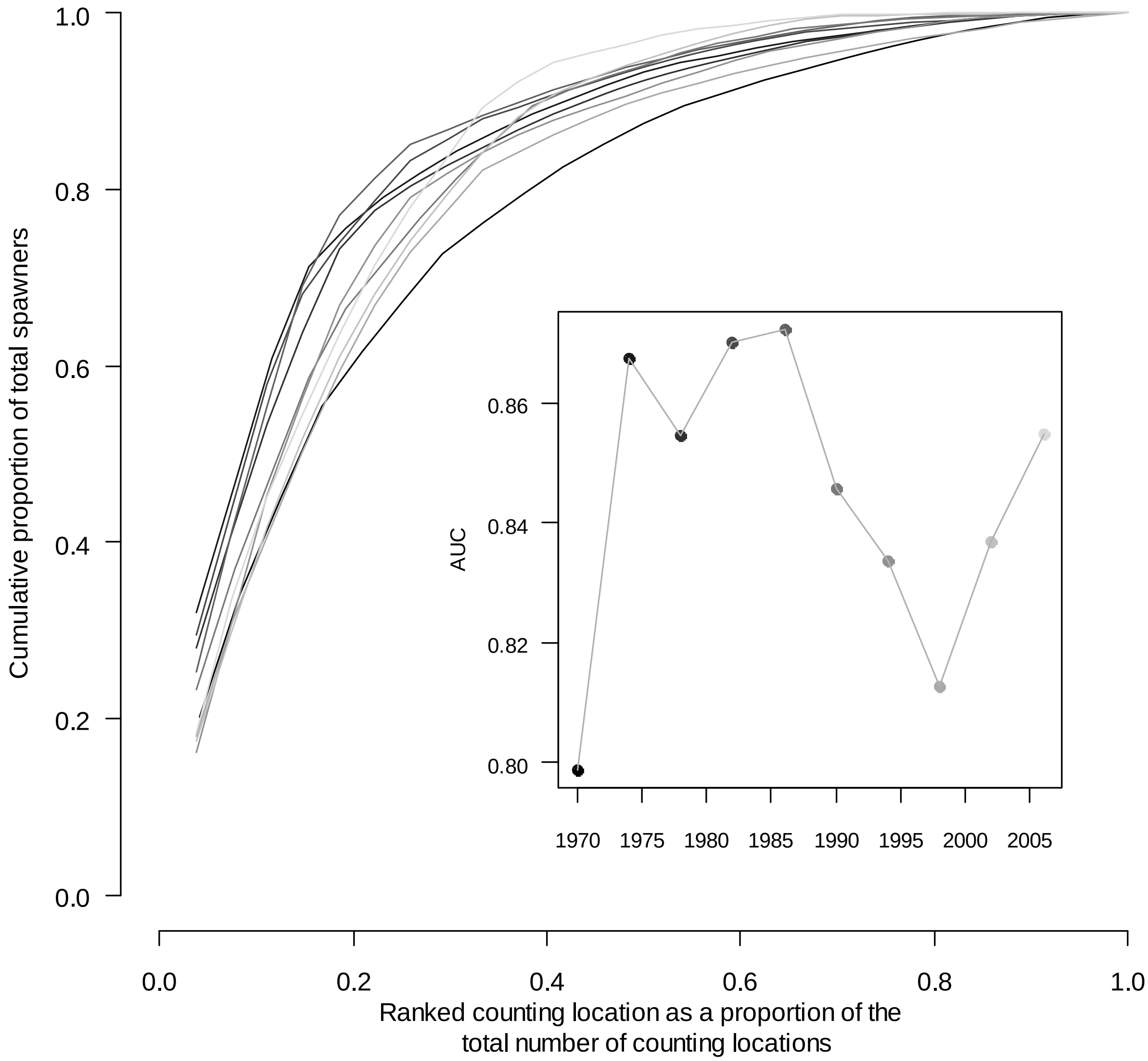

Figure C 8. Cumulative proportion of total spawners from each selected counting location, ranked in decreasing order of abundance for the ten most recent generations of spawners in the Takla/Trembleur EStu sockeye CU. The inset plot shows the change in area-under-the- curve (AUC) over time. Each curve represents a generation, with the shade matching the corresponding AUC in the inset. The non-overlapping mean for each generation was used for clarity.

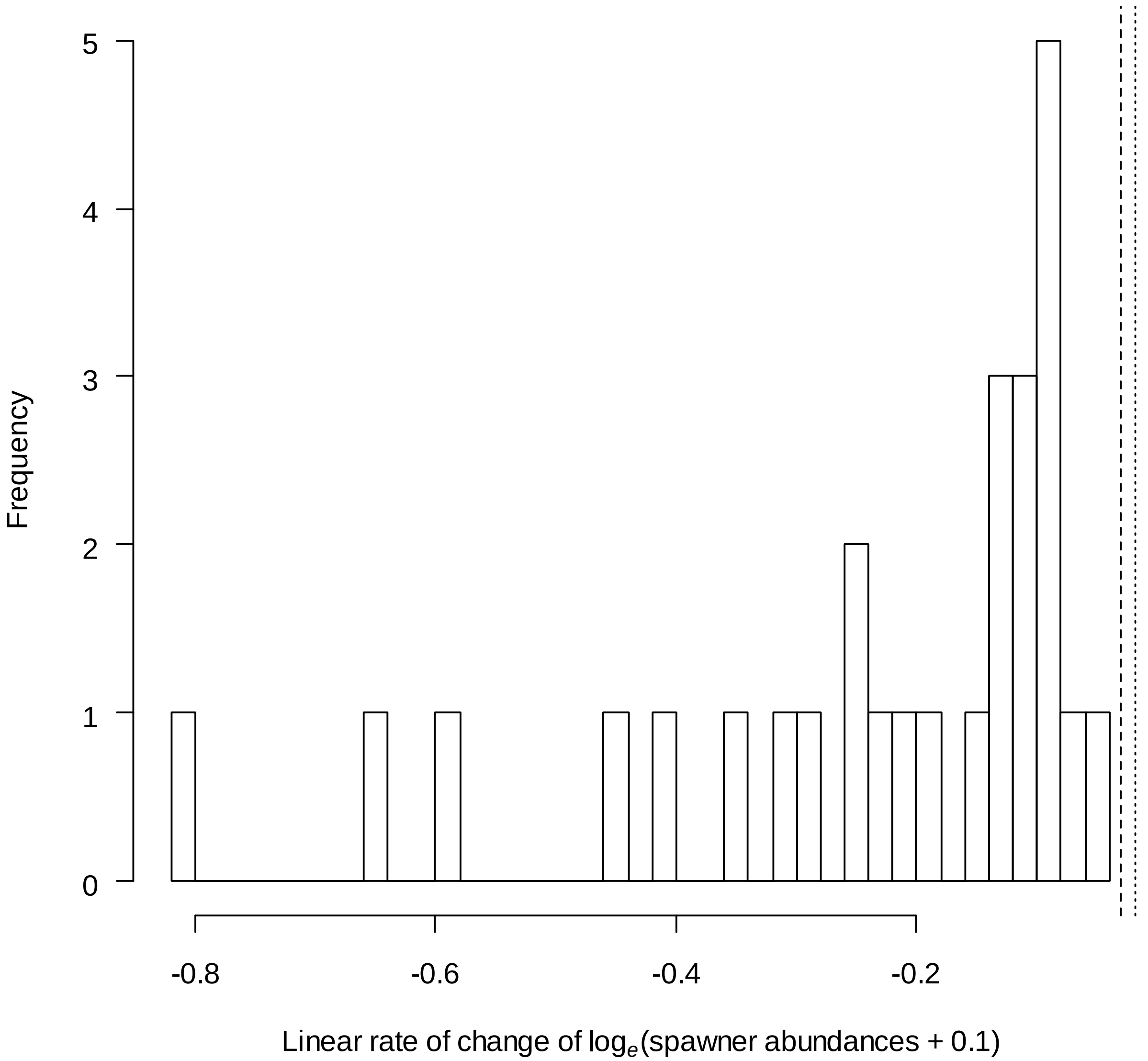

Figure C 9. Histogram of linear rates of change of log-transformed spawner abundances (smoothed with a four-year running mean) over the past three generations for all selected counting locations in the Takla/Trembleur EStu sockeye CU. The linear rates of change associated with 20% and 30% declines in abundances over three generations are shown with the dotted and dashed lines, respectively. In this case, 100% of selected counting locations had rates of declines greater than those that required for COSEWIC vulnerable designation. This is consistent with recent declines in abundance observed in Figure C 6. However, when the trends were extended to 10 generations, only 25.9% of counting locations had rates of decline greater than COSEWIC's vulnerable designation.