Monitoring for fisheries or for fish? Declines in monitoring of salmon spawners continue despite a conservation crisis

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Abstract

Monitoring of salmon in Pacific Canada has been declining for decades. Spawner timeseries enable researchers to quantify impacts of local stressors, identify when and where management interventions are required to avoid extirpations, and evaluate the efficacy of recovery efforts. These data are more important now than ever, as uniquely adapted spawning populations underlie salmon resilience and their ability to adapt to climate change, and fine-scale data can inform terminal fisheries being revitalized by First Nations. We revisit the state of spawner data from the Yukon to southern BC. Almost two-thirds of salmon populations that were historically monitored have no reported estimates in 2013-2022 – the worst decade for data since monitoring programs began in the 1950s. We found strong correlations between the number of populations monitored and catch for each species, suggesting that monitoring is primarily motivated by commercial fisheries management. We recommend clarifying monitoring objectives and strategic investments to improve monitoring outcomes for salmon and communities. We emphasize data stewardship, as ensuring access to these baseline data is a cornerstone for rebuilding wild Pacific salmon.

Key words: Pacific salmon, long-term monitoring, Wild Salmon Policy, population dynamics, marine fisheries, marine conservation

Introduction

Collecting baseline, fishery-independent data is a pillar of sustainable fisheries management, providing the foundation for evidence-based decisions about the conservation and management of aquatic species (Hilborn and Walters 1992; Punt et al. 2020; Punt 2023). Commercial fisheries data are important components of sustainable management frameworks, but relying on catch data alone is broadly acknowledged as insufficient to meet sustainable fisheries objectives (Walsh et al. 2018; Free et al. 2020; Ovando et al. 2021). In a recent example underlining this point, Canada's Pacific salmon fishery was forced to withdraw from the Marine Stewardship Council certification program in 2022, in large part due to a lack of sufficient data to assess salmon abundance trends (Raincoast Conservation Foundation 2019; Marine Stewardship Council 2022). The history of colonial fisheries and their management in Canada is punctuated with consequential failures resulting from insufficiently considering the biology of fished species and the harvest levels they can sustain. From the 1990s collapse of Atlantic cod (Hutchings and Rangeley 2011) to the mid-2000s decline of Fraser sockeye in the Pacific (Peterman and Dorner 2011; Castañeda et al. 2020), retrospective reviews emphasized the importance of decision-making grounded in robust, data-driven science. Maintaining up-to-date and quality-controlled datasets, required for rigorous science, is crucial to effectively managing fish populations. Even in the absence or decline of commercial fisheries, as in the case of wild salmon in Pacific Canada (Walters et al. 2019), baseline data remain instrumental to stewarding populations through stressors such as climate change and habitat degradation.

Pacific Canada is home to thousands of distinct Pacific salmon (*Oncorhynchus* spp.) populations across five species – Chinook (*O. tshawytscha),* chum (*O. keta),* coho (*O. kisutch),* pink (*O. gorbuscha)*, and sockeye (*O. nerka) –* which exhibit extraordinary diversity in their life histories (Groot and Margolis 1991). Pacific salmon inhabit diverse freshwater habitats to which

they are locally adapted through characteristics such as body size, colouration, age-at-maturity,

spawn timing, and duration of freshwater residence. This diversity provides the ingredients for

Pacific salmon to withstand and adapt to environmental change, and it distributes the risk of

extinction due to local catastrophes. In other words, Pacific salmon never have all their eggs in

one basket (or redd). The diversity among and within Pacific salmon species also provides

stability to salmon social-ecological systems, sustaining coastal and inland communities and

cultures for millenia (Castañeda et al. 2020; Atlas et al. 2021; Reid et al. 2022).

Multiple types of data inform efforts to study, monitor, and manage Pacific salmon. The federal

department of Fisheries and Oceans Canada (DFO) tracks how many fish are caught in

commercial fisheries and fin-clip or scale samples from captured fishes provide information on

their genetic origins. Coded wire tags, pit tags, and acoustic tags provide detailed information on

ocean survival and movement. These data, and more, help to sustainably manage commercial

fisheries and are critical to understand, track, and conserve the diversity and distribution of

salmon. An evidence-based approach to conserving wild salmon, however, also requires simply

counting them. Fortunately for us, and unique from other marine fishes, salmon show up in our

backyards each year for us to count as they return home to spawn (Fig. 1).

In Pacific Canada, the history of counting salmon – in one way or another – as they return to

spawn extends back thousands of years. Since time immemorial, First Nations communities

have developed deep-rooted knowledge of salmon over generations, informed by diverse

approaches to monitoring local populations (Atlas et al. 2021; Reid et al. 2022). This paper

focuses on salmon counting programs that extend back to the 1930s, which is relatively modern

history but a period for which centrally compiled, broad-scale, and publicly accessible data are

available. The evolution of salmon counting coordinated by the federal government over the last

one hundred years feeds directly into the data available today. Beginning in the 1920s, the

"Annual Reports of Salmon Stream and Spawning Grounds," commonly known as the "BC16s"

for the number on the physical reports, were released (Fig. 2). Initially, reports were sent as

personal letters to federal fisheries supervisors, describing runs as "good", "average", "well

seeded", etc. (McNairnay 1987). In the early 1930s, the reports were formalized to provide an

estimated range for the approximate number of spawners on the spawning grounds. This shift

was not intended to produce actual estimates of abundance but rather to allow considerations of

watershed size, given that "a small stream well seeded could probably have one hundred parent

salmon, but a larger stream equally well seeded would have perhaps five hundred parent

salmon…" (McNairnay 1987). By the 1980s, the estimates for most populations had transitioned

to "point estimates" of the number of individual spawning salmon (Fisheries and Oceans

Canada 2023). In 1995, responsibility for salmon counting moved to DFO's Science branch, and

counting data were brought together into what is now known as the New Salmon Escapement

Database (NuSEDS), including details of estimation methods and other descriptive information.

Today, NuSEDS houses the most spatially and temporally comprehensive spawner abundance

estimates available for Pacific salmon in Canada. The database is publicly available online and

is intended to be updated annually (Fisheries and Oceans Canada 2024a). In the current

Canadian context, NuSEDS is fundamental to assessing salmon status (Box 1), estimating

population-level effects of localised stressors (Box 2), and evaluating the efficacy of recovery

actions (Box 3).

While rarely acknowledged directly, the importance of counting salmon is implicitly woven into

the policy history of Pacific salmon in Canada, most recently embodied in the Wild Salmon

Policy and its plan for implementation (Fisheries and Oceans Canada 2005, 2018). The Wild

Salmon Policy formalised a shift, from viewing salmon simply as "stocks" to be harvested,

toward conservation of the inherent diversity and distribution of wild Pacific salmon. This shift

required federal policy to consider what it means to define, restore, and maintain diverse salmon

populations. One step in this process included defining "Conservation Units" (CUs) – genetically

and ecologically distinct groups of salmon unlikely to recolonize within a human lifetime if

extirpated (Fisheries and Oceans Canada 2005). Delineating CUs at biologically and socially

relevant scales is not a trivial task and has been a focus of extensive research (Holtby and

Ciruna 2007; Weinstein 2007; Fisheries and Oceans Canada 2009). While imperfect, CUs laid

the foundation for implementing the Wild Salmon Policy and, once defined, begged the

questions: What data are required to monitor and manage CUs? In what state are those data?

Indeed, the first strategy of the Wild Salmon Policy is to "[standardize] monitoring of wild salmon

status" (Fisheries and Oceans Canada 2005). For over 20 years, researchers and salmon

advocates have noted that the number of populations monitored in regions of BC has steadily

declined (Harvey and MacDuffee 2002; Price et al. 2008, 2017; English 2016; Atkinson et al.

2020). However, a coastwide assessment of the trajectory of salmon counting as captured by

NuSEDS has not been published. Such an assessment is necessary to understand whether

previous calls for increased monitoring have led to change, especially in light of substantial

recent investments by the federal and provincial governments through the Pacific Salmon

Strategy Initiative ($647 million) and the BC Salmon Restoration and Innovation Fund ($143

million).

Inspired by the late Dr. Jeffrey Hutchings and his commitment to investigating the scientific and

policy connections between data and decision-making, we set out to produce an updated,

broad-scale assessment of the state of Pacific salmon spawner abundance data in Canada. We

focused on NuSEDS, the most comprehensive database of spawner counts in Pacific Canada.

We assessed the number of populations and CUs monitored annually from 1926-2022, and the

correlation between this monitoring effort and commercial salmon catches in Canada. Finally,

we provide recommendations for optimizing monitoring to meet the conservation objectives laid

out in Canada's Wild Salmon Policy and for improving data management to ensure that timely

and accurate information can be shared publicly and appropriately in the coming decades.

Boxes

Box #1: Assessing salmon status

The primary metric used to assess biological status of CUs is current spawner abundance (Holt

et al. 2009; Pestal et al. 2023; Pacific Salmon Foundation 2024). Estimates of CU-level

abundance can be compared to benchmarks – generally set from historical abundances or

social-biologically relevant reference points (e.g. the number of fish that maximise fisheries

yield) – to determine the status of CUs and determine the potential for fisheries (Chum

Technical Committee 2023; Chinook Technical Committee 2024) or the need for conservation

intervention. This seemingly simple goal involves hidden complexity and assumptions required

to estimate CU-level abundance. In some cases, such as status assessments of geographically

constrained lake-type sockeye, spawner abundance can be obtained from a single survey or

indicator population that is representative of the aggregate stock or CU. However, in most

cases, assumptions must be made to "expand" counts from a limited number of spawner

surveys to estimate spawners for an aggregate unit, such as a CU, Stock Management Unit, or

region. The expanded estimates are also often required for calculating total returns and

exploitation rates, because harvest of salmon does not discriminate between fish that are

returning to monitored and unmonitored streams (with the exception of some mark-selective

fisheries). Thus, to ensure that catch and spawner data correspond to the same component

populations and can be added together, spawner abundance must be extrapolated to

unmonitored populations. Although common expansion approaches are fairly robust (Peacock

et al. 2020), a severe reduction in the number of monitored populations or decline in monitoring

effort over time can invalidate the assumptions of these expansions and create uncertainty

around the estimated aggregate spawner abundance. For example, in 2021, only one out of 61

spawning populations was monitored for the West Haida Gwaii chum CU, with a count of 500

spawners (Salmon Watersheds Program 2023). Based on the historical proportional contribution

of the monitored stream to the CU, these 500 spawners were expanded to a CU-level

abundance of over 40,000 spawners. Of particular concern is the tendency to stop monitoring

declining salmon populations and focus on more abundant populations, which may overestimate

the expanded number of spawners and present conservation risks to the aggregate on top of

potential undocumented extinctions of individual populations (Price et al. 2008).

175   Box #2: Assessing impacts on salmon

The spatial and temporal breadth of spawner counts in Pacific Canada has enabled a wide body

of research into the effects of local stressors on the responses of Pacific salmon populations. By

comparing spawner abundances, or recruits-per-spawner for individual populations, across a

range of exposure to a given stressor, the impacts of that stressor on salmon can be estimated.

With this approach, research has leveraged salmon abundance data to investigate, for example,

the population level-effects of climate change (Hinch and Martins 2011; Malick et al. 2017),

parasite transmission from salmon farms (Connors et al. 2010; Krkošek and Hilborn 2011;

Peacock et al. 2013), marine mammal predation (Nelson et al. 2019), and forestry (Holtby 1988;

Bradford and Irvine 2000; Wilson et al. 2021). All these studies examined stressors that show a

range of effect sizes at fine spatial resolution in freshwater or near-shore marine environments

(e.g., watersheds or inlets), and many relied on salmon spawner abundance records assembled

and maintained by DFO in the New Salmon Escapement Database (NuSEDS) to quantify

salmon responses at an appropriate spatial resolution. More spatially constrained data, such as

survival estimates from coded wire tags of select indicator stocks, or data with coarser spatial

resolution, such as catch within Pacific Fisheries Management Areas, fail to represent the effect

sizes and resolution of many pressures. The decline of spawner abundance monitoring in

Pacific Canada limits the ability to quantify effects of localised freshwater and near-shore

stressors on salmon abundance and productivity.

Box #3: Assessing the efficacy of recovery actions

Monitoring spawner abundances before and after recovery actions is essential to measure their

efficacy. In the past five years, the Canadian government has renewed efforts to address the

declining abundance of Pacific salmon by establishing systematic planning processes such as

rebuilding plans, prescribed in revisions to the *Fisheries Act,* and Integrated Salmon Ecosystem

Plans, piloted under the Pacific Salmon Strategy Initiative (Fisheries and Oceans Canada 2022,

2024b). For example, resource-intensive efforts led by DFO are underway to create a rebuilding

plan for West Coast Vancouver Island Chinook salmon and pilot Integrated Salmon Ecosystem

Plans for the Thompson-Shuswap, Nicola, and Yukon watersheds. While historical spawner

abundance data may be sufficient to inform planning and implementation, assessing the

success of interventions may be impossible if monitoring declines continue. The efficacy of

recovery actions undertaken at finer spatial scales, such as localized habitat restoration or water

management interventions, can only be understood by monitoring the affected populations

rather than aggregate stocks. Mismatches between recovery strategies and monitoring

coverage, both temporally and spatially, may result in instances where significant investments

are made in recovery planning and implementation but the success of such efforts cannot be

demonstrated and may be unable to inform future actions.

Methods

The terminology used for different biological and management scales of salmon is a common source of confusion in analyses such as ours, so we begin with some definitions. We define "populations" as unique combinations of CUs and spawning sites (e.g., stream, river, or lake). These populations mostly reflect the biological unit for which spawner abundances are reported in NuSEDS (Fisheries and Oceans Canada 2024a), except that we consider pink salmon counted at the same site in even- and odd-years as separate populations, consistent with the evidence for genetically distinct even- and odd-year lines (Beacham et al. 2012). There was a relatively small number (n = 82) of NuSEDS populations that could not be reliably assigned to a CU and were excluded from our analyses (cf. Appendix).

We downloaded two datasets from NuSEDS on January 22nd, 2024 (Fisheries and Oceans Canada 2024a). The first dataset (*all_areas_nuseds*) contains the annual counts (e.g. number of natural adult and jack spawners) for each population. The second dataset (*conservation_unit_system_sites*) associates each population to its respective CU and site. We merged the two datasets to associate each population's time series to its CU. There were numerous errors and omissions between these two datasets including duplicate time series, abundance estimates assigned to wrong populations or CUs, or missing CU information. We undertook a systematic review of the data to identify and correct these cases (cf. Appendix details and access to R code). The resulting cleaned spawner survey data are available online (Carturan and Peacock 2024).

We assigned each population to one of nine broad-scale regions based on the site location (latitude/longitude) in NuSEDS to assess broad spatial patterns in monitoring (Figure 1) . The final dataset contained spawner abundance data from 1926 to 2022 for the five Pacific salmon

species (Chinook, chum, coho, pink, and sockeye), 390 CUs, 6,766 populations, and 2,300 sites

(Table 1).

From the cleaned NuSEDS data, we calculated the annual "number of populations monitored"

as the number of populations having a numeric estimate in any of the following fields: natural

adult spawners, natural jack spawners, total natural spawners, adult broodstock removals, jack

broodstock removals, total broodstock removals, other removals, or total return to river. There

were 2,992 yearly counts (2%) with a maximum value of zero across these fields. We found

suspicious changes in the frequency of zeroes starting in certain years and only for certain

regions and species (e.g., Fig. A7). Given the available information, it was not possible to

determine whether these zeros represented monitored populations with true zero counts. As

such, we opted to conduct the analysis under two different assumptions: in the main text we

present results assuming that counts of zero indicate no monitoring and in the Appendix, we

present results under the assumption that monitoring did occur when zero spawners are

reported.

We divided the number of populations monitored each year by the total number of populations

monitored to obtain the annual "proportion of populations monitored". The annual "proportion of

CUs monitored" was the number of CUs with at least one population monitored divided by the

total number of CUs (which differed in even and odd years because pink salmon CUs are only

monitored every other year). We only considered NuSEDS data in this analysis. In many

regions, monitoring may be undertaken but the data are either not submitted to or not included

in NuSEDS. This potential reporting bias is addressed in recommendation #4 in the Discussion.

We summarised declines in monitoring for each species and region as the average change per

year in the number of populations monitored. We estimated the average change per year as the

slope of a linear regression model fitted to the number of populations monitored each year from

the peak of monitoring in 1986 to 2022.

We downloaded catch data from the North Pacific Anadromous Fish Commission website

(NPAFC; 2024) in July 2024. We considered the Canadian, commercial catches expressed in

thousands of individuals for each of the five Pacific salmon species. We quantified the temporal

association between the number of populations surveyed and catches using the non-parametric

Spearman correlation coefficient.

We used R (version 4.3.1; R Core Team 2023) and the R packages `tidyr` 1.3.1 (Wickham et

al. 2024) and `dplyr` 1.1.4 (Wickham et al. 2023) to handle and analyse the datasets and

produce the figures. We used the R package `sf` 1.0-14 (Pebesma and Bivand 2023) to group

sites in their respective region. The workflow is fully reproducible by accessing the R scripts and

datasets in the Zenodo repository at https://zenodo.org/records/14248905.

Findings

Monitoring and reporting of salmon spawner abundances throughout BC and the Yukon peaked

in the mid-1980s, with over 2,700 individual populations across ~1,300 unique sites being

monitored annually (Fig. 2). Since 1986, there has been a marked decline in the number of

populations monitored annually, with an average loss of 42 populations per year in the NuSEDS

data from 1986 to 2022. Across 6,766 unique populations (Table 1), only 37% have spawner

records in the most recent decade (2013-2022) compared to 70% in the period 1980-1989.

Coho and chum populations saw the greatest decline in monitoring, particularly for Vancouver

Island & Mainland Inlets, the Central Coast, and Haida Gwaii (Fig. 3c,f,g, Fig. A1b,c). Pink

salmon also saw major reductions in monitoring on the Central Coast, Skeena, and Haida Gwaii

(Fig. 3c,f,e, Fig. A1d). Fraser Chinook and Fraser sockeye saw the only increases in monitoring

since the 1980s among all regions and species (Fig. 4), although the number of Fraser Chinook

populations monitored peaked later, in 2000, and has also since declined (Fig. 3h).

Differences in monitoring effort across species and regions through time tend to reflect changes

in commercial catches (Fig. 2). For example, declines in coho monitoring in the early 2000s

coincided with the moratorium on coho fisheries following a period of low marine survival that

started in the 1990s (Decker et al. 2014). While there was no longer a need to inform

management of coho fisheries, the reduction in monitoring may have had unintended

consequences: chum salmon monitoring appears to have declined concurrently, most obviously

on Vancouver Island & Mainland Inlets (Fig 3g). Chum salmon have similar spawn timing to

coho and may have been monitored opportunistically during surveys that target coho. Many

coho populations increased in the late 2000s and 2010s, with the reduction of harvest and more

recent shift in ocean condition, however spawner surveys have not resumed. As the Interior

Fraser coho Management Unit recently exceeded escapement targets for the first time (Connors

et al. 2024), we anticipate the resumption of fisheries. Whether the diversity and distribution of

coho within the Fraser watershed have also recovered, and how vulnerable this stock is to

another collapse, are difficult to assess in the absence of broad-scale river-level monitoring

(Boxes #2-3). Pervasive declines of chum salmon over the past five years (North Pacific

Anadromous Fish Commission 2023; Connors et al. 2024) have added to the urgent need to

better understand the abundance and distribution of these two species in late-season spawner

surveys.

The hypothesis that monitoring effort reflects economically important fisheries is supported by a

significant positive correlation between the number of monitored populations and commercial

catch at a broad scale for all species (Fig. 5). Overall, there is a strong temporal component to

this relationship, with more recent years having low monitoring effort and catches. The

correlation is the strongest for coho, which likely reflects the decline described above. Chinook

and sockeye show the lowest levels of correlation among species between monitoring effort and

fisheries catch, a pattern that seems to reflect the relatively low monitoring of these species in

the early part of the time series when catches were moderate, and relatively high levels of

monitoring as catch declined in the 1990s and 2000s. These latter increases in monitoring may

reflect international obligations under the Pacific Salmon Treaty (Pacific Salmon Commission

2023).

The relationship between monitoring effort and catch occurs not only among years (Fig. 5) but

also through space, with monitoring often focused on numerically abundant populations. These

abundant populations tend to be "indicator stocks", many of which are subject to catch sharing

arrangements and monitoring obligations dictated by treaties (e.g., Pacific Salmon Commission

2023). As such, these indicator stocks are prioritised for monitoring, and their assessment

consumes the majority of the limited resources available. For example, 14 of the 30 most-

monitored Chinook populations in the Vancouver Island & Mainland Inlets region are "indicator

stocks" reported on by the PSC's Chinook Technical Committee, with an average of 63 years of

data per indicator population. By contrast, the 246 Chinook populations in the region that are not

indicator stocks have an average of 17 years of data, and 69% of them have not been

monitored at all in the most recent decade (2013-2022).

Even within streams, monitoring tends to increase in years with more abundant brood lines. As

a result, pink salmon are often predominantly monitored in either even or odd years (e.g., Fig.

3b-h). In the Fraser region, for example, monitoring of pink salmon occurred exclusively in odd

years, whereas in the nearby Vancouver Island & Mainland Inlets, monitoring was historically

predominant in even years, following the dominant return year (Fig. A3e,f). "Cyclic" sockeye in

the Fraser River, which show marked patterns across four brood lines, tend to have higher

monitoring effort in the higher-abundance "dominant" years, a pattern that has intensified since

the early 2000s (Fig. 3h).

In some regions, patterns in monitoring may reflect a reporting bias rather than an actual

reduction in effort, although it is difficult to disentangle the two if the data are not made

available. For example, no data have been included in NuSEDS for Yukon populations since

2008 (Fig. 3a), yet spawner surveys are reported in other publications (JTC 2024). In other

cases, the apparent disappearance of monitoring may reflect a shift towards aggregate

assessments at more downstream locations. This is the case for Fraser River pink salmon, for

which monitoring of individual spawning populations appears to have stopped in the 1990s (Fig.

3h) when the Pacific Salmon Commission began recording pink salmon abundance using a

hydroacoustic station near the mouth of the Fraser. Although this method provides rapid and

accurate counts of the number of pink salmon returning to the Fraser, and is used to inform

fisheries management, the survival of those fish to their spawning grounds and distribution

throughout the Fraser River basin is now unknown.

A corollary of "monitoring for fisheries" is the dearth of data for less abundant populations.

These monitoring data are, however, essential for understanding patterns of salmon distribution

and diversity, which include both large and small runs. Monitoring only abundant populations

reduces the power to detect abundance shifts, such as shifts in dominance for pink salmon

(Irvine et al. 2014), or declines in biodiversity, such as the erosion of sub-dominant and off-cycle

lines for Fraser sockeye (Ricker 1997), that may affect the sustainability of management

decisions and the resilience of salmon. Furthermore, ground-based salmon counting surveys

provide valuable information beyond abundance counts. They are an opportunity to monitor the

system more broadly, including documenting disease events, river blockages, and high

temperatures. Less-abundant or declining populations have been termed "ghost streams" in

reference to their undetermined status and potential for extirpations to go unrecorded (Price et

al. 2008).

The proportion of CUs with at least one population monitored has also broadly declined since

the mid-1980s across all regions and species (Fig. 6). CUs were only defined after the

implementation of Canada's Wild Salmon Policy in 2005 (Fisheries and Oceans Canada 2005),

which emphasized the importance of monitoring these ecologically and genetically unique

groups of populations. Despite this recognition, monitoring of CUs has declined since 2005,

continuing even after 2018 when DFO renewed its commitment to the policy with the release of

the Wild Salmon Policy Implementation Plan (Fisheries and Oceans Canada 2018).

Retaining observations with zero counts in the NuSEDS data yields similar results overall (Figs.

A4-A6). The main differences pertain to sockeye populations in the Fraser, which accounts for

58% of the zero counts, all recorded after 1998 (Fig. A7). This abrupt reporting of zero counts

dampens the magnitude of fluctuations in monitoring effort after 2000 (Fig. A4), increases

average annual change in monitored population since 1998 (Figure A5), and eliminates the

correlation between monitoring effort and catch (Fig. A6). While these differences do not

undermine our conclusions, they underscore the extent to which the interpretation of results

hinges on the consistency and reliability of how zero counts versus NAs are reported.

Discussion

Spawner abundance monitoring has historically focused on informing commercial fisheries

management, resulting in monitoring efforts being concentrated on economically important

species and numerically abundant populations. Commercial catches of salmon in BC and the

Yukon have collapsed in recent years (Walters et al. 2019; JTC 2024), along with the effort

towards collecting and sharing spawner data that was previously used to inform management of

those fisheries. While well-managed salmon fisheries will continue to be sustainable into the

future, the current magnitude of commercial fisheries is very different than it once was, and

monitoring priorities must shift to reflect the changing seascape of salmon fisheries. As public

interest and funding shifts towards salmon conservation and recovery planning, the limitations of

past, commercial fishery-oriented monitoring objectives are becoming apparent: we currently

lack the data to assess the status of diverse Conservation Units or understand threats to their

survival (Boxes #1-2). In the absence of this information, recovery planning – and assessing the

effectiveness of recovery actions (Box #3) – is challenging.

We recognize that the patterns we observed may be due to a combination of declining

monitoring effort and potential reporting bias. Data take time to be verified and entered into

NuSEDS, creating the possibility of lag that may be misinterpreted as a decline in effort.

However, the long time period over which we observed the declines in monitoring – more than

40 years – suggests that such a lag is not the only factor at play. We did observe some regions

and species where monitoring appears to have declined or completely stopped but where we

know that spawner surveys have continued and are reported elsewhere. For example, in the

Yukon and Transboundary regions, many spawner surveys are reported on by the Technical

Committees tasked with informing salmon management under the Pacific Salmon Treaty

(Transboundary Technical Committee 2022; JTC 2024), but the very same surveys are

inconsistently updated in NuSEDS (Peacock et al. *in press*). Regardless of whether data

continue to be collected, their usefulness to research and broad-scale prioritization and planning

is undermined if they are not compiled and included in NuSEDS. Access to public data should

not be the bottleneck in these processes.

As climate change pushes salmon to adapt, keeping track of changes in salmon distribution and

diversity through spawner surveys has never been more relevant. Monitoring programs that rely

on a handful of key indicator stocks may miss potential changes in diversity, which underpins

the resilience of salmon social-ecological systems (Schindler et al. 2010; Nesbitt and Moore

2016). Numerically abundant indicator populations may persist as surrounding (unmonitored)

populations decline, and aggregate stocks may continue to have large returns even as the

diversity of their components is undermined (Price et al. 2021). This can lead to apparently

healthy populations, until a tipping point is reached or a catastrophic event threatens the viability

of the aggregate stock. For example, preceding the collapse of Atlantic cod fisheries in eastern

Canada, aggregate offshore surveys continued to point to healthy cod stocks, but local

extirpations were noted by inshore fishers – proverbial canaries in the coal mine (Hutchinson

2008). Climate changes are now exacerbating other pressures on salmon, but there is a lack of

data to understand the adaptive capacity – or fragility – of salmon populations.

Here, we provide recommendations with the goal to encourage and enable strategic

investments in spawner abundance monitoring that can support informed, evidence-based

decisions about salmon conservation and recovery.

432   Recommendations

We, the authors, are non-Indigenous researchers with extensive technical experience working

with large salmon datasets to serve the scientific objectives of a broad range of groups including

academic researchers, non-governmental organisations, federal and provincial governments,

First Nations, and other Indigenous organizations. We are best positioned to make

recommendations that would improve the technical utility of salmon abundance data generally

and NuSEDS in particular. We also recognize that data (and their handling) are intertwined with

the decisions they inform, and we draw on our experience and on a growing body of literature

on Indigenous Data Sovereignty to offer suggestions intended to be respectful of Indigenous

rights.

Solutions to the evident decline in monitoring will involve investment in boots on the ground, but

the burden of enormous costs can be mediated by strategic investments in collecting data,

employing new technologies, and making improvements to how data are processed and shared.

Recommendation #1: Clarify the objectives of spawner monitoring to include assessment

of salmon diversity, for the purpose of maintaining it. We have shown that, historically,

spawner survey efforts have mirrored commercial catches through time and across populations.

As catches have declined to zero in some regions, this approach has undermined our ability to

assess salmon status, understand threats, and implement effective recovery plans. Clarifying

monitoring objectives to include assessing salmon biodiversity would help inform conservation

and recovery efforts to maintain that diversity, while promoting sustainable management of

modern-day fisheries – balancing local and regional objectives, First Nations rights, and both

recreational and commercial interests, now and in the future.

Annual spawner surveys of all ~2,300 locations listed in NuSEDS (Table 1) may not be feasible,

but strategic monitoring programs can be designed to meet clearly stated objectives with

minimal costs, making the most of limited resources. Spawner monitoring that is focused on

assessing the status of Conservation Units, as outlined in the Wild Salmon Policy, would

provide a starting point for assessing and conserving salmon diversity that is necessary to

support sustainable fisheries and ensure salmon resilience in the face of environmental change.

With almost 400 individual CUs (Baxter and Hamilton 2024), many of which are remote and

logistically challenging to monitor, annual monitoring may not be possible. When prioritisation

among CUs is necessary, monitoring could aim to distribute effort across all salmon-bearing

regions rather than focus on the regions of highest human population density.

Some CUs encompass hundreds of spawning populations and thus monitoring a single site is

likely insufficient. In such cases, the total number of populations of interest may exceed the

capacity for monitoring, but techniques such as "rotating panel" monitoring designs (Peacock

and Holt 2012) can be employed to maximize the information obtained with limited resources.

Previous research has shown that detecting contractions in the spatial distributions of spawners

is efficiently achieved using rotating panel designs where some indicator populations are

assessed annually while other populations are assessed on a rotating basis (Peacock and Holt

2012).

Recommendation #2: Provide sufficient resources to spawner monitoring programs to

meet stated objectives. The Wild Salmon Policy set out a forward-looking roadmap for the

conservation of wild Pacific salmon that included monitoring and assessment of Conservation

Units, but the challenge of following that roadmap has arguably not been met with sufficient

resources. Ironically, there have recently been historic investments in salmon through the

Pacific Salmon Strategy Initiative (Government of Canada 2021) and BC Salmon Restoration

and Innovation Fund (Government of Canada et al. 2019). We argue that these investments,

while unprecedented in their total amount, have not led to the stable long-term funding and

coordinated approach that rebuilding salmon monitoring in Pacific Canada requires.

Investment to reinvigorate spawner monitoring across BC and the Yukon is a common sense

approach to salmon conservation and management. It is also a practical opportunity to create

local jobs in the many rural coastal and inland communities working to expand and diversify

labour opportunities. Stream-walking jobs to monitor spawning salmon are community based,

provide connection between people and place, and have the potential to be purposeful,

meaningful occupations for people in Pacific Canada. Reviving salmon counting will likely

involve reinvesting in DFO-led stock assessment programs, but in many salmon watersheds the

practical solution may involve supporting local communities and First Nations already

stewarding watersheds and salmon. Many of these community-based salmon counters are

funded through DFO contracts that have shrunk in amount and scope year-over-year (e.g., Billy

Proctor, *personal communication*, 2022). Nonetheless, these groups often have ample expertise

and enthusiasm, and sufficient investment can enable them to count more populations.

Recommendation #3: Invest in new technologies that can improve monitoring efficiency.

The rapid advancement of computer analysis and remote sensing has significant potential to

improve the quality of data and reduce costs. Historically, new monitoring technologies have

focused on providing more in-depth knowledge about survival of particular stocks, rather than

improving broad-scale coverage of monitoring. For example, coded wire tags, pit tags, and

acoustic tags provide detailed information on ocean survival and movements but are only

deployed on a limited number of stocks, requiring strong assumptions (e.g. about the

representativeness of coded wire tag stocks) to extrapolate findings to broader scales.

Emerging technologies, on the other hand, may make monitoring more efficient, thereby

allowing for increased coverage. The application of computer vision and deep learning to

process salmon sonar and video data, collected at in-river weirs, can reduce the need for

manual review of hundreds of hours of footage, with potential to reduce costs significantly

(Atlas et al. 2023). Uncrewed aerial vehicles (UAVs), commonly known as drones, have been

shown – in amenable systems – to provide reliable indices of salmon spawner abundance for

relatively low cost (Ponsioen et al. 2023). Environmental DNA, or eDNA, is another emerging

technology that may be suitable for detecting, and potentially estimating abundance of,

salmonids (Levi et al. 2019).

Although these technologies are in their infancy, and cost savings may not be immediate,

investing in their development and application in Canada could speed up broad-scale

application and its associated benefits. To ensure salmon abundance data maintain their value

as long time series, it will be critical that new technologies are applied together with existing

monitoring approaches to validate and calibrate between methods.

Recommendation #4: Compile and maintain high-quality spawner data across

government divisions and organisations.

In some cases, monitoring gaps may be due to a failure to integrate existing spawner

abundance data into NuSEDS, a process which is slow or inconsistent across regions. NuSEDS

represents the most comprehensive dataset on salmon abundance, and yet we found many

instances where data were not contributed to NuSEDS despite being published by DFO in other

reports or made available on request. We mentioned examples in the Yukon and

Transboundary regions above, but the monitoring gaps for Columbia sockeye and Chinook

salmon (Fig. 3i) can also be filled by looking at alternative sources (Hyatt and Stockwell 2019;

Matylewich et al. 2019). For Fraser chum salmon the most recent data in NuSEDS are from

2020, three years behind collection, and the last year of data currently available for Harrison

sockeye salmon (a major sockeye population of the Fraser watershed) is 2015, almost 10 years

ago. This lack of data centralisation limits the power and application of the data to improve our

understanding and timely management of Pacific salmon (e.g. Boxes #1-3). In the context of

this study, it also hinders our ability to document putative declines in monitoring effort. Following

the collapse of Atlantic cod and declines in Pacific salmon, several noted experts recommended

that all scientific information on stock abundances be made public as soon as it is presented to

DFO (Hutchings et al. 1997). Even 'interim' or 'provisional' data are valuable for timely detection

of conservation risks, and should be made available. Any errors could be corrected in future

versions of the data. As an excellent example of this proactive approach, the Pacific Salmon

Commission Secretariat releases 'in-season' estimates of Fraser sockeye abundance that are

retroactively finalized and re-released pending estimates of pre-spawn mortality (Pacific Salmon

Commission 2024). Institutions responsible for publicly funded monitoring are ultimately

accountable to ensure that resulting data are open and accessible in a timely manner.

In our analyses, we found numerous errors in NuSEDS that needed correction, including

duplicate entries and mis-assigned population identifiers (undermining the efficacy of the slow-

release approach discussed in the last paragraph). Data anomalies also included inconsistent

use of zero and "NA" values, complicating efforts to discern whether monitoring occurred in

these cases. Inconsistent use of zeroes and NAs hampers even simple investigations of

monitoring efforts such as our analysis. Although many of these errors were easily corrected

once identified, there seems to be little effort dedicated to improving data quality across the

dataset. At a minimum, a transparent forum for documenting data errors (and ideally a

mechanism to correct those errors!) is needed. As monitoring becomes increasingly distributed

across DFO, First Nations, and non-governmental organisations (e.g., academic researchers,

community groups, etc.), integrating data into NuSEDS will require increased investment in

capacity to review and clean data to respect investment in monitoring. Being more willing to

share "preliminary" data, embracing crowd-source error checking, instituting a streamlined

mechanism to correct identified errors, and implementing modern version control could help to

moderate the investment required.

Recommendation #5: Work to develop data sharing protocols that facilitate data use

while respecting Indigenous Data Sovereignty.

FAIR data are Findable, Accessible, Interoperable, and Reusable - a set of principles that has

been lauded by the scientific community for almost a decade (Wilkinson et al. 2016). More

recently, to address concerns around Indigenous Data Sovereignty, the CARE principles for

Indigenous Data Governance have also been developed. CARE stands for data that are used

for **collective** benefit, where Indigenous People maintain their **authority** to control their data,

non-Indigenous institutions and individuals share a **responsibility** to engage respectfully, and

data are applied following Indigenous Peoples' **ethics** (Carroll et al. 2021). These two sets of

principles can be complementary, and given that salmon are core to Indigenous livelihoods and

cultures and salmon data are often collected by First Nations staff or members, both FAIR and

CARE principles are applicable here (Carroll et al. 2021).

Facilitating access to salmon data requires understanding the hesitations and concerns of the

data owners and custodians and this must be approached contextually. Fear of misuse or

misinterpretation of data is an oft-cited explanation from DFO for limiting access to data, but

ensuring that data are well documented with appropriate caveats and limitations is a logical

antidote that is supported by existing government policy (Fisheries and Oceans Canada 2013).

The Pacific Salmon Commission Fraser River Panel's online tools for viewing and downloading

both in-season and annual data on Fraser pink and sockeye abundance and timing (Pacific

Salmon Commission 2024) demonstrate that timely, transparent, and appropriately caveated

sharing of data is entirely feasible given appropriate resourcing. Rather than lead to

misunderstanding, publicly distributed data often provide common baseline information upon

which complex decision making discussions can be based.

Conclusion

Salmon are a foundational species in Pacific Canada, and counting them each year as they return home to spawn is a cornerstone of assessing and tracking their status, managing local and regional fisheries, estimating the impact of myriad stressors, and evaluating recovery efforts. With the ongoing decline of monitoring salmon populations, both realised and potential knowledge gained from decades of counting salmon is eroding. Until now, conventional monitoring and management by DFO has focused on managing commercial harvest. By available public records, the proportion of salmon populations counted over the past decade (at the scale of individual populations spawning in their respective rivers/streams/lakes *or* the coarser scale of Conservation Units) is at the lowest it has been since the growth of counting programs in the 1950s. Pervasive salmon declines and the collapse of commercial salmon fishing demand that we shift monitoring priorities to support the admirable blueprint set forth by the Wild Salmon Policy. As salmon distributions appear to be contracting, with pervasive declines at coarse scales (Connors et al. 2024), there is a need for *increased* monitoring of at-risk populations to avoid the undocumented erosion of salmon diversity. Revitalizing salmon spawner abundance monitoring – through redefined priorities, focused investments in salmon communities, and robust data practices – has the potential to advance shared goals and benefit both salmon themselves and the people and ecosystems that depend on them.

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614 Competing interests

615   The authors declare no competing interests.

616 Author contributions

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Data curation – BC, SP

Formal analysis – BC, SP

Funding acquisition – KC, EA

Investigation – EA, BC, EH, AB, SP

Methodology – BC, EA, SP, EH, AB

Project administration – EA

Resources – EA, KC

Software – BC, SP, EA

Supervision – SP, KC

Validation – SP, BC

Visualization – BC, EA, SP

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Data availability statement

Cleaned spawner survey data are available at https://zenodo.org/records/14194638. Additional data and R code to reproduce all our analyses for this submission are archived at https://zenodo.org/records/14248905.

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Figure 1. Map of Pacific Canada showing the nine broad-scale regions (colours) and 2,300 sites (points) where spawner monitoring is recorded in NuSEDS. Open circles reflect sites which were not monitored at least once within the 2013-2022 decade.

Figure 2. A timeline of the number of populations for which spawner counts appear in NuSEDS (blue) and total commercial salmon catch (brown) in Pacific Canada, highlighting notable events pertaining to abundance monitoring. A population is a grouping of salmon that can return to breed in the same spawning location, usually a stream or river (but sometimes a smaller geographic area). The blue line depicts the number of populations monitored over time (as inferred from the number of records in NuSED, see Methods for full details). The brown line depicts total commercial salmon fishery catch among five salmon species over time as reported by the North Pacific Anadromous Fish Commission (NPAFC 2024). This figure focuses specifically on contemporary salmon abundance monitoring as curated in NuSEDs but many of these populations have been monitored, in one way or another, for thousands of years.

Figure 3. The annual number of salmon populations monitored in NuSEDS broken down by region (panels a through i) and by species (Chinook, chum, coho, pink, and sockeye).

Figure 4. The average annual change in populations monitored since 1986 as estimated via linear regression for each species and region. Dots and horizontal bars represent the slopes and their 95% confidence intervals, respectively.

Figure 5. Correlation between the number of populations monitored and the number of fish commercially caught since 1960 per species (n = 62). Also show is the Spearman correlation coefficient (ρ) and associated P values (*: P < 0.05; **: P < 0.01; ***: P < 0.001). The correlation is calculated since 1960 in order to show the synchrony between the decline in survey and fishing efforts.

Figure 6. Annual proportion of conservation units (CUs) with at least one population monitored in NuSEDS.

Table 1. Number of Conservation Units (CUs), populations, and sites present in the NuSEDS data in each region after cleaning. Sites are unique locations where spawners from one or more CUs may be counted. Populations are unique combinations of CUs and sites.

Region	Number of CUs	Number of populations	Number of sites
Yukon	15	60	54
Transboundary	22	64	37
Haida Gwaii	28	748	233
Nass	20	312	90
Skeena	53	772	260
Central Coast	110	1621	392
Vancouver Island & Mainland Inlets	83	2247	656
Fraser	56	940	577
Columbia	2	2	1
Total	389	6,766	2,300

Appendix: Monitoring for fisheries or for fish? Declines in monitoring of salmon spawners continue despite a conservation crisis

Emma M. Atkinson, Bruno S. Carturan, Clare P. Atkinson, Andrew W. Bateman, Katrina Connors, Eric Hertz, Stephanie J. Peacock

Appendix figures

Figure A1. Annual number of salmon stream populations monitored over time in NuSEDS.

11   **Figure A2.** Annual proportion of salmon stream populations assessed over time in NuSEDS.

Figure A3. Annual number of pink salmon populations in odd and even years monitored in

NuSEDS and broken down by region (panels a through f).

16   **Figure A4.** Annual number of salmon populations monitored in NuSEDS broken down by region

17   (panels a through i) and by species (Chinook, chum, coho, pink, and sockeye), including

18   observations recorded as zero counts in the NuSEDS dataset.

Figure A5. The average annual change in populations monitored since 1986 as estimated via

linear regression for each species and region, including observations recorded as zero counts in

the NuSEDS dataset. Dots and horizontal bars represent the slopes and their 95% confidence

intervals, respectively.

Figure A6. Correlation between the number of populations monitored and the number of fish

commercially caught since 1960 per species (n = 62), including observations recorded as zero

counts in the NuSEDS dataset. Also show is the Spearman correlation coefficient (ρ) and

associated P values (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). The correlation is calculated since

1960 in order to show the synchrony between the decline in survey and fishing efforts.

Year

Figure A7. Pattern in zero counts (MAX_ESTIMATE) for Fraser sockeye populations (n = 335)

in the cleaned NuSEDS data before filtering out zeros.

NuSEDS Data Processing

The R script containing the code for the NuSEDS data processing procedure described below is

available in a Zenodo repository (https://zenodo.org/records/14194638).

Cleaning Procedure

The objective of the procedure is to obtain the yearly counts of each salmon population in their

respective sampling site and associate these populations to their corresponding conservation

unit (CU). The NuSEDS data is separated into two datasets. The **all_areas_nuseds** dataset

contains the observed yearly counts (related fields: NATURAL_ADULT_SPAWNERS,

NATURAL_SPAWNERS_TOTAL, etc.) for each population (related fields: SPECIES, POP_ID,

POPULATION) in their respective site (related fields: AREA, GFE_ID, WATERBODY,

GAZETTED_NAME, etc.), along with the associated methods used (related fields:

ESTIMATE_METHOD, ESTIMATE_CLASSIFICATION, ENUMERATION_METHODS).

We first define the unique yearly count field **MAX_ESTIMATE** for each population as the

maximum value of the count-related fields in all_areas_nuseds, i.e.,

NATURAL_ADULT_SPAWNERS, NATURAL_JACK_SPAWNERS,

NATURAL_SPAWNERS_TOTAL, ADULT_BROODSTOCK_REMOVALS,

JACK_BROODSTOCK_REMOVALS, TOTAL_BROODSTOCK_REMOVALS,

OTHER_REMOVALS and TOTAL_RETURN_TO_RIVER. MAX_ESTIMATE is the only count-

related field we use in the rest of the procedure. A population's MAX_ESTIMATE data points is

referred to as its "**time series**".

The second dataset, **conservation_unit_system_sites,** links each population (related fields:

POP_ID, population) to their respective CU (related fields: CU_NAME, FULL_CU_IN,

CU_LONGT, CU_LAT, etc.) and site (related fields: GFE_ID, SYSTEM_SITE, X_LONGT,

Y_LAT). Ideally, attributing each time series in all_areas_nuseds its corresponding CU and

location's coordinates in conservation_unit_system_sites would simply consist in merging the

two datasets using the population and location identification number POP_ID and GFE_ID,

respectively. Unfortunately, numerous time series are **problematic**, which occurs when:

-   A time series is present in all_areas_nuseds but its POP_ID and GFE_ID association is

absent in conservation_unit_system_sites.

-   Multiple time series of a same population (i.e. same POP_ID) are observed in multiple

locations (i.e. different GFE_IDs), which should not occur because a POP_ID should be

defined for a unique location.

The observation of problematic time series revealed inconsistencies such as missing,

duplicated, and conflicting data points (i.e. different counts in a same year). In order to rescue

as much data as possible, we attempted to solve these issues by either (*i*) **deleting**, (*ii*)

combining or (*iii*) **summing** a problematic series to an **alternative series** (i.e., a time series

present in all_areas_nuseds that shares either the same POP_ID or GFE_ID and species), or

(*iv*) **creating** a new reference to the time series in conservation_unit_system_sites. In each

case, we used all the information available in the different fields and made assumptions based

on our professional judgment. Below are more details about the different interventions applied to

problematic time series:

- We **deleted** a problematic time series (or a portion of it) from all_areas_nuseds when (1)

it was a duplicate of another time series, (2) it had less than four data points and was not

spotted during the cleaning process, or (3) the lack of information prevented to combine

or merge it to an alternative series or to create a new series in

conservation_unit_system_sites (e.g. if run timing was unknown).

- We **combined** a problematic time series with an alternative series when data points

were not in conflict (i.e. different value for a same year) and the information available in

the other fields was not prescriptive (e.g. the population belong to the same CU, the

locations have similar names or spatial coordinates, the runtimings are not different).

- We **summed** a problematic time series to an alternative series having different POP_ID

but same GFE_ID and CU_NAME and with conflicting data points.

- We **created** a new reference of the problematic time series in

conservation_unit_system_sites (i.e. a new row with a unique POP_ID - GFE_ID

combination) when it could not be deleted, merged or combined to an alternative series.

The diverse and idiosyncratic nature of these problematic cases prevented the establishment of

a systematic and simple cleaning process. Many of these cases were resolved individually by

observing and comparing time series and accounting for the information available. We

proceeded in consecutive steps in which we applied the different types of intervention

mentioned above, either after visually inspecting individual time series or by applying a

systematic procedure. These steps are detailed below:

1. Remove the time series (i.e. unique POP_ID - GFE_ID associations) with only NAs

values for MAX_ESTIMATE in all_areas_nuseds (n = 102845; 25%)

2. Assess all the references to time series present in conservation_unit_system_sites but

absent in all_areas_nuseds (n = 259)

112   2.2. Cases with presence of alternative series in NUSEDS (n = 4)

113   –   Each case was assessed visually.

114   2.3. Cases with no alternative time series in all_areas_nuseds (n = 254)

115   –   The rows corresponding to these time series are removed from

116   conservation_unit_system_sites.

117   2.4. Case with multiple GFE_ID for a single POP_ID (n = 1)

118   –   The problematic time series was simply removed from

119   conservation_unit_system_sites.

121   3. Case of time series with a same POP_ID but different GFE_IDs in

122   conservation_unit_system_sites and present in all_areas_nuseds (n = 1).

123   –   Two time series had the same POP_ID but different GFE_ID. Both time series

124   were kept because they are not compatible and have many and recent data

125   points.

127   4. Assess all the time series present in all_areas_nuseds but absent in

128   conservation_unit_system_sites (n = 171)

129   4.1. Remove series with < 4 data points (n = 94)

130   4.2. Cases of series with alternative POP_ID and no alternative GFE_ID (n = 6)

131   –   Each case was assessed visually.

132   4.3. Cases of series with alternative GFE_ID with or without alternative POP_ID (n = 34)

133   –   Problematic series with the same POP_IDs (e.g. series with POP_ID = 47925

134   and GFE_ID = 15, 31516 ad 31740, respectively) having the same alternative

135   series (e.g. series with POP_ID = 47925 and GFE_ID = 14) are assessed

136   together.

137   4.4. Cases with no alternative series (n = 37)

138   –   These series were removed from all_areas_nuseds.

5. Merge all_areas_nuseds and conservation_unit_system_sites.

6. Assess time series with a same CU_NAME and GFE_ID (n = 62).

-   Case 1: there is only one data point in one of the series; if it is compatible, then merge to

the alternative series, otherwise remove it from all_areas_nuseds.

-   Case 2: One of the series is 100% duplicated with the other one: to remove from

all_areas_nuseds.

-   Case 3: the rest of the series are merged; adding the values when data points are in

conflict.

Finally we merged all_area_nuseds and conservation_unit_system_sites using the fields

POP_ID and GFE_ID.

152   Attribution of the geographic regions to CUs

153   We matched the CUs in the cleaned NuSEDS data with the CUs defined in the Pacific Salmon

154   Explorer, which are associated with a given region (PSE; https://salmonexplorer.ca). We used

155   the fields POP_ID, FULL_CU_IN and CU_NAME. We removed the data for the 22 CU_NAME

156   values we could not match to any CUs in the PSE, corresponding to 82 populations and 1102

157   data points.

158   Managing NA and zero counts

159   For the analysis presented in the main text, we excluded data points where MAX_ESTIMATE =

160   NA (n = 152,992) or 0 (n = 2,992). In contrast, the analysis presented here excludes only those

161   data points with MAX_ESTIMATE = NA.