Evaluating the consequences of common assumptions in run reconstructions on Pacific-salmon biological status assessments

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Abstract

Under Canada's Wild Salmon Policy, biological status of salmon Conservation Units (CUs) is determined by expert consensus based on quantitative metrics, considering the associated assumptions, uncertainties, and risks. This process takes time and resources and has been completed for <10% of CUs. Data-driven approaches that rely on a standardized subset of metrics can provide transparent, timely, and accessible assessments on those metrics, but lack rigorous review by experts on a CU-by-CU basis. Thus, it is important to understand how status outcomes from data-driven assessments may be biased by underlying assumptions. We used a stochastic simulation model to quantify how common assumptions in "run reconstructions" around imputing missing spawner data, expanding observed spawner abundance to CUs, assigning catch to CUs, and quantifying age-at-return biased assessments. We found that data-driven assessments based on spawner abundances are robust to most common assumptions in run reconstructions, but overestimating catch to CUs may increase rates of status misclassification. Further research is needed to understand the implications for more complex run-reconstruction models that incorporate spatial and temporal variability in return timing.

Introduction

Timely and effective management of fish and wildlife relies on accurate information about the current biological status of populations. However, complete information on abundance, trends, and demographic parameters is rarely available for those populations or species that need to be assessed. Therefore, assumptions have to be made when assessing status. Evaluating the impact of assumptions on resulting status outcomes is critical to understanding the potential biases, uncertainty, and limitations of status assessments (Chen et al. 2003; Wetzel and Punt 2011).

Wild Salmon Policy – Monitoring and Assessing Biological Status

Pacific salmon are a highly exploited group of species and many populations have experienced declines in recent decades due to overfishing, changing ocean conditions, and freshwater habitat degradation (e.g., COSEWIC 2016, 2017; Brown et al. 2019). The management of Pacific salmon is challenging, in part due to the rich ecological, genetic, and life-history diversity within species that must be conserved and considered when devising fisheries management strategies (Gustafson et al. 2007). Canada's Wild Salmon Policy (WSP) provides a framework for maintaining salmon biodiversity through the preservation of Conservation Units (CUs) – groups of wild salmon that, if lost, are unlikely to recolonize within an acceptable timeframe (Fisheries and Oceans Canada 2005). Standardized monitoring and assessment of the biological status of CUs is a critical element of the WSP (Fisheries and Oceans Canada 2005, 2018).

Status assessments under the WSP - called integrated status assessments - use expert-driven processes to combine a suite of metrics into an overall status assessment given uncertainties in each metric (e.g., DFO 2015, 2016, 2018a). Although these integrated status assessments are thorough and ensure the unique context of each CU and associated data are taken into consideration, the required resources and time (typically 1-3 years) have limited their broad application to all 462 Pacific salmon CUs. Only 9% Pacific salmon CUs have had their biological status assessed through an integrated status assessment since the WSP was released nearly 15 years ago, and reports are often already 2-4 years out of date when they are released (DFO 2019). Given the multiple pressures facing Pacific salmon and the declining status of many populations, there is an urgent need for more timely and transparent measures of biological status that can be broadly applied to salmon CUs to inform conservation and management decisions when up-to-date integrated status assessments are not available.

Using robust, standardized, and objective measures to quantify the biological status of CUs is critical for supporting the implementation of the WSP. Furthermore, the outcomes of status assessments are more impactful if they are broadly, and freely, available to the public through open-access platforms. In BC, a novel open-access data visualization platform called the Pacific Salmon Explorer (see www.salmonexplorer.ca) has been developed by the Pacific Salmon Foundation to provide timely, data-driven assessments of the current status of Pacific salmon CUs on a subset of metrics. This approach has many benefits, but the trade-off is that a thorough expert review of the assumptions and limitations unique to the assessment of each CU, as is undertaken in integrated status assessments, is not always possible. We refer to biological status assessments that do not undergo review by experts to interpret and combine different indicators as “data-driven” status assessments. Similar data-driven approaches are also applied by DFO and stakeholders in other contexts (e.g., local management, Marine Stewardship Council certification (www.msc.org), and for the Pacific Salmon Treaty (PSC 2019)).

Data-driven biological status assessments may be prone to biases from compounding assumptions around the imputation of data, which is of concern given that they are not subject to the same level of scrutiny as integrated status assessments. Here, we aim to explicitly quantify potential biases in data-driven biological status assessments due to common assumptions in reconstructing salmon abundance, relative to the uncertainty inherent to ecological systems.

Metrics and benchmarks for assessing biological status

Under the WSP’s biological status assessment framework, quantifiable metrics are calculated from available data and compared against biological reference points, or “benchmarks”, to arrive at a status outcome of red, amber, or green (Fisheries and Oceans Canada 2005; Figure 1). A red status indicates that a CU has low spawner abundance and/or reduced spatial distribution and management intervention is required to avoid extirpation. A green status indicates that the CU is able to sustain maximum annual catch under existing environmental conditions. The specific benchmarks delineating these status zones must consider uncertainties in metrics and risk tolerance, and depend on the biological characteristics of the CU being assessed.

Multiple metrics of biological status have been proposed under the WSP. These metrics fall under four broad classes of indicators: current spawner abundance, trends in abundance over time, distribution of spawners, and fishing mortality (Holt et al. 2009). The PSE has focused on biological status assessments based on a single indicator class, current spawner abundance, using two types of benchmarks that have been widely applied: spawner abundances associated with maximum sustainable yield, derived from stock-recruitment analyses (Holt et al. 2009), and percentiles of historical spawner abundance (Connors et al. 2013, 2018, 2019; Holt et al. 2018; Figure 1).

Common assumptions in estimating biological status

Pacific salmon are anadromous and semelparous, returning from ocean rearing grounds to spawn in freshwater before dying, and are typically vulnerable to fisheries upon their return to coastal waters. Data imputation and expansion are necessary to assess and manage Pacific salmon and many other fisheries (Chen et al. 2003; Wetzel and Punt 2011). The data required to assess biological status of Pacific salmon can include annual estimates of the number of returning adult salmon to individual rivers, fisheries catch or harvest rates, and the age composition of returning salmon (needed for stock-recruitment analyses). Often, these data are incomplete and require imputation (e.g., Figure 2). Furthermore, the calculation of harvest rates (i.e., the proportion of the total return caught in fisheries) requires expanding estimates of observed spawner abundance to account for observer efficiency and spawning sites that may not be monitored for spawners. “Run reconstructions” have been undertaken for salmon CUs to expand spawner abundances to the entire CU and estimate recruitment (Cave and Gazey

1994; English et al. 2007, 2016, 2018). The exact procedure undertaken depends on the life-history traits and available data for each CU, and can include complexities such as spatial and temporal variability in returns among spawning populations.

Investigating the impact of assumptions on status outcomes (and therefore management actions) is essential to understand potential biases and minimize the risk of overharvesting or unnecessarily constraining fisheries. The combined influence of assumptions in run reconstruction models on our ability to accurately assess the status of CUs is unknown. In this study, we use a simulation approach to quantify the consequences of common assumptions in simple run-reconstruction models that we considered most likely to affect status assessments. As a case study, we tailored our simulation model to represent a generic chum salmon CU from the central coast of British Columbia (Figure 3) because these CUs have recently been assessed using a data-driven approach (Connors et al. 2018) and have a relatively simple run-reconstruction model that does not include run timing. Furthermore, there are conservation concerns for both north and central coast chum salmon, which have not recovered despite significant reductions in harvest rates over the past two decades (DFO 2018b). Thus, central coast chum salmon offer a useful case study for an initial investigation of basic assumptions underlying biological status assessments. However, our simulation model is flexible enough that it can accommodate different species and life-history traits of Pacific salmon. We further explore a broad range of biological (e.g., trends in capacity) and management (e.g., monitoring coverage) scenarios to yield more general insight into the circumstances under which assumptions may bias status assessments. Our results suggest that efforts to provide timely and objective data-driven assessments of biological status are robust to most underlying assumptions, although improving estimates of CU-level harvest rates would reduce potential misclassifications of status.

Methods

Benchmark calculations and assumptions

In this study, we consider two types of benchmarks for the spawner-abundance metric (Figure 1) that have been frequently applied to determine biological status of Pacific salmon CUs, including in the Pacific Salmon Explorer (PSE; Connors et al. 2013, 2018, 2019). The first type of benchmark is associated with maximum sustainable yield, derived from a stock-recruitment relationship (Figure 2b). An upper stock-recruitment (SR) benchmark of 80% of the spawner abundance that is projected to maintain long-term maximum yield, or 80% S_{MSY}, has been recommended by Holt et al. (Holt et al. 2009, 2018) and will be applied to future assessments in the PSE (previous PSE assessments have applied $\mathrm{S}_{\mathrm{MSY}}$; Connors et al. 2018, 2019). S_{MSY} can be calculated explicitly from the productivity and density-dependence parameters of the Ricker spawner recruitment relationship (Scheuerell 2016). Multiple lower benchmarks have been suggested (Holt et al. 2009, 2018), and here we focus on a lower benchmark of the spawner abundance that leads to S_{MSY} in one generation in the absence of fishing mortality, or S_{GEN} (Korman and English 2013; DFO 2015) as applied in the PSE.

The second type of benchmarks we considered, referred to as historical spawners (HS), also called percentile benchmarks (Clark et al. 2014; Holt and Folkes 2015; Holt et al. 2018), are based on historical spawner abundance (Figure 2a). The upper and lower benchmarks we considered were the 50th and 25th percentiles of historical spawner abundance, respectively. The calculation of these benchmarks has fewer data requirements, as the stock-recruitment relationship need not be estimated (i.e. there is no need for age-at-return or harvest data). As such, the HS benchmarks can be applied to data-limited CUs for which spawner data are patchy or age and harvest data are not available.

Here, we focus on a basic run-reconstruction model and associated assumptions that are commonly made when assessing spawner abundance against the benchmarks above (Figure 2c; Table 1). At a minimum, in order to apply HS benchmarks, a time series of total spawner abundance at the CU scale is required. Conservation Units are typically comprised of multiple spawning populations that may or may not be monitored in any given year. Spawning populations in individual streams (henceforth “populations”) may exhibit unique dynamics as their productivity is (in part) limited by density-dependent processes in freshwater. A simple sum of the observed spawner abundance within a CU may be misleading if the same populations are not monitored consistently. On the north and central coast, monitored populations have been designated as either “indicator streams” or “non-indicator streams”, with indicator streams being prioritized for monitoring and thus having more continuous and reliable spawner estimates (English 2016). In addition, there may be populations that have never been monitored and for which spawner abundance is unknown. To reconstruct spawner abundance to the CU, three “Expansion Factors” have been applied to account for (1) spawners returning to indicator streams that are not monitored in a given year, (2) spawners returning to non-indicator streams, and (3) observation efficiency and populations that are never monitored (Table 1).

The application of stock-recruitment benchmarks also requires timeseries of the total number of salmon returning to the CU, including those caught in fisheries and those that make it to spawn but are not counted, to reconstruct recruitment. The number of returning salmon in a CU that are caught in fisheries is estimated based on the catch statistics for Pacific Fisheries Management Areas (PFMAs) adjacent to the geographic location of the CU (Figure 3). It is assumed that salmon caught in an PFMA were destined to spawn in streams that empty into that PFMA, although there is the potential for bias in that fish may be caught while migrating through the PFMA or fish destined for streams in the focal PFMA may be caught in other PFMAs. Furthermore, in most cases, there is not a perfect spatial correspondence between PFMAs and CUs (Figure 3). Streams in multiple CUs may flow into a single PFMA, which is common for small CUs, such as with sockeye salmon (Holtby and Ciruna 2007). In the simplest case, the catch from that PFMA may be assigned to CUs based on the relative spawner abundance to each CU. However, differences in run-timing among CUs may complicate the assignment of catch and necessitate more complex run-reconstruction models. A single CU may also be comprised of populations that are caught in multiple PFMAs, particularly for species with large CUs such as pink and chum salmon (Figure 3), in which case an average harvest rate across PFMAs may be applied. The impact of observation bias in the catch assigned to each CU on status assessments in unknown and is a focal aspect of this study (see Sensitivity analyses, below).

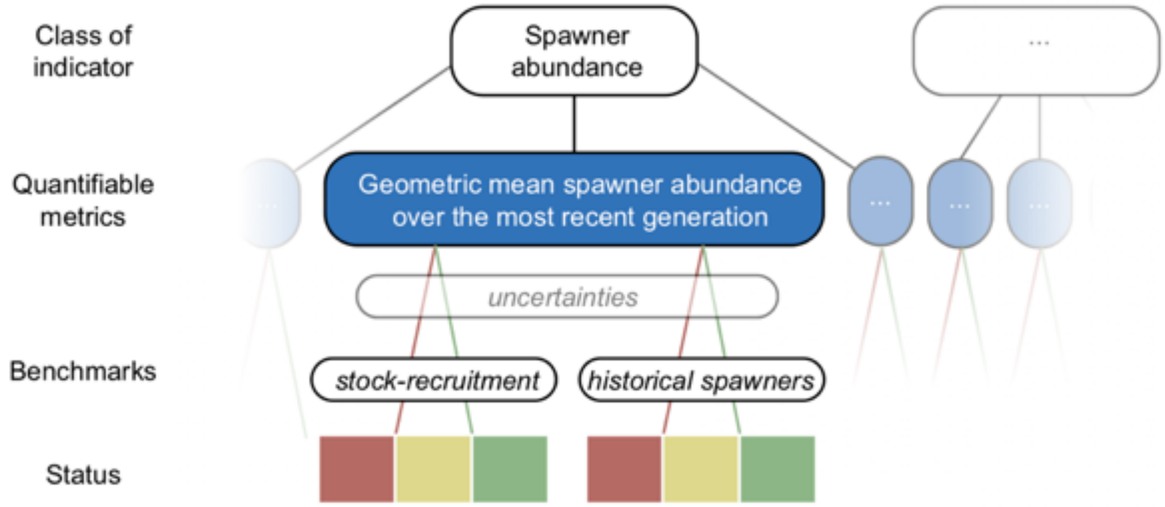


Figure 1. Illustration of the WSP status assessment framework (adapted from Holt et al. 2009). We focused on the geometric mean spawner abundance (metric, blue) under the spawner abundance indicator. This metric was assessed against two types of benchmarks: stock-recruitment and historical spawners (see Figure 2). Faded boxes represent other types of metrics and indicators that may be included in integrated status assessments but were beyond the scope of what we considered.

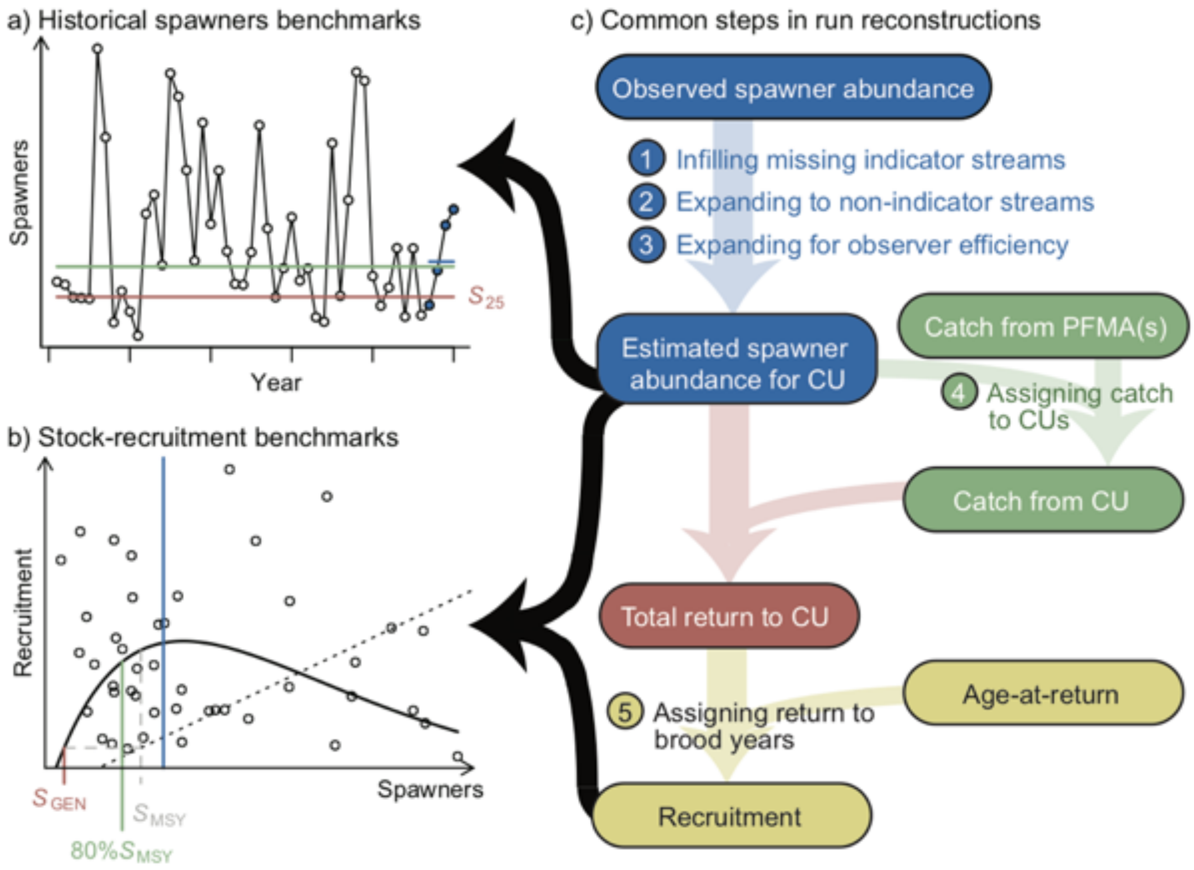


Figure 2. a) Historical spawners benchmarks are the 50th (horizontal green line) and 25th (horizontal red line) percentiles of historical spawner abundance (points). The current spawner abundance is calculated as the geometric mean spawner abundance over the most recent generation (4 years, blue points and line). b) Stock-recruitment benchmarks are based on the shape of the Ricker stock-recruitment relationship (solid line) fit to data on spawner abundance (x-axis) and corresponding recruitment (catch + escapement, y-axis). The upper and lower benchmarks are 80% S_{MSY} *(green) and* S_{GEN} *(red), respectively.* S_{GEN} *is defined as the spawner abundance that leads to* S_{MSY} *(grey) in one generation in the absence of fishing mortality. Under both types of benchmarks, the current spawner abundance in the example shown is above the upper benchmark, and this CU would be assessed as 'green'. c) The calculation of historical spawners benchmarks and stock-recruitment benchmarks requires run reconstruction to expand observed spawners abundances, assign catch to CUs, and calculate recruitment (Table 1).*

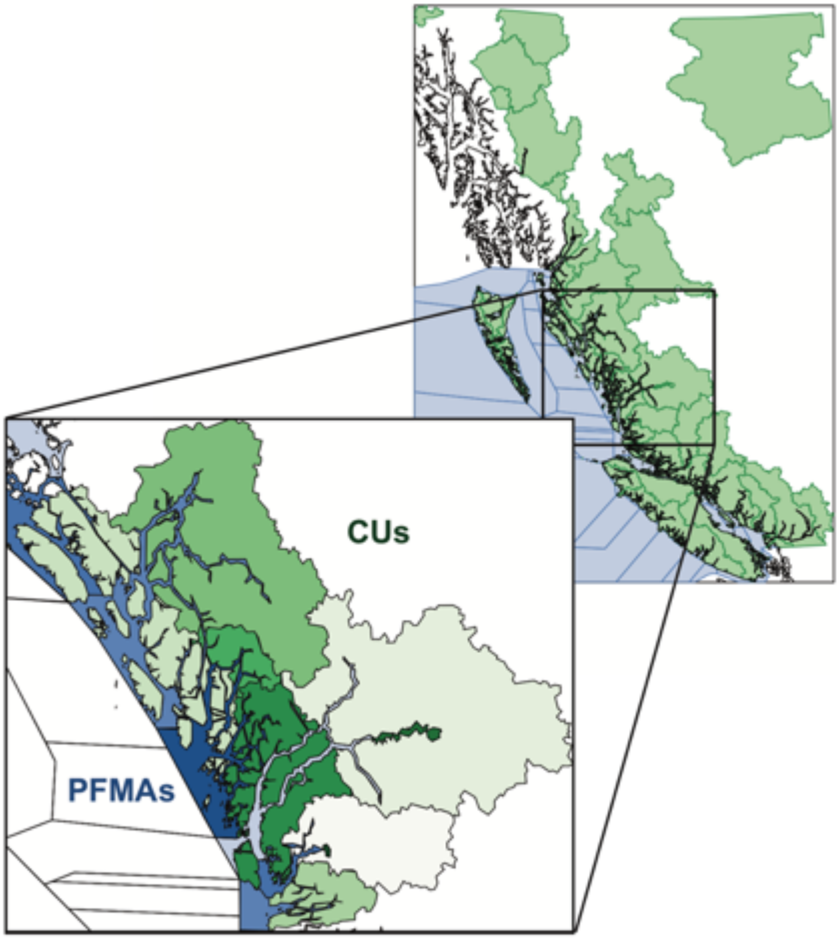


Figure 3. Our study focused on central coast chum salmon Conservation Units (CUs) as a case study for how common run-reconstruction assumptions affect the assessment of biological status. Chum salmon CUs (green; different CUs shaded differently in central coast inset) are relatively large, and do not correspond to the Pacific Fishery Management Areas (PFMAs; white or light blue shaded regions) for which catch is reported. Therefore, assumptions have to be made when assigning catch to CUs that may result in under- or over-estimation of catch. Map produced using PBSmapping (Schnute et al. 2015) with data from Fisheries and Oceans Canada (Martin Huang, pers. comm. <Martin.Huang@dfo-mpo.gc.ca>).

Finally, to calculate recruitment for a given cohort of spawners, assumptions about the age-at-return of spawners in any given year are required (except in the case of pink salmon, which have a fixed 2-year generation time). The total return in a given year is assigned to brood years based on the proportion of fish that return at a certain age, but these proportions are often not estimated every year. For chum salmon on the central coast, the distribution of age-at-return is assumed to be constant over time and is based on the average of available data (English et al. 2018). In this case, interannual variability in age-at-return may introduce uncertainty into the calculation of brood-year recruitment and bias resulting assessments of status (Zabel and Levin 2002). Temporal shifts in age-at-maturity, as have been widely observed in Pacific salmon (Ohlberger et al. 2018; Cline et al. 2019), may also introduce directional bias into status assessments.

Simulation model

We developed and applied a stochastic simulation model of salmon population dynamics that allows control over various biological and management factors that may influence the accuracy of status assessments. This approach built on previous studies that evaluated uncertainties in fisheries management (e.g., Holt and Peterman 2008) and other factors influencing the performance of metrics and benchmarks under the Wild Salmon Policy (e.g., Peacock and Holt 2012; Holt and Folkes 2015; Holt et al. 2016, 2018). The simulation model is comprised of submodels for salmon population dynamics, observation of spawners, assessment, harvest, and performance (Figure 4).

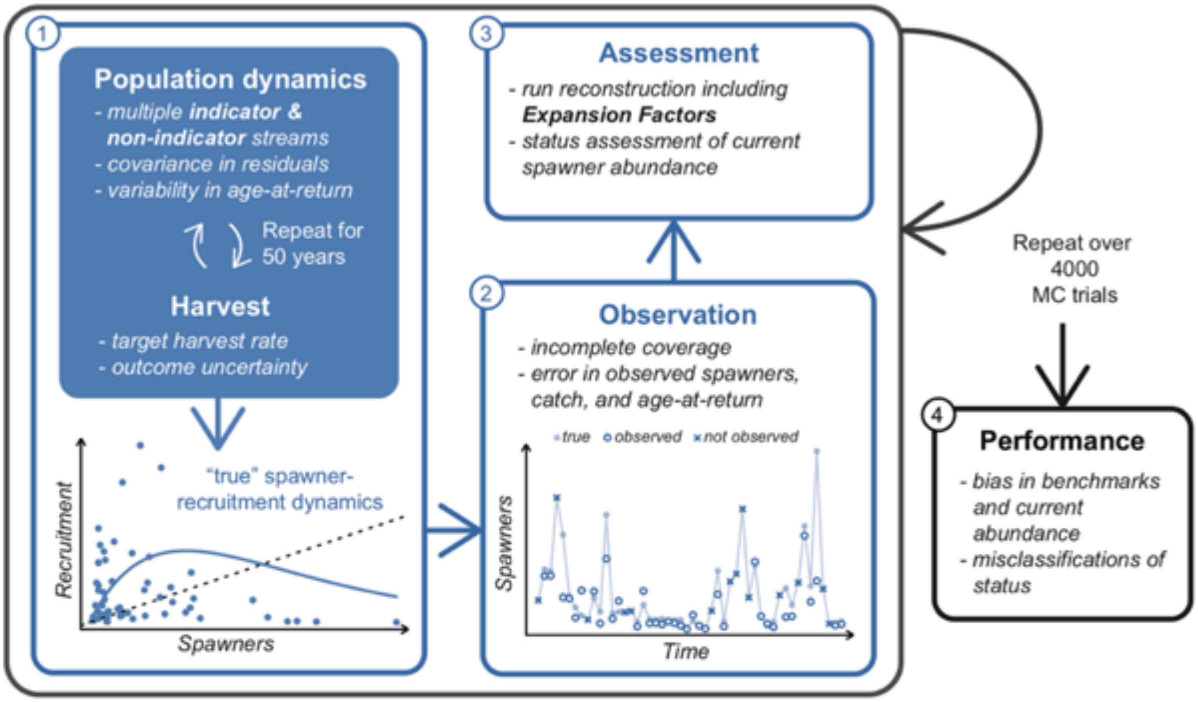


Figure 4. Schematic of the simulation model comprised of submodels for population dynamics (including harvest), observation, assessment, and performance. Adapted from Holt et al. (2016).

Population dynamics

We simulated the dynamics of multiple spawning populations returning to indicator or non-indicator streams within a single hypothetical CU. Although some CUs consist of just a single spawning population (e.g., lake-type sockeye salmon), many CUs (especially pink and chum salmon) span hundreds of kilometers (Figure 3) and can include multiple spawning populations whose dynamics may differ due to local adaptation and finite rearing and spawning habitats.

We based our simulations on the life history of chum salmon, which generally return as 3-, 4-, or 5-year-olds. The number of salmon returning to spawn in return year t and population j, $R_{t,j}$, was calculated as:

$$R_{t,\,j} = {R'}_{t-3,\,j}\ p_{t-3,\,3} + {R'}_{t-4,\,j}\ p_{t-4,\,4} + {R'}_{t-5,\,j}\ p_{t-5,\,5}, \tag{1}$$

where $p_{y,g}$ is the proportion of recruits from brood year y returning at age g. Throughout this model description, we use R to denote returns, or catch plus escapement of fish returning in a year, and R' to denote recruitment, or the total number of offspring from a brood year that survive to return to spawn.

We assumed that the annual proportion of recruits returning at a given age was the same among populations, but incorporated interannual variability in age-at-maturity by allowing the proportion of recruits that return as g year-olds to vary among brood years, y:

$$p_{y,g} = \frac{\overline{p}_g \exp(\overline{\omega}\, \varepsilon_{y,g})}{\sum_{G=3}^{5} \overline{p}_G \exp(\overline{\omega}\, \varepsilon_{y,G})}, \tag{2}$$

where $\overline{p}_g$ is the average proportion of individuals maturing as g year-olds, $\overline{\omega}$ is a parameter that controls interannual variability in proportions of fish returning at each age (Figure S4) and $\varepsilon_{y,g}$ are standard normal deviates (Schnute and Richards 1995).

The number of salmon that escape the fishery and return to spawn was calculated as:

$$S_{t,j} = \left(1 - h_{t,j}\right)\, R_{t,j}, \tag{3}$$

where $R_{t,j}$ is the number of returning salmon from eq. (1) and $h_{t,j}$ is the realized harvest rate for population *j* in year t. We incorporated outcome uncertainty (i.e., deviations from the target harvest rates) by drawing the realized harvest rates each year from a Beta distribution with mean equal to a target harvest rate, h_t' (Holt and Peterman 2008).

We considered two different scenarios for determining the target harvest rate (Figure 5). First, we considered a simple, abundance-based harvest control rule (HCR) where h_t' increased with the total return to the CU from a minimum of 0.05 (to account for bycatch and unavoidable mortality and also avoid problems associated with low target HRs when incorporating Beta-distributed outcome uncertainty) up to an asymptote, h_{MAX} (Holt and Peterman 2008):

$$h_t' = \max\left(h_{MAX} \left\{1 - \exp\left[m \textstyle\sum_j R_{t,j}\right] \right\}, 0.05\right), \tag{4}$$

where m is the shape parameter of the HCR. The low harvest rates at low returns under this HCR prevented the CU from declining to red status in simulations, and so as to broaden our results to include CUs with true red status, we also considered a constant high target harvest rate of $h_t' = 0.60$ regardless of the total return (Figure 5). In the Supplementary Material, we present an intermediate scenario with a constant moderate target harvest of $h_t' = 0.42$.

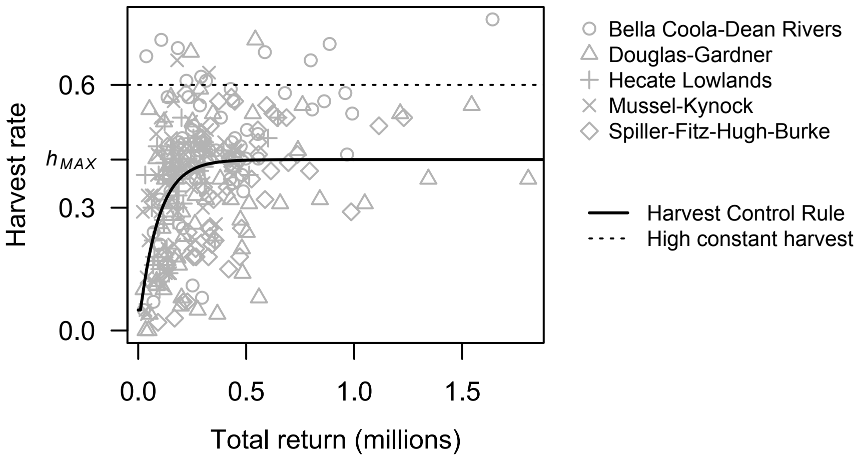


Figure 5. The two harvest cases we simulated were (1) a simple Harvest Control Rule (eq. (4); solid line) with parameters estimated from historical harvest rates and total return from five central coast chum CUs (grey points), (2) a constant high target harvest rate of $h'_t = 0.6$ *(dotted line).*

Each population in our model was harvested in proportion to its abundance, such that the true total catch of fish that would have returned to streams within the CU was calculated as:

$$C_t = h_{t,j} \sum_j R_{t,j}. \tag{5}$$

Although realized harvest rates differed among populations, we did not incorporate persistent biases in realized harvest rates among populations and thus assumed that all populations were equally vulnerable to the fishery. The extent to which this assumption is violated will depend the size of the CU, the number of populations within it, the magnitude of variation in run-timing among populations, and where fisheries are prosecuted. Any such biases among populations within a CU would likely be small because run-timing was a consideration when delineating CUs (Holtby and Ciruna 2007). However, biases among CUs may be significant and we investigate this by varying the observation bias in the total catch to the CU (see Sensitivity analyses, below).

Finally, we assumed the stock-recruitment dynamics followed a Ricker relationship (Ricker 1954) yielding the number of recruits from brood year y and population j:

$$R'_{y,j} = S_{y,j}\ \exp\left(a_j - b_{j,y}\, S_{y,j}\right)\ \exp\left(\phi_{y,j}\right), \tag{6}$$

where a_j is the $\log_e$ recruits per spawner at low spawner abundance (i.e., productivity), $b_{j,y}$ is the time-varying density-dependence parameter, and $\phi_{y,j}$ are the normally distributed recruitment deviates applied for year y and population j (eq. (7)).

We allowed productivity to differ among populations, where $a_j \sim N(\overline{a}, \sigma_a)$. We constrained $a_j \geq 0.4$ by re-drawing values of $a_j < 0.4$ because SR benchmarks are not calculable for very low productivity (Holt and Ogden 2013; Holt et al. 2018). For central coast chum salmon, we found only 1% of spawning populations (2/181) had $a_j < 0.4$ (Online Supplement). A linear change in the density-dependence parameter was simulated for some populations as a decline in the capacity of the stream (i.e., $S_{MAX,j,y} = 1/b_{j,y}$, or the spawner abundance that leads to maximum recruitment). This decline in capacities captured the potential consequences of cumulative stressors to freshwater habitat among watersheds on the central coast (Connors et al. 2018). For all populations, the initial capacity $S_{MAX,j,1}$ was drawn from a lognormal distribution whose mean and standard deviation differed for populations in indicator versus non-indicator streams, as indicator streams tend to be larger systems (English 2016; see

Parameterization). The productivity and density-dependence parameters were drawn independently for each MC iteration of the model.

We incorporated temporal autocorrelation in recruitment deviates:

$$\phi_{y,j} = \tau\, \phi_{y-1,j} + \upsilon_{y,j}, \tag{7}$$

where τ is the temporal autocorrelation coefficient and $\upsilon_{y,j}$ is a multivariate normal random variable with mean zero and variance-covariance matrix:

$$\Sigma_{j\times j} = \begin{bmatrix} \sigma_\upsilon^2 & \rho\,\sigma_\upsilon^2 & \dots & \rho\,\sigma_\upsilon^2 \\ \rho\,\sigma_\upsilon^2 & \sigma_\upsilon^2 & \dots & \rho\,\sigma_\upsilon^2 \\ \vdots & \vdots & \ddots & \vdots \\ \rho\,\sigma_\upsilon^2 & \rho\,\sigma_\upsilon^2 & \dots & \sigma_\upsilon^2 \end{bmatrix}_{j\times j}. \tag{8}$$

Here, σ_υ is the standard deviation in recruitment deviates without autocorrelation (Ricker 1975, Holt and Bradford 2011) and ρ is the correlation in recruitment deviates among populations.

We simulated the 'true' population dynamics over 50 years, after an initialization period of seven years to seed eq. (6) given the variable age-at-return of chum salmon. For each year in this initialization, we assumed that the number of spawners was equal to 20% of S_{MAX} for population j. For the first year of the initialization, we set $\phi_{y-1,j}$ from eq. (7) to zero.

Observation submodel

In the observation submodel, we incorporated both incomplete monitoring coverage of streams and imperfect observation of spawners in streams that were monitored. In any given year, population *j* was observed with probability $\psi_{y,j}$. We included a linear decline in monitoring coverage (i.e., the probability of a population being observed) over time based on observations of declining monitoring coverage on the north and central coast (Price et al. 2008, 2017; English 2016). We calculated the annual probability of being monitored separately for indicator and non-indicator streams based on observations that monitoring coverage of non-indicator streams is generally lower and has declined more severely than coverage of indicator streams (English 2016). See Parameterization for further details.

Spawner abundances were 'observed' with log-normal error:

$$\hat{S}_{y,j} = z_{y,j}\ [S_{y,j}\ \exp(\delta_{y,j})], \tag{9}$$

where $z_{y,j} \sim \text{Bernoulli}(\text{prob} = \psi_{y,j})$, $\delta_{y,j} \sim N(\overline{\delta},\ \sigma_\delta)$, $\overline{\delta}$ is the mean observation error, and σ_δ is the standard deviation in observation error of spawner abundances. Thus, this combines both the probability of a population being monitored and the distribution of observation errors around true spawner abundances if monitored. We included a negative bias in the observation of spawners ($\overline{\delta} \leq 0$) such that the mean observed spawner abundance is on average lower than the true spawner abundance. In general, it is challenging to enumerate spawners in all reaches of a stream and in all streams within a CU. The reported spawner abundance is considered an underestimate of the total spawners in a CU, which motivates the application of Expansion Factor III for observer (in)efficiency when performing run reconstructions (Table 1). The calculation of Expansion Factor I required that we impose the constraint that at least one indicator stream was monitored each year, so if $z_{y,j}$ = 0 for all indicator streams in a year, we randomly selected one indicator stream to be monitored.

The catch to the entire CU in return year t was observed with log-normal error:

$$\hat{C}_t = C_t \, \exp(\chi_t), \tag{10}$$

where $\chi_t \sim N(\bar{\chi}, \sigma_\chi)$, σ_χ is the standard deviation in catch error, and $\bar{\chi}$ is a bias in catch. We assumed a default value of $\bar{\chi}$ =0, but in sensitivity analyses we varied this parameter to simulate scenarios in which fish are caught from other CUs or fish from the focal CU were caught in other PFMAs.

Previous models (e.g., Holt et al. 2018) have included error in the “estimated age-at-return” separately for each return year. For central coast chum salmon, annual age-at-return data are rarely sampled comprehensively so the same average is generally applied across all years (Peacock et al. 2014; English et al. 2018). Therefore, for each year in a Monte Carlo (MC) trial we applied the same age-at-return, which was drawn independently for each MC trial using eq. (2) with observation error, $\overline{\omega_r}$ (Table A1).

Assessment submodel

As described above, the minimum requirement to calculate benchmarks and assess population status using HS benchmarks is a time-series of spawner abundance to the CU. For SR benchmarks, harvest rates and age-at-return must also be estimated in order to calculate recruitment. The basic procedure of these run reconstructions is outlined in Table 1, and begins by expanding observations of spawners to indicator streams to the total spawner abundance to the CU by applying three Expansion Factors. The equations and criteria governing these Expansion Factors are detailed in the Online Supplement and in English et al. (2012, 2016, 2018). Briefly, Expansion Factor I ($F'_{t,d}$) imputes for populations in unmonitored indicator streams and is calculated for each year, t, within a decade, d, of the spawner time series. It relies on the decadal contribution of each indicator-stream population to the total escapement to all indicator streams (English et al. 2016). Expansion Factor II (F''_{d}) expands observations of spawners from indicator streams to include populations in non-indicator streams that are less frequently monitored, and is the same for each year within a decade, d. Expansion Factor II is calculated as the average proportion of total monitored spawners (in indicator and non-indicator streams) that are in non-indicator streams for that decade. For decades with insufficient information to calculate either of these Expansion Factors, for example due to declining monitoring coverage, a reference decade may be used. Expansion Factor III (F''') is determined by the regional DFO staff familiar with the escapement monitoring techniques used in each statistical area and is assumed to be constant through time (English et al. 2018). In our model, we assumed that all populations were at least partially monitored, and that Expansion Factor III accounted for observation (in)efficiency, but in reality, Expansion Factor III may also account for populations in unmonitored streams.

The observed number of salmon returning in year t is the sum of observed catch and expanded escapement to the CU:

$$\hat{R}_t = \hat{C}_t + F'_{t,d}\, F''_d\, F''' \sum_{j \in I} \hat{S}_{t,j}, \tag{11}$$

where the summation includes observed spawner abundance to the I indicator streams only, with the non-indicator streams being accounted for through Expansion Factor II, F''_d.

We do not explicitly account for en route or pre-spawning mortality of fish that escaped the fishery, and assume that pre-spawning mortality is relatively small and accounted for in the productivity of the population through the Ricker stock-recruitment dynamics. Observed recruitment for brood year y is calculated as the sum of age 3, 4, and 5 fish returning in years $y + 3$, $y + 4$, and $y + 5$, respectively:

$$\hat{R}'_y = \hat{R}_{y+3}\, \widehat{pr}_3 + \hat{R}_{y+4}\, \widehat{pr}_4 + \hat{R}_{y+5}\, \widehat{pr}_5, \tag{12}$$

yielding the ‘reconstructed’ spawner-recruit pairs for brood year y.

To calculate estimated SR benchmarks, we fit a linearized Ricker model to the observed data at the aggregate CU-level. The estimated productivity and density-dependence parameters were used to calculate upper and lower SR benchmarks (80% of S_{MSY} and S_{GEN}) for the CU.

Performance submodel

For each MC simulation, we estimated status using both SR and HS benchmarks calculated from the observed stock-recruitment pairs for the CU, including observation biases and incomplete monitoring coverage. Estimated status under both types of benchmarks was compared to the true status, which was calculated by comparing the current true spawner abundance (without observation error) against the upper and lower SR benchmarks (80% of S_{MSY} and S_{GEN}) from the underlying stock-recruitment parameters. Because we simulated the true dynamics at the scale of spawning populations and there was no “true” CU-level value for the Ricker parameters, calculating the true S_{MSY} (and thus the SR benchmarks) at the CU-level was not straightforward. We chose to calculate the true SR benchmarks for each population from the underlying Ricker parameters for that simulation and then summed the benchmarks across all populations to yield the “true” CU-level benchmarks. Although this CU-level benchmark will underestimate the level required to maintain all component populations above their individual benchmarks in any given year, the objective of the WSP is to maintain the overall CU and populations within CUs are generally assumed be recolonizable within reasonable time frames (Fisheries and Oceans Canada 2005). We evaluated estimates of HS benchmarks against the true underlying benchmarks derived from ”true” SR parameters. When declines in capacity were included in the simulation, we calculated true status from the initial capacity parameters before the decline in order to avoid a shifting baseline in benchmarks.

Performance was evaluated in two ways that capture the difference between estimated and true status:

a) Proportion of MC simulations for which status was correctly assessed as green, amber, or red, and the proportion of simulations for which status was either underestimated (pessimistic) or overestimated (optimistic).

b) Percent relative bias of observed average spawner abundance (S_{AVG}) and of the four benchmarks (S_{GEN}, 80% S_{MSY}, S_{25}, S_{50}) compared to their true values for each MC simulation.

For each parameterization investigated (see below) we ran 4000 MC trials, which was sufficient to ensure the mean percent error in performance measures was < 3% (Figure S3).

Parameterization

Some of the parameters in our simulation model were unknown or unknowable, in which case we followed assumptions made for southern BC chum salmon by Holt et al. (2018). Other parameters were available specifically for central coast chum salmon or could be estimated from raw data; details of parameter estimation are given in the Online Supplement. As mentioned above, in order to understand the assessment biases under different true statuses we considered two cases: (1) high productivity and a conservative harvest control rule (HCR), which we refer to as the "base case" because it is most representative of central coast chum salmon, and (2) low productivity and a constant high target harvest rate, which represented a CU at high risk of extirpation. In the Online Supplement, we also present results from a third case intermediate between these two with low productivity and moderate harvest. Unless otherwise indicated in the sensitivity analysis (below), parameters defaulted to the values described here and listed in the Appendix, Table A1.

The mean proportion of adults maturing at ages 3, 4, and 5 in eq. (2) was 0.23, 0.64, and 0.13, respectively, based on the average age-at-return applied in run reconstructions of central coast chum (Challenger et al. 2018; English et al. 2018).

We estimated the parameters in the HCR (Figure 5) from harvest rates and total return sizes for five central coast chum CUs (English et al. 2018; Salmon Watersheds Program - Pacific Salmon Foundation 2019).

To estimate the stock-recruitment parameters for spawning populations (eq. (6)), we fit a linearized Ricker model to population-level spawner-recruit pairs from nine central coast chum CUs with individual productivity and density-dependence parameters for each population (Figure S5). From these model fits, we calculated (1) mean and variance in productivity among populations, (2) mean and variance in the initial capacity (i.e., $1/S_{\mathrm{MAX}}$) for indicator and non-indicator streams, (3) the residual variance within populations, (4) the correlation in residuals among populations, and (4) the temporal autocorrelation in residuals within populations. The mean population-level productivity was $\bar{a}$ = 1.40 (Figure S5), which we applied in our base case. For the low-productivity case, we chose $\bar{a}$ = 0.56, which was the 2.5th percentile of population-level productivity estimates (Figure S5). The correlation in residuals among populations was estimated at $\rho = 0.46$, but we also investigated lower ($\rho = 0$) and higher ($\rho = 0.9$) levels of synchrony in the Online Supplement.

As the default case, we considered a decline in the capacity of streams (i.e., inverse density-dependence parameter of the Ricker model) that reflected observed declines in freshwater habitat (Office of the Auditor General of Canada 2004). Within the central coast chum CUs, 29% of watersheds are considered to be at moderate risk, and 21% at high risk, of cumulative habitat pressures over the last 60 years from stressors such as logging, water licenses for withdrawal of water from streams, and stream crossings (Connors et al. 2018). We hypothesized that declines in capacity that differ among spawning populations may affect the accuracy of Expansion Factors I and II, particularly in combination with declining monitoring coverage (Price et al. 2017). We incorporated a linear decline in capacity (i.e., $S_{\mathrm{MAX}} = 1/b$) between 25% and 50%, representing a moderate decline, for 29% of populations (the percentage of central coast chum watersheds deemed to be at moderate risk of cumulative habitat pressures by Connors et al. 2018) and a linear decline between 50% and 75%, representing severe decline, for 21% of populations (the percentage deemed to be at high risk) over the 50-year simulation. The exact percent decline for each population was randomly drawn from a uniform distribution within the above range for each MC simulation. The remaining 50% of populations had stable capacity over the 50-year simulation. In a sensitivity analysis, we investigated four additional scenarios for declining capacity (Table 2).

In the observation submodel, we chose the bias in the observation of spawners to match Expansion Factor III, which corrects for observer efficiency, with a range of values explored in a sensitivity analysis (below). The value of Expansion Factor III applied in status assessments has been constant at F’’’ = 1.5 for all central coast chum CUs (English et al. 2016), and so we applied a default value of $\bar{\delta} = \log_e(1/1.5) = -0.4$. The majority of central coast chum streams are surveyed visually by ground (fish counts or other sampling) with some aerial (fish counts) or boat (fish counts or other sampling) surveys (English 2016), similar to southern BC chum streams (Holt et al. 2018). We assumed $\sigma_\delta = 0.5$ following Holt et al. (2018), which is the maximum estimated uncertainty for visually surveyed spawners (Cousens et al. 1982; Szerlong and Rundio 2008).

We incorporated a linear decline over the last 27 years of simulations in the proportion of indicator and non-indicator streams monitored each year from 0.76 and 0.72, respectively, to 0.72 and 0.05 based on English (2016). These declines are representative of overall declines in monitoring across species, but we also consider the trends specific to chum salmon in the Online Supplement (Figure S6).

We assumed no bias in the observation of catch ($\bar{\chi}$ = 0) by default, but consider a range of bias in sensitivity analyses (below). The standard deviation in the observation error of catch accounts for differences between observed (i.e., reported) and actual catch due to uncertainties with mixed-stock fisheries and in reporting and estimation of recreational fisheries and subsistence use. We set this to σ_{χ} = 0.2 (Holt et al. 2018), which is less than the observation error in spawners.

Sensitivity analyses

We examined the sensitivity of status assessments over a range of values for several different model parameters that we considered most likely to affect status assessments due to their influence on the assumptions in run reconstructions (Table 1; Table 2). We investigated each of the questions below under both the base case and low-productivity high-harvest case described above, with other parameters at their default values (Table A1) unless otherwise noted. The specific questions that we addressed were:

1. How does the number of spawning populations and the proportion designated as indicator streams affect status assessments? The lower the proportion of streams that are indicators, the greater the magnitude of Expansion Factor II.
2. How does a decline in monitoring coverage affect status assessments? The fewer indicator streams that are monitored, the greater the magnitude of Expansion Factor I and the potential uncertainty in expanded spawner abundance. Here, we consider two scenarios (Table 2; Figure S6): constant monitoring coverage at historical proportions among all streams and an observed decline in coverage starting in the mid-1980s as has been observed on the north and central coast (English 2016; Figure S6). In the Online Supplement we consider two additional scenarios: observed declines in monitoring specific to chum salmon streams and a sharp, recent decline in monitoring of indicator streams.
3. How do declines in capacity affect status assessments? The application of Expansion Factors I and II assumes that the relative contributions of populations to aggregate abundance in the CU does not change over time, but declines in capacity that differ among populations may violate this assumption.
4. How does spawner observation bias affect status assessments, given that the value of Expansion Factor III is fixed over time and often the same among CUs (English et al. 2018)?
5. How does catch observation bias (e.g., over- or under-estimating catch of salmon) affect status assessments? This represents scenarios where there are errors in estimates of CU proportions in the aggregate catch in a mixed-stock fishery, or violation in the

assumption of homogenous spatial and temporal distribution of CUs when CU proportions are not monitored in such fisheries.

6. How does interannual variability in age-at-return affect status assessments?

We investigated the impact of declines in monitoring coverage (question #2 above) in combination with declines in capacity of spawning populations (question #3) in a bivariate sensitivity analysis.

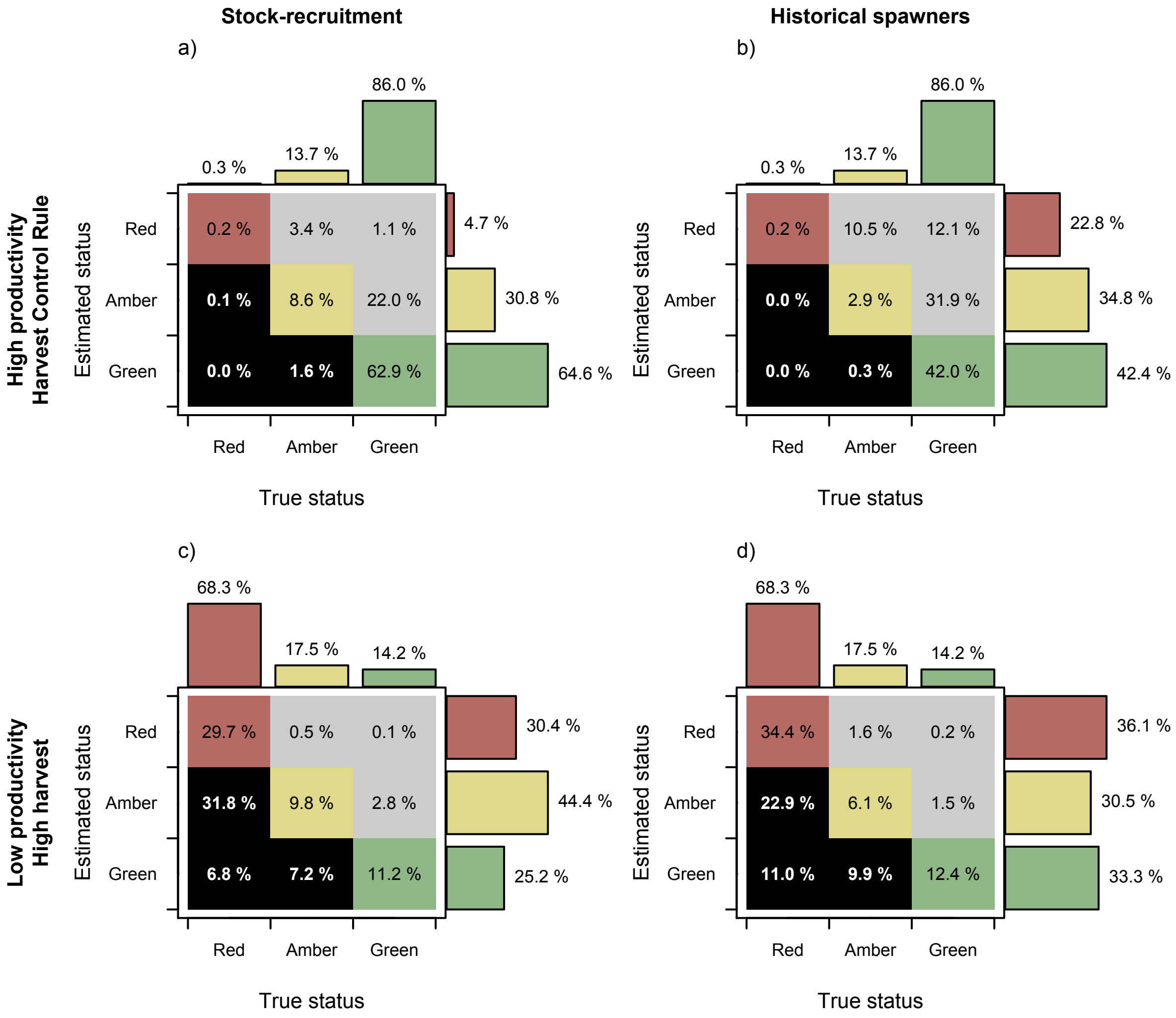
Results

The different productivity and harvest rate combinations that we considered led to different true statuses for the CU. Under high productivity and an abundance-based harvest control rule (HCR) – the base case corresponding to central coast chum salmon – 86.0% of simulations resulted in true green status (Figure 6a,b). Conversely, under low productivity and high harvest rates, 68.3% of simulations resulted in true red status (Figure 6c,d).

Under the base case when true status was mostly green, misclassifications resulted in estimated status lower than the true status meaning assessments were biologically pessimistic (henceforth referred to as “pessimistic misclassifications”). This was particularly true of the historical spawners (HS) benchmarks, for which 54.5% of simulations resulted in a pessimistic misclassification with 12.1% of simulations having misclassified green status as red. Pessimistic misclassifications were due to positive bias in benchmarks and not bias in the current spawner abundance (Figure 7), resulting in status being underestimated. For productive populations (as in the base case), most observed spawner abundances tend to be far above lower benchmarks and closer to equilibrium values. As a result, HS benchmarks of 25th and 50th percentile of historical spawner abundance tend to overestimate the "true" SR-based benchmarks.

When true status was mainly red, under low productivity and high harvest rates, biologically optimistic misclassifications (henceforth "optimistic misclassifications") were more common, which may be riskier from a conservation and management standpoint. For example, 45.8% and 43.8% of simulations had an estimated status higher than true status under the stock-recruitment (SR) and HS benchmarks, respectively (Figure 6c,d). These more frequent optimistic misclassifications were due to a negative bias in benchmarks, in particular the lower SR benchmark of S_{GEN} (Figure 7a), likely due to a poor ability to estimate S_{MSY} under low productivity when spawner abundances tend to cluster near the origin.

Under both types of benchmarks, bias did not decrease when monitoring coverage was held constant at 100% (Figure S9), suggesting that the application of Expansion Factors I and II were not contributing factors.



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550 *Figure 6. Estimated status according to the stock-recruitment benchmarks (left) and the historical spawners*
551 *benchmarks (right), over the true status for each of two cases (high productivity and an HCR (a-b) and low*
552 *productivity and high harvest rates (c-d)). Grey cells indicate pessimistic misclassifications, which may lead to overly*
553 *conservative management actions, and black cells indicate optimistic misclassifications, which may lead to overly*
554 *risky management actions. Coloured cells indicate correct classifications for red, amber, and green zones,*
555 *respectively.*

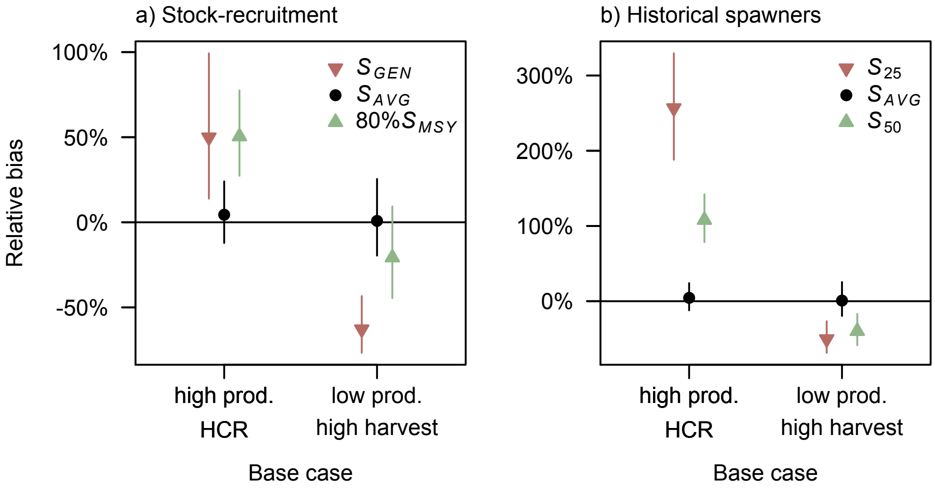

Figure 7. Relative bias in stock-recruitment benchmarks (a), historical spawners benchmarks (b), and current spawner abundance (S_{AVG}; black) (median ± interquartile range among 4000 MC simulations) for the base case (high productivity and an HCR) and the low-productivity high-harvest case.

Sensitivity analyses

The number of spawning populations within the CU and the proportion of those populations spawning in indicator streams had little impact overall on status assessments (Figure S10). Under the base case, the relative bias in estimates of S_{MSY} and S_{GEN} were lower in larger CUs, presumably because the effect of recruitment deviations for individual spawning populations on the aggregate stock-recruitment relationship was diminished when there were more component populations. This decline in bias resulted in half as many pessimistic misclassifications for larger CUs under the SR benchmarks (40% for 10 populations versus 20% for 140 populations with 30% indicator streams; Figure S10a). This trend was not, however, observed in the low-productivity high-harvest case when true status was predominantly red (Figure S12).

The monitoring-coverage scenarios that we considered, representative of observed declines in monitoring on the north and central coast, had no effect on status outcomes or the relative bias in benchmarks. This was true in the base case (Figure 8, Figure S13) and under low productivity (Figures S14 – S15). Even under severe declines in capacity of 50% to 75% for all spawning populations, our results suggest that the observed declines in monitoring coverage on the north and central coast are unlikely to influence the accuracy of status assessments. This result held regardless of whether the recruitment deviates among component populations within the CU were not correlated (ρ = 0; Figure S16) or highly correlated (ρ = 0.9; Figure S17).

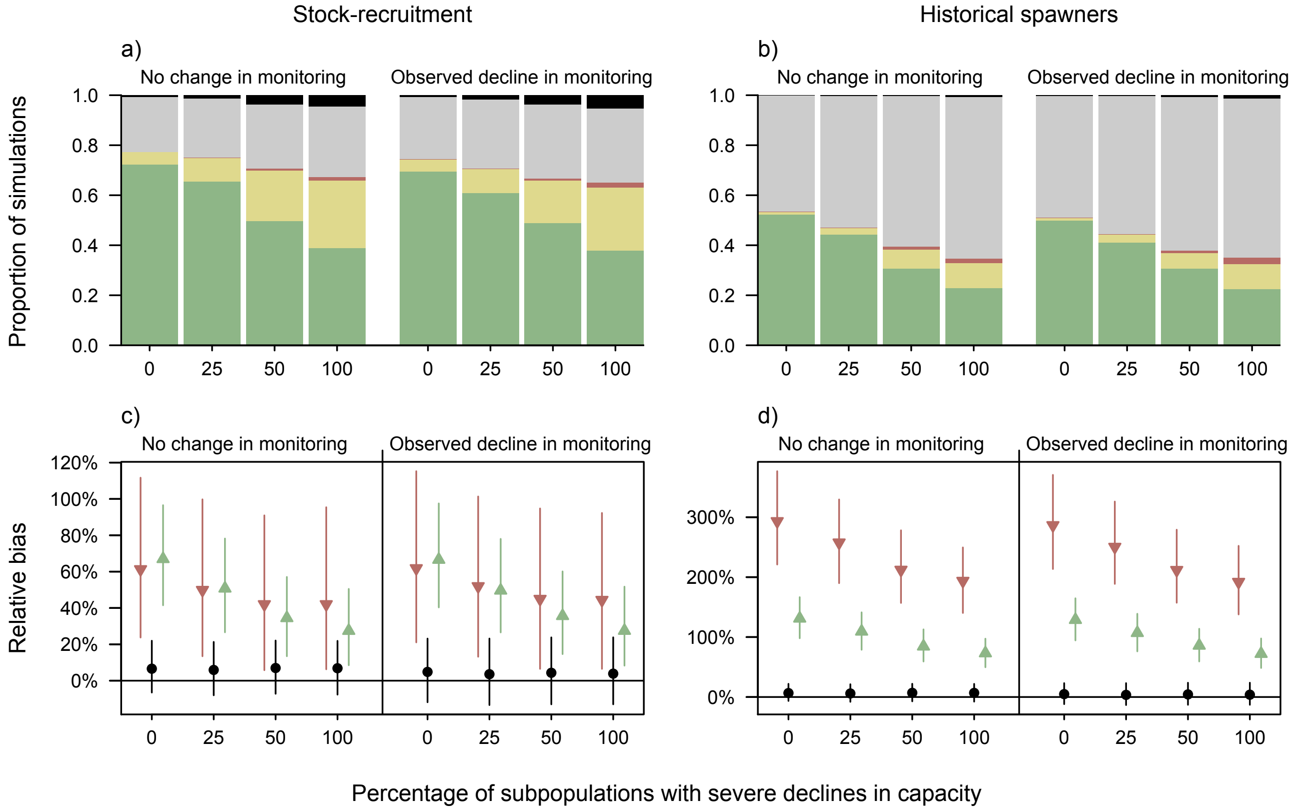

Figure 8. The effect of monitoring coverage (no change and decline; Table 2) and the percentage of spawning populations with severe declines in capacity (x-axis) on performance measures under the base case of high productivity and HCR. (a-b) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks (a) and HS benchmarks (b). (c-d) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}; black) and lower and upper benchmarks (red and green, respectively) under the SR benchmarks (c) and the HS benchmarks (d). See Online Supplement for results under the low-productivity high-harvest case.

Under the base case, declines in capacity of the CU were associated with poorer estimated status and an increase in misclassification rates (Figure 8a-b). Pessimistic misclassifications increased because CUs more frequently had a true status of amber but were misclassified as red. Optimistic misclassifications increased, particularly under the SR benchmarks (Figure 8a), because the relative bias in the current spawner abundance (S_{AVG}) remained unchanged, but the bias in benchmarks decreased (Figure 8c-d). In the low-productivity high-harvest case, the results were similar but with biologically optimistic misclassifications dominating as status was predominantly amber or red (Figure S15).

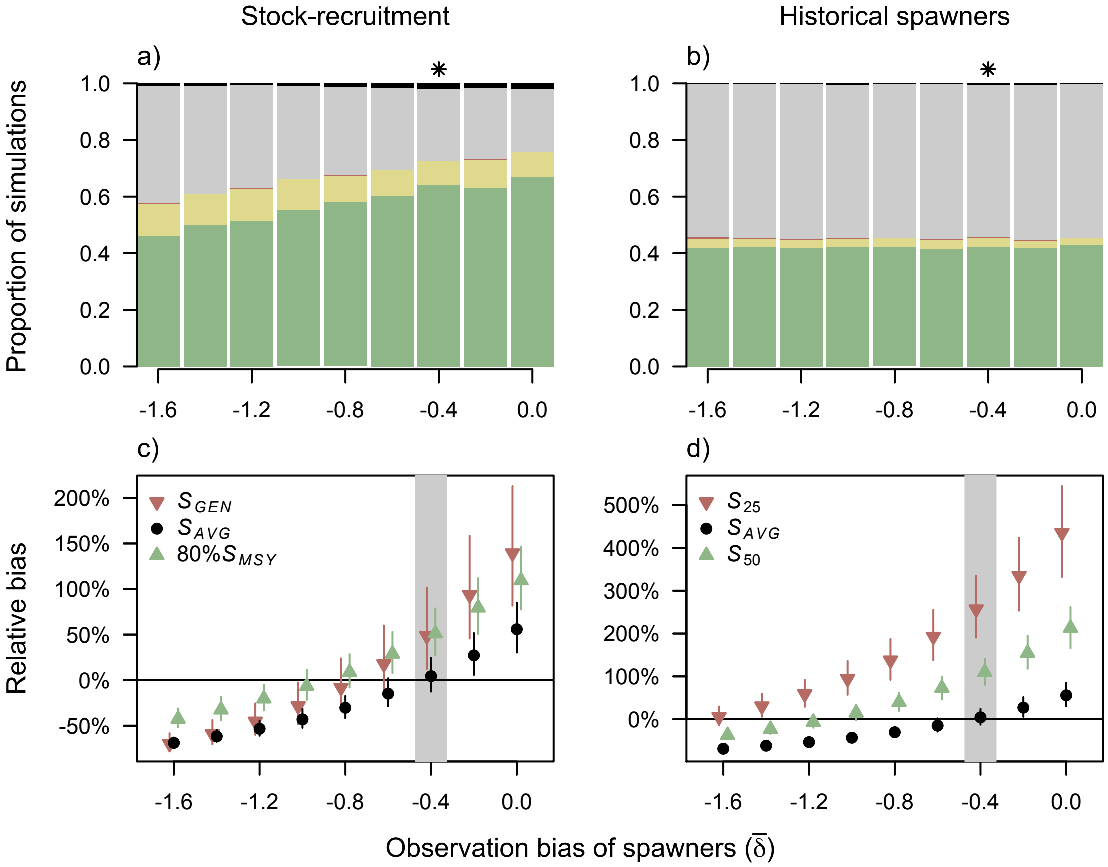

Figure 9. The effect of observation bias in the number of spawners (x-axis) on performance measures under the base case. (a-b) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks (a) and HS benchmarks (b). (c-d) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}; black circle) and lower and upper benchmarks (red and green, respectively) under the SR benchmarks (c) and the HS benchmarks (d). The Asterisk (*) in (a-b) and grey zone in (c-d) indicate the default parameter value of $\bar{\delta}$ = -0.4, and the bias that matches the Expansion Factor III of F''' = 1.5 applied in all simulations. See Online Supplement for results under the low-productivity high-harvest case (results were similar).

As the bias in the observation of spawners approached zero ($\bar{\delta} \rightarrow 0$), misclassifications under the SR benchmarks declined in all cases, even as the observation bias became less than the Expansion Factor III applied to correct for it (Figure 9a, Figures S18-S19). The relative bias in the current spawner abundance was minimized when the observation bias matched the assumed value of Expansion Factor III ($\bar{\delta}$ = -0.4 corresponding to F''' = 1.5; Figure 9c-d). When observed spawner abundance was biased low ($\bar{\delta}$ = -1.6), the relative bias in the upper benchmark of 80% S_{MSY} was higher than the relative bias in current spawner abundance (S_{AVG}) or the lower benchmark (S_{GEN}), and thus CUs with a true green status were more likely to be misclassified as amber. Status outcomes under the HS benchmarks were unaffected by changes in observation bias of spawners (Figure 9b); the bias in both benchmarks and current abundance showed similar changes as observation bias declined (Figure 9d) such that the resulting status outcome was unchanged. In the Online Supplement, we also investigated a change in observation bias halfway through the simulation (Figure S20), but a change from the base value of $\bar{\delta}$ = -0.4 to $\bar{\delta}$ = -1.6, -0.7, and 0 did not have any impact on status outcomes or biases in benchmarks (Figure S21).

Underestimation of catch (i.e., negative values of $\bar{\chi}$) resulted in fewer misclassifications than overestimating catch (Figure 10, Figures S22 – S23). As the catch bias increased from $\bar{\chi}$ = -1.0 (63% underestimation) to $\bar{\chi}$ = 1.0 (271% overestimation), the relative bias in the lower SR benchmark of S_{GEN} declined while the relative bias in the upper benchmark of 80% S_{MSY} increased (Figure 10b). This is due to the errors in variables that occur when catch is underestimated: productivity and recruitment tend to be underestimated, thus leading to lower estimates of S_{MSY} and higher estimates of S_{GEN} (Holt and Folkes 2015). Under the base case, the true status was green in the majority of simulations and so the increasing bias in the upper benchmark dominated the overall status assessments and led to the increase in pessimistic misclassifications with increasing $\bar{\chi}$. In the low-productivity high-harvest case, true status was mostly red and so the increasingly negative bias in S_{GEN} resulted in more optimistic misclassifications as the observation bias in catch increased (Figure S23). In both cases, overestimating catch by ~80% (i.e., $\bar{\chi}$ = 0.6) led to a ~5% increase in misclassification rate (Figure S24). Although these changes in misclassification rates may seem small, there is potential for large catch errors in run reconstructions, especially when multiple CUs overlap with a single PFMA. Catch does not factor into the calculation of HS benchmarks, so status under the HS benchmarks was unaffected by changing catch bias.

Finally, increasing interannual variability in age-at-maturity resulted in more frequent status misclassifications, but the effect was relatively small. Under the base case, increasing $\bar{\varpi}$ from 0.2 to the default value of 0.8 resulted in an increase in misclassifications from 25.2% to 29.8%, but very little change in the bias in benchmarks (Figure S25). Further increasing the interannual variability to $\bar{\varpi}$ = 1.6 led to 32.1% of simulations being misclassified, but this level of interannual variability is high (see Figure S4 for example) compared to data on age-at-return for central coast chum salmon (Challenger et al. 2018; English et al. 2018). The increase in misclassifications was smaller under the low-productivity high-harvest case (Figure S25).

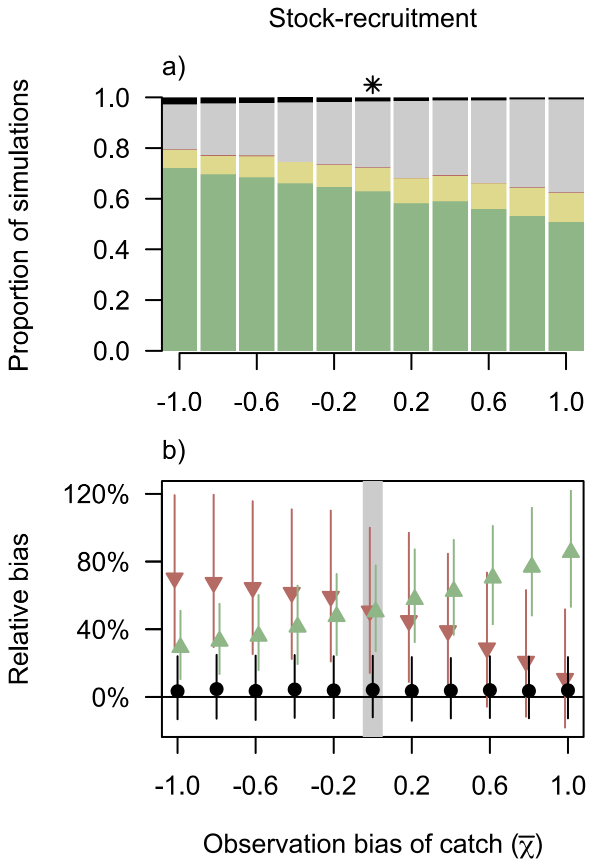

Figure 10. The effect of observation bias in catch (x-axis) on performance measures under the base case. (a) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks . (b) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}) and upper and lower benchmarks under the SR benchmarks. The asterisk in (a) and grey zone in (b) indicate the default parameter value of $\bar{\chi}$ = 0. See Online Supplement for results under the low-productivity high-harvest case.

Discussion

Complete knowledge of the dynamics of wild fish populations and fisheries is unattainable, and thus assumptions must be made when assessing biological status to inform conservation and management (Chen et al. 2003). Integrated status assessments of Pacific salmon Conservation Units (CUs) under Canada's Wild Salmon Policy (WSP) rely on the judgement of selected experts to help evaluate status, considering multiple indicators and the quality and quantity of available data (DFO 2015, 2016, 2018a), but this process is time and resource intensive, slowing the broad application of integrated status assessments. Other types of assessments rely on a data-driven approach focused on specific metrics without extended expert elicitation to evaluate the potential uncertainty and biases arising from assumptions around imputing spawner abundances and calculating recruitment (i.e., run reconstruction). These run-reconstructions have been adopted by, for example, local management organisations, Marine Stewardship Council (www.msc.org), the Pacific Salmon Treaty (PSC 2019), COSEWIC (e.g., COSEWIC 2016, 2017), and the Pacific Salmon Foundation (PSF). The PSF, in particular, have undertaken a widespread effort to apply a data-driven approach to assessing spawner abundance under the WSP framework, with results for the north and central coast openly available through their Pacific Salmon Explorer (Connors et al. 2013, 2018, 2019), and are currently expanding their assessments to the south coast of BC.

The benefits of this data-driven approach to biological status assessment include transparent and repeatable methodology, standardized and comparable results across CUs, and the ability to update status assessments in a timely manner. However, the impact of compound assumptions on the assessment of biological status needs to be quantified to lend confidence and credibility to status outcomes. In this study, we quantified the impact of common assumptions in basic run reconstructions (Figure 2c; Table 1) on resulting biological status outcomes.

Implications for status assessments

In general, the common assumptions in salmon run reconstructions that we hypothesized might introduce biases (Table 1) had little effect on status outcomes on our simulated populations, suggesting that attempts to assess status in the face of limited data are worthwhile. In particular, there was almost no effect of declines in monitoring coverage to the extent that has been observed on the accuracy of benchmarks or resulting status outcomes, even in the face of different trends in capacity and reduced synchrony (i.e., zero autocorrelation in recruitment deviates) among spawning populations within the CU. This result suggests that the application of Expansion Factors accurately infills gaps in spawner abundances, even when there are changes over time in the dynamics of populations in indicator and non-indicator streams. More extreme declines in monitoring may impact assessments – certainly, if no spawning populations are monitored then our ability to assess status will inevitably be compromised – but the current approach to infilling and expanding spawner abundances proved robust to declines in monitoring coverage in the range documented for the north and central coast (English 2016; Price et al. 2017).

Perhaps unexpectedly, misclassifications were not minimized when the value of Expansion Factor III, correcting for observer efficiency, accurately reflected the true observation bias in the underlying simulation. Rather, misclassifications under the stock-recruitment (SR) benchmarks declined as the observation bias in spawners approached zero. This result is due to the combination of bias in current spawner abundance, which *is* minimized when observation bias matches Expansion Factor III, and biases in benchmarks, which depend on underlying status. Status outcomes under the historical spawners (HS) benchmarks were unaffected by observation bias, as this bias was assumed to be constant over time and affected the current and historical spawner abundances equally.

Under high productivity and an abundance-based harvest control rule (HCR) consistent with historical central coast chum salmon harvest rates, most simulations had a true green status, but misclassifications as amber were common under both SR and HS benchmarks. The estimated status from our simulations roughly matched the status outcomes for seven central coast chum CUs from that period, with the majority of CUs having green status under the SR benchmarks and amber status under the HS benchmarks (Connors et al. 2018). (Note that status of central coast chum salmon CUs has since declined; see the Pacific Salmon Explorer (www.salmonexplorer.ca) for the most up-to-date assessments.) Consistent with the real status assessments, status under the HS benchmarks tended to be poorer than status under the SR benchmarks. Our simulations attributed this to a higher relative bias in HS benchmarks, consistent with a similar simulation study of south-coast chum salmon that found estimated HS benchmarks tended to be biased high under high-productivity scenarios, resulting in pessimistic misclassifications of biological status (Holt et al. 2018). These pessimistic misclassifications may result in overly conservative management actions that are less risky from a conservation standpoint, consistent with the Precautionary Principle (Foster et al. 2000). However, high probabilities of pessimistic misclassification are not always desirable as they may result in foregone harvest (Walters et al. 2019).

We extended our results beyond the base case, representative of central coast chum salmon, by including simulations with low productivity and high harvest rates. These simulations revealed that misclassifications strongly depend on the true status of the CU. For example, when we manipulated productivity and target harvest rates to mimic a CU with poor biological status (i.e., true red), the bias in benchmarks was negative, resulting in a high proportion of *optimistic* misclassifications. This represents a high-risk management scenario from a conservation standpoint, particularly as the true underlying status is red. Similarly, the absolute biases in benchmarks were more severe under declines in capacity when status was predominantly red (productivity low) compared to predominantly green (productivity high). The bias in SR benchmarks was particularly sensitive to the underlying true status, presumably because productivity and recruitment, which influence status, also affect the bias in stock-recruitment parameters (Subbey et al. 2014) that arises due to recruitment-spawner linkage inherent in the data (Walters 1985; Korman et al. 1995) and/or due to error in spawner estimates (Walters and Ludwig 1981; Kehler et al. 2002; Kope 2006).

Our results suggest that overestimating catch should be avoided. In particular, under low productivity and high harvest rates when status is mainly red, optimistic misclassifications associated with oversestimating catch and therefore underestimating the lower benchmark, S_{GEN}, may put populations at further risk. In contrast, under the base case of high productivity and an HCR, overestimating catch resulted mainly in more frequent pessimistic misclassifications as the upper benchmark (S_{MSY}) was overestimated, resulting in CUs with a true green status being estimated as amber. In both cases, the impact of overestimating catch has the potential to significantly bias assessments: overestimating catch by ~80% led to a ~5% increase in misclassification rates. This level of catch overestimation (and higher levels) may occur when fish caught in a Pacific Fisheries Management Area (PFMA) and assigned to the CU that overlaps with that PFMA were actually bound for other CUs. This could occur in mixed-stock fisheries if genetic stock identification is not undertaken to validate assumptions regarding run-timing and migration patterns. Increased efforts to quantify catch composition, run timing, and spatial distribution of Pacific salmon CUs are therefore needed to more accurately estimate harvest rates and minimize misclassifications of biological status.

Limitations, challenges, and future research

As is inevitable when trying to accurately model the stochastic dynamics of salmon spawning populations within CUs, we made a number of assumptions and so there remain several limitations to our modelling approach. We considered true stock-recruitment dynamics to operate at the spatial scale of spawning populations (i.e., individual streams), but there is evidence that the processes influencing productivity and density-dependence may operate at broader, regional spatial scales (e.g., Malick and Cox 2016). Other simulation models have incorporated straying among spawning populations within a CU (e.g., Peacock and Holt 2012; Holt and Folkes 2015). While that approach incorporates density-dependence that may occur at broader spatial scales, it also requires additional assumptions to be made about the probabilities of straying among streams, which is largely unknown.

Simulating true dynamics at the scale of individual spawning populations also complicates the calculation of true status at the CU-level from SR benchmarks. We chose to calculate SR benchmarks at the spawning-population-level and then sum across spawning populations to calculate S_{MSY} and S_{GEN} at the CU-level. There are other approaches to calculate aggregate benchmarks, but each has its own potential biases. For example, stock-recruitment relationships could be fit to the "true" data aggregated at the CU-level and SR benchmarks calculated from the resulting CU-level estimates of productivity and density dependence. The way in which spawning-population-level benchmarks are aggregated to CU-level benchmarks may affect performance in our simulations, and a full exploration of how different methods of aggregation affect our results warrants future consideration.

Despite these limitations, the simulation model that we adapted and applied is flexible enough that it can accommodate different Pacific-salmon species and life-history traits, opening the door to future work investigating the impact of different assumptions and the impact of the assumptions that we focused on under additional scenarios. Here, we considered a relatively simple run-reconstruction model, but further work is needed to quantify how observation errors and uncertainty in the spatial and temporal distribution of returns affects status outcomes when more complex run-reconstruction models are used. Temporal shifts in biological parameters, including age-at-return (e.g., associated with environmental change and selective fisheries) and productivity (non-stationarity has been widely observed in Pacific salmon; e.g., Peterman and Dorner 2012; Malick and Cox 2016; Dorner et al. 2017), are also areas that warrant further exploration. Additional simulations could also help inform methods in the assessment process, such as the optimal time-series length for detecting changes, whether benchmarks should be updated with each assessment, and the best analytical approach to calculate SR benchmarks (e.g., Bayesian hierarchical models vs. single-stock ordinary least squares).

Conclusions

Pacific salmon are one of the most data-rich groups of fish due to their high economic, social, and cultural value, but nonetheless our knowledge of their dynamics is uncertain. Assessing the biological status of Pacific salmon CUs is a conservation and management priority given the continued declines of many stocks (e.g., COSEWIC 2016, 2017) and escalating threats to salmon conservation. Status assessments are also central to the implementation of Canada's WSP, which requires information on current biological status in order to inform management strategies that can help to maintain salmon biodiversity. Current government-led approaches to assessing the status of salmon CUs are either time and resource intensive (e.g., integrated assessments) or are not clearly documented in a consistent way (e.g., in assessment bulletins), which has limited their application to all 460+ Pacific salmon CUs in Canada. It is unlikely that integrated status assessments will be undertaken in a timely manner for all salmon CUs. Given the importance of current information on biological status, more rapid approaches for assessing biological status are required.

The PSF has developed a timely and standardized approach for assessing biological status based on the indicators and benchmarks recommended under the WSP. Similar approaches have also been adopted by other management and conservation organizations (e.g., Marine Stewardship

Council, COSEWIC, Pacific Salmon Commission). These data-driven approaches to assessing biological status require assumptions to be made to estimate spawner and recruitment timeseries for CUs. We found that the data-driven biological status assessments applied here were relatively insensitive to common assumptions in expanding spawner abundances within the parameter ranges we explored, but misclassification rates depend on the underlying status of the CU and may be of greater concern for CUs with poor status. To ensure the accuracy of data-driven status assessments, increased efforts to collect data on catch composition, age-at-return, and maintain timeseries of spawner abundances are needed. Such information will help, for example, to define plausible ranges of error in catch estimation to lend confidence to estimates of recruitment and thus assessments under SR benchmarks. Nonetheless, our research suggests that current efforts to assess status in the face of imperfect and incomplete data are worthwhile for central coast chum salmon and other similar stocks, and can provide a timely approach to assessing status for CUs that complements more thorough integrated status assessments.

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Literature cited

Brown, G.S., Baillie, S.J., Thiess, M.E., Bailey, R.E., Candy, J.R., Parken, C.K., and Willis, D.M. 2019. Pre-COSEWIC review of southern British Columbia Chinook Salmon (*Oncorhynchus tshawytscha*) conservation units, Part I: background. DFO Can. Sci. Advis. Sec. Res. Doc. 2019/11: vii + 67 pp. Available from http://publications.gc.ca/collections/collection_2019/mpo-dfo/fs70-5/Fs70-5-2019-011-eng.pdf [accessed 1 December 2019].

Cave, J.D., and Gazey, W.J. 1994. A preseason simulation model for fisheries on Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **51**(7): 1535–1549. doi:10.1139/f94-153.

Challenger, W., Mochizuki, T., English, K., and Bychkov, Y. 2018. North and Central Coast Salmon Database and Analysis System User Manual. Sidney, BC. Available from https://salmonwatersheds.ca/libraryfiles/lib_449.pdf [accessed 1 December 2019].

Chen, Y., Chen, L., and Stergiou, K.I. 2003. Impacts of data quantity on fisheries stock assessment. Aquat. Sci. 65(1): 92–98. doi:10.1007/s000270300008.

Clark, R., Eggers, D., Munro, A., Fleischman, S., Bue, B., and Hasbrouck, J. 2014. An evaluation of the percentile approach for establishing sustainable escapement goals in lieu of stock productivity information. Alaska Dep. Fish Game, Fish. Manuscr. No. 14–06. Anchorage, AK. doi:10.4027/amdlfs.2016.08.

Cline, T.J., Ohlberger, J., and Schindler, D.E. 2019. Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. Nat. Ecol. Evol. **3**(6): 935–942. doi:10.1038/s41559-019-0901-7.

Connors, B.M., Pickard, D.C., Porter, M., Farrell, G., Bryan, K., Casely, S., and Huang, S. 2013. Skeena Salmon Conservation Unit Snapshots. Report prepared by ESSA Technologies Ltd. for the Pacific Salmon Foundation. v + 70p. Available from https://salmonwatersheds.ca/libraryfiles/lib_420.pdf [accessed 1 December 2019].

Connors, K., Hertz, E., Jones, E., Honka, L., Kellock, K., and Alexander, R. 2019. The Nass Region: Snapshots of salmon population status. The Pacific Salmon Foundation, Vancouver, BC. Available from https://salmonwatersheds.ca/libraryfiles/lib_453.pdf [accessed 1 December 2019].

Connors, K., Jones, E., Kellock, K., Hertz, E., Honka, L., and Belzile, J. 2018. BC Central Coast: A Snapshot of Salmon Populations and Their Habitats. The Pacific Salmon Foundation, Vancouver, BC. Available from https://salmonwatersheds.ca/library/lib_442/ [accessed 1 December 2019].

COSEWIC. 2016. COSEWIC Assessment and Status Report on the Coho Salmon *Oncorhynchus kisutch*, Interior Fraser population, in Canada. Committee on the Status of Endangered Wildlife in Canada Ottawa, ON. Available from https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/coho-salmon-interior-fraser-2016.html [accessed 1 December 2019].

COSEWIC. 2017. COSEWIC assessment and status report on the Sockeye Salmon *Oncorhynchus* *nerka*, 24 Designatable Units in the Fraser River Drainage Basin, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, On. Available from https://www.sararegistry.gc.ca/virtual_sara/files/cosewic/srSockeyeSalmon2017e.pdf [accessed 1 December 2019].

Cousens, N.B.F., Thomas, G.A., Swann, C.G., and Healey, M.C. 1982. A Review of Salmon Escapement Estimation Techniques. Can. Tech. Rep. Fish. Aquat. Sci. **1108**: 1–128.

DFO. 2015. Wild Salmon Policy Biological Status Assessment for Conservation Units of Interior Fraser River Coho Salmon (*Oncorhynchus kisutch*). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2015/022. Available from https://waves-vagues.dfo-mpo.gc.ca/Library/364851.pdf [accessed 1 December 2019].

DFO. 2016. Integrated Biological Status of Southern British Columbia Chinook Salmon (*Oncorhynchus tshawytscha*) Under the Wild Salmon Policy. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/042. Available from https://waves-vagues.dfo-mpo.gc.ca/Library/40595419.pdf [accessed 1 December 2019].

DFO. 2018a. The 2017 Fraser sockeye salmon (*Oncorhynchus nerka*) integrated biological status re-assessment under the Wild Salmon Policy. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/017. Available from https://waves-vagues.dfo-mpo.gc.ca/Library/40712163.pdf [accessed 1 December 2019].

DFO. 2018b. Northern BC Salmon Integrated Fisheries Management Plan. Fisheries and Oceans Canada, Vancouver, BC. Available from https://waves-vagues.dfo-mpo.gc.ca/Library/40797168.pdf [accessed 1 December 2019].

DFO. 2019. Wild Salmon Policy 2018-2022 Implementation Plan: Annual Report 2018-2019. Available from https://www.pac.dfo-mpo.gc.ca/fm-gp/species-especes/salmon-saumon/wsp-pss/annual-annuel/2018-2019-eng.html [accessed 1 December 2019].

Dorner, B., Catalano, M.J., and Peterman, R.M. 2017. Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the northeastern Pacific Ocean. Can. J. Fish. Aquat. Sci. **75**(7): 1082–1095. doi:10.1139/cjfas-2017-0197.

English, K.K. 2016. Review of escapement indicator streams for the North and Central Coast salmon monitoring program. Report prepared by LGL Limited for the Pacific Salmon Foundation and Fisheries and Oceans Canada. Available from https://salmonwatersheds.ca/libraryfiles/lib_440.pdf [accessed 1 December 2019].

English, K.K., Bailey, R.E., and Robichaud, D. 2007. Assessment of Chinook Salmon returns to the Fraser River watershed using run reconstruction techniques, 1982-04. Can. Sci. Advis. Sec. Res. Doc. 2007/020: vi + 76. Available from https://www.psf.ca/sites/default/files/RES2007_020_e.pdf [accessed 1 December 2019].

English, K.K., Peacock, D., Challenger, W., and Mochizuki, T. 2016. North and Central Coast Salmon Escapement, Catch, Run Size and Exploitation Rate Estimates for each Salmon Conservation Unit for 1954-2014. Report prepared by LGL Limited for the Pacific Salmon Foundation and Fisheries and Oceans Canada. Available from https://salmonwatersheds.ca/libraryfiles/lib_435.pdf [accessed 1 December 2019].

English, K.K., Peacock, D., Challenger, W., Noble, C., Beveridge, I., Robichaud, D., Beach, K., Hertz, E., and Connors, K. 2018. North and Central Coast Salmon Escapement, Catch, Run Size and Exploitation Rate Estimates for each Salmon Conservation Unit for 1954-2017. Report prepared by LGL Limited for the Pacific Salmon Foundation. Available from https://salmonwatersheds.ca/library/lib_451/ [accessed 1 December 2019].

Fisheries and Oceans Canada. 2005. Canada's Policy for Conservation of Wild Pacific Salmon. Vancouver, BC. Available from https://www.pac.dfo-mpo.gc.ca/fm-gp/species-especes/salmon-saumon/wsp-pss/policy-politique/index-eng.html [accessed 1 December 2019].

Fisheries and Oceans Canada. 2018. Wild Salmon Policy 2018 to 2022 Implementation Plan. Available from https://www.pac.dfo-mpo.gc.ca/fm-gp/species-especes/salmon-saumon/wsp-pss/ip-pmo/intro-eng.html [accessed 1 December 2019].

Foster, K.R., Vecchia, P., and Repacholi, M.H. 2000. Science and the Precautionary Principle. Science **288**(5468): 979–981. Available from https://www.jstor.org/stable/3075092 [accessed 1 December 2019].

Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., and Hard, J.J. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. Conserv. Biol. **21**(4): 1009–1020. doi:10.1111/j.1523-1739.2007.00693.x.

Holt, C., Davis, B., Dobson, D., Godbout, L., Luedke, W., Tadey, J., and Van Will, P. 2018. Evaluating Benchmarks of Biological Status for Data-limited Populations (Conservation

Units) of Pacific Salmon, Focusing on Chum Salmon in Southern BC. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/011: ix + 87. Available from http://www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2018/2018_011-eng.html [accessed 1 December 2019].

Holt, C.A., Brooke, D., and Cox-Rogers, S. 2016. Adapting benchmarks of biological status for persistent changes in productivity and variability in exploitation history with a focus on data-limited populations (Conservation Units) of Pacific salmon in north and central BC. Draft final report for the PSC. Can. Sci. Advis. Secr. Res. Doc. 86. Available from https://www.psc.org/fund-project/adapting-benchmarks/ [accessed 1 December 2019].

Holt, C.A., Cass, A., Holtby, L.B., Riddell, B.E., and Holtby, B. 2009b. Indicators of status and benchmarks for Conservation Units in Canada’s Wild Salmon Policy. Can. Sci. Advis. Sec. Res. Doc. 2009/058: viii+74. Available from https://www.psf.ca/sites/default/files/339096.pdf [accessed 1 December 2019].

Holt, C.A., and Folkes, M.J.P. 2015. Cautions on using percentile-based benchmarks of status for data-limited populations of Pacific salmon under persistent trends in productivity and uncertain outcomes from harvest management. Fish. Res. **171**: 188–200. doi:10.1016/j.fishres.2015.01.002.

Holt, C.A., and Ogden, A. 2013. Software for Assessing Status of Conservation Units under Canada’s Wild Salmon Policy: Instructional Manual. Can. Tech. Rep. Fish. Aquat. Sci. *In Prep.*

Holt, C.A., and Peterman, R.M. 2008. Uncertainties in population dynamics and outcomes of regulations in sockeye salmon (*Oncorhynchus nerka*) fisheries: implications for management. Can. J. Fish. Aquat. Sci. **65**(7): 1459–1474. Available from https://www.nrcresearchpress.com/doi/full/10.1139/F08-053 [accessed 1 December 2019].

Holtby, L.B., and Ciruna, K.A. 2007. Conservation Units for Pacific salmon under the Wild Salmon Policy. Can. Sci. Advis. Sec. Res. Doc. 2007/070: viii+74. Available from http://www.dfo-mpo.gc.ca/csas-sccs/publications/resdocs-docrech/2007/2007_070-eng.htm [accessed 1 December 2019].

Kehler, D.G., Myers, R.A., and Field, C.A. 2002. Measurement error and bias in the maximum reproductive rate for the Ricker model. Can. J. Fish. Aquat. Sci. **59**(5): 854–864. doi:10.1139/f02-060.

Kope, R. 2006. Cumulative effects of multiple sources of bias in estimating spawner-recruit parameters with application to harvested stocks of Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Res. **82**(1–3): 101–110. doi:10.1016/j.fishres.2006.08.016.

Korman, J., and English, K. 2013. Benchmark Analysis for Pacific Salmon Conservation Units in the Skeena Watershed. A report prepared for the Pacific Salmon Foundation, Vancouver, BC. Available from https://salmonwatersheds.ca/libraryfiles/lib_318.pdf [accessed 1 December 2019].

Korman, J., Peterman, R.M., and Walters, C.J. 1995. Empirical and theoretical analyses of correction of time-series bias in stock-recruitment relationships of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **52**(10): 2174–2189. doi:10.1139/f95-810.

Malick, M.J., and Cox, S.P. 2016. Regional-Scale Declines in Productivity of Pink and Chum Salmon Stocks in Western North America. PLoS One **11**(1): e0146009. doi:10.1371/journal.pone.0146009.

Office of the Auditor General of Canada. 2004. 2005 Report of the Commissioner of the Environment and Sustainable Development. In Fisheries and Oceans Canada — salmon stocks, habitat, and aquaculture. Chapter 5 [online]. Available from http://www.oag-bvg.gc.ca/internet/docs/c20041005ce.pdf [accessed 8 April 2019].

Ohlberger, J., Ward, E.J., Schindler, D.E., and Lewis, B. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. Fish Fish. **19**(3): 533–546. doi:10.1111/faf.12272.

Peacock, S.J., Connors, B.M., Krkošek, M., Irvine, J.R., and Lewis, M.A. 2014. Can reduced predation offset negative effects of sea louse parasites on chum salmon? Proc. R. Soc. B Biol. Sci. **281**: 20132913. doi:10.1098/rspb.2013.2913.

Peacock, S.J., and Holt, C.A. 2012. Metrics and sampling designs for detecting trends in the distribution of spawning Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. **69**(4): 681–694. doi:10.1139/f2012-004.

Peterman, R.M., and Dorner, B. 2012. A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. Can. J. Fish. Aquat. Sci. **69**(8):

1255–1260. doi:10.1139/F2012-063.

Price, M.H.H., Darimont, C.T., Temple, N.F., and MacDuffee, S.M. 2008. Ghost runs: management and status assessment of Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts. Can. J. Fish. Aquat. Sci. **65**: 2712–2718. doi: 10.1139/F08-174.

Price, M.H.H., English, K.K., Rosenberger, A.G., MacDuffee, M., and Reynolds, J.D. 2017. Canada's Wild Salmon Policy: an assessment of conservation progress in British Columbia. Can. J. Fish. Aquat. Sci. **74**(10): 1507–1518. doi:10.1139/cjfas-2017-0127.

PSC. 2019. Treaty Between the Government of Canada and the Government of the United States of America Concerning Pacific Salmon. Pacific Salmon Commision, Vancouver, BC. Available from http://www.psc.org/ [accessed 1 December 2019].

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Canada **11**(5): 559–623. Available from https://www.nrcresearchpress.com/doi/abs/10.1139/f54-039 [accessed 1 December 2019].

Salmon Watersheds Program - Pacific Salmon Foundation. 2019. Salmon Watersheds Data Library. Available from http://data.salmonwatersheds.ca/data-library/ [accessed 1 December 2019].

Scheuerell, M.D. 2016. An explicit solution for calculating optimum spawning stock size from Ricker's stock recruitment model. PeerJ **4**(1): e1623. doi:10.7717/peerj.1623.

Schnute, J.T., Boers, N., and Haigh, R. 2015. PBSmapping: Mapping Fisheries Data and Spatial

Analysis Tools. Available from https://cran.r-project.org/package=PBSmapping [accessed 1 December 2019].

Schnute, J.T., and Richards, L.J. 1995. The influence of error on population estimates from catch-age models. Can. J. Fish. Aquat. Sci. **52**(10): 2063–2077. doi:10.1139/f95-800.

Subbey, S., Devine, J.A., Schaarschmidt, U., and Nash, R.D.M. 2014. Modelling and forecasting stock–recruitment: current and future perspectives. ICES J. Mar. Sci. **71**(8): 2307–2322.

Szerlong, R.G., and Rundio, D.E. 2008. A statistical modeling method for estimating mortality and abundance of spawning salmon from a time series of counts. Can. J. Fish. Aquat. Sci. **65**: 17–26. doi:10.1139/F07-141.

Walters, C., English, K., Korman, J., and Hilborn, R. 2019. The managed decline of British Columbia’s commercial salmon fishery. Mar. Policy **101**: 25–32. doi:10.1016/j.marpol.2018.12.014.

Walters, C.J. 1985. Bias in the Estimation of Functional Relationships from Time Series Data. Can. J. Fish. Aquat. Sci. **42**(1): 147–149. doi:10.1139/f85-018.

Walters, C.J., and Ludwig, D. 1981. Effects of Measurement Errors on the Assessment of Stock-Recruitment Relationships. Can. J. Fish. Aquat. Sci. **38**(6): 704–710.

Wetzel, C.R., and Punt, A.E. 2011. Performance of a fisheries catch-at-age model (Stock Synthesis) in data-limited situations. Mar. Freshw. Res. **62**(8): 927. doi:10.1071/mf11006.

Zabel, R.W., and Levin, P.S. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia **133**(3): 349–355. doi:10.1007/s00442-002-1051-0.

Tables

1027 *Table 1. Summary of common steps in run reconstructions (Figure 2) and associated assumptions and potential biases that we investigated.*

Step in run recon-struction	**Description**	**Assumption**	**Potential biases**	**Associated factor(s) investigated in this study**
(1) Expansion Factor I	Infills observed spawner abundances in indicator streams to account for indicator streams that were not monitored in a given year.	The contribution of each indicator-stream population to total escapement is constant within a decade.	May be biased if contributions are changing due to, for example, changes in capacity or productivity that differ among populations. Under low monitoring coverage, the magnitude of expansion is greater and thus we expect that any potential bias would be larger.	→ Diverging capacities of populations through time → Declining monitoring coverage
(2) Expansion Factor II	Expands spawner abundances from (1) to include spawners in non-indicator streams.	The contribution of non-indicator-stream populations to total escapement is constant within a decade.	May be biased if contributions are changing due to, for example, changes in capacity or productivity that differ between populations in indicator and non-indicator streams.	→ Diverging capacities of populations through time → Declining monitoring coverage

				→ Number of streams and proportion that are indicators
(3) Expansion Factor III	Expands spawner abundances from (2) to account for observer efficiency and for populations that are never monitored, yielding the estimated total spawner abundance for the CU.	The proportion of total spawner abundance estimated in (2) is known, constant over time, and independent of spawner abundance.	May be biased if observer efficiency is not known or poorly estimated, if survey methods change over time (e.g., a weir to overhead counts), or if observation bias varies with total spawner abundance.	→ Bias in the observation of spawners (under the same value of Expansion Factor III) → Declining monitoring coverage
(4) Catch assignment to CUs	Catch from PFMAs is assigned to CUs in proportion to the spawner abundance for that CU.	Fish caught in an PFMA were destined to spawn in streams that flow into that PFMA.	Over- or under-estimation of catch due to different run timing among CUs that flow into the same PFMA (if information on run timing is uncertain, unavailable, or not incorporated into run-reconstruction models).	→ Bias in the observation of catch

(5) Calculating recruitment using age-at-return	The total return to the CU is assigned to brood years based on the proportion of fish returning at different ages.	Often, annual age-at-return data are not available for each CU, and so age-at-return is assumed to be constant over time, using the average of available data.	Variability in brood year recruitment will be underestimated if there is high inter-annual variability, or temporal changes, in age-at-return that is not accounted for in assessments.	→ Inter-annual variability in age-at-return

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Table 2. Summary of factors that we investigated in sensitivity analyses to determine their impact on bias in status assessments.

Factor	**Scenario**	**Details**
Number of populations and proportion that spawn in indicator streams	Central coast chum*	35 populations, 15 (43%) indicator streams
	Small/Low	10 populations, 3 (30%) indicator streams
	Small/High	10 populations, 8 (80%) indicator streams
	Large/Low	140 populations, 42 (30%) indicator streams
	Large/High	140 populations, 119 (85%) indicator streams
Monitoring coverage	Constant	**Indicator**: historical 76% with no change **Non-indicator**: historical 72% with no change
	Observed decline*	**Indicator**: 76% with a change of -5% over the last 26 years **Non-indicator**: 72% with a change of -67% over the last 26 years
Declines in capacity†	0	All spawning populations have stable capacities
	25	25% of populations severe and 25% moderate declines, and 50% stable capacity
	50	50% of populations severe and 50% moderate declines in capacity
	100	100% of populations display severe declines in capacity
Bias in observation of spawners	Range in bias from $\bar{\delta}$ = -1.6, which would correspond to the maximum value of Expansion Factor III that has been applied (F’’’ = 5.0,; English et al. 2018) to $\bar{\delta}$ = 0 in increments of 0.2 (*default value $\bar{\delta}$ = -0.4, corresponding to F’’’=1.5)	
Bias in observation of catch	Range in bias from $\bar{\chi}$ = -1.0 (63% underestimation) to $\bar{\chi}$ = 1.0 (271% overestimation) in increments of 0.2 (*default value $\bar{\chi}$ = 0).	

Interannual variability in age-at-return	Range in variability from $\overline{\varpi}$ = 0.2 to $\overline{\varpi}$ = 1.6 in increments of 0.2 (*default value $\overline{\varpi}$ = 0.8; Figure S4)

*Default values. †The default values for decline in capacity did not correspond exactly to the scenarios considered in the sensitivity analyses, but were based on habitat assessments for central coast (21% of populations having severe declines and 29% of populations having moderate declines (Connors et al. 2018)).

Figure captions

Figure 1. Illustration of the WSP status assessment framework (adapted from Holt et al. 2009). We focused on the geometric mean spawner abundance (metric, blue) under the spawner abundance indicator. This metric was assessed against two types of benchmarks: stock-recruitment and historical spawners (see Figure 2). Faded boxes represent other types of metrics and indicators that may be included in integrated status assessments but were beyond the scope of what we considered.

Figure 2. a) Historical spawners benchmarks are the 50th (horizontal green line) and 25th (horizontal red line) percentiles of historical spawner abundance (points). The current spawner abundance is calculated as the geometric mean spawner abundance over the most recent generation (4 years, blue points and line). b) Stock-recruitment benchmarks are based on the shape of the Ricker stock-recruitment relationship (solid line) fit to data on spawner abundance (x-axis) and corresponding recruitment (catch + escapement, y-axis). The upper and lower benchmarks are 80% S_{MSY} (green) and S_{GEN} (red), respectively. S_{GEN} is defined as the spawner abundance that leads to S_{MSY} (grey) in one generation in the absence of fishing mortality. Under both types of benchmarks, the current spawner abundance in the example shown is above the upper benchmark, and this CU would be assessed as 'green'. c) The calculation of historical spawners benchmarks and stock-recruitment benchmarks requires run reconstruction to expand observed spawners abundances, assign catch to CUs, and calculate recruitment (Table 1).

Figure 3. Our study focused on central coast chum salmon Conservation Units (CUs) as a case study for how common run-reconstruction assumptions affect the assessment of biological status. Chum salmon CUs (green; different CUs shaded differently in central coast inset) are relatively large, and do not correspond to the Pacific Fishery Management Areas (PFMAs; white or light blue shaded regions) for which catch is reported. Therefore, assumptions have to be made when assigning catch to CUs that may result in under- or over-estimation of catch. Map produced using PBSmapping (Schnute et al. 2015) with data from Fisheries and Oceans Canada (Martin Huang, pers. comm. <Martin.Huang@dfo-mpo.gc.ca>).

Figure 4. Schematic of the simulation model comprised of submodels for population dynamics (including harvest), observation, assessment, and performance. Adapted from Holt et al. (2016).

Figure 5. The two harvest cases we simulated were (1) a simple Harvest Control Rule (eq. (4); solid line) with parameters estimated from historical harvest rates and total return from five central coast chum CUs (grey points), (2) a constant high target harvest rate of h_t'=0.6 (dotted line).

Figure 6. Estimated status according to the stock-recruitment benchmarks (left) and the historical spawners benchmarks (right), over the true status for each of two cases (high productivity and an HCR (a-b) and low productivity and high harvest rates (c-d)). Grey cells indicate pessimistic misclassifications, which may lead to overly conservative management actions, and black cells indicate optimistic misclassifications, which may lead to overly risky management actions. Coloured cells indicate correct classifications for red, amber, and green zones, respectively.

Figure 7. Relative bias in stock-recruitment benchmarks (a), historical spawners benchmarks (b), and current spawner abundance (S_{AVG}; black) (median ± interquartile range among 4000 MC simulations) for the base case (high productivity and an HCR) and the low-productivity high-harvest case.

Figure 8. The effect of monitoring coverage (no change and decline; Table 2) and the percentage of spawning populations with severe declines in capacity (x-axis) on performance measures under the base case of high productivity and HCR. (a-b) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks (a) and HS benchmarks (b). (c-d) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}; black) and lower and upper benchmarks (red and green, respectively) under the SR benchmarks (c) and the HS benchmarks (d). See Online Supplement for results under the low-productivity high-harvest case.

Figure 9. The effect of observation bias in the number of spawners (x-axis) on performance measures under the base case. (a-b) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks (a) and HS benchmarks (b). (c-d) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}; black circle) and lower and upper benchmarks (red and green, respectively) under the SR benchmarks (c) and the HS benchmarks (d). The Asterisk (*) in (a-b) and grey zone in (c-d) indicate the default parameter value of δ = -0.4, and the bias that matches the Expansion Factor III of F’’’ =

1.5 applied in all simulations. See Online Supplement for results under the low-productivity high-harvest case (results were similar).

Figure 10. The effect of observation bias in catch (x-axis) on performance measures under the base case. (a) The proportion of simulations with correct green, amber, or red status or pessimistic misclassifications (grey) and optimistic misclassifications (black) under the SR benchmarks . (b) The percent relative bias (median ± interquartile range among 4000 MC simulations) in the current spawner abundance (S_{AVG}) and upper and lower benchmarks under the SR benchmarks. The asterisk in (a) and grey zone in (b) indicate the default parameter value of $\chi = 0$. See Online Supplement for results under the low-productivity high-harvest case.

Appendices

Appendix A: Table of default parameter values

Table A1. Default values for parameters in the simulation model that were used unless otherwise specified (e.g., in sensitivity analyses). See text for further explanation of the values and the Online Supplement for details of estimation for those based on raw data. For parameters that were part of sensitivity analyses, the range in parameter values that was explored is highlighted.

Submodel	**Parameter**	**Symbol**	**Default value**	**Range**	**Ref.**
General	Years over which the simulation is run	t : return year y : brood year	50	-	
	Number of indicator streams	I	15	1 – 41	1
	Number of non-indicator streams	J	20	1 - 100	1
Population dynamics	Productivity	$\bar{a}$	1.40	-	2
		σ_a^2	0.22	-	2
	$a_i \sim N(\bar{a}, \sigma_a^2)$				
	Density dependence (initial)	$\mu_{b,I}$	7.95	-	2
		$\sigma_{b,I}^2$	2.07	-	2
	$b_{i,t=0} = 1/S_{MAX_i}$				
	$\log S_{MAX_i} \sim N\left(\mu_{b,I}, \sigma_{b,I}^2\right)$	$\mu_{b,J}$	6.95	-	2
		$\sigma_{b,J}^2$	1.39	-	2

	Temporal autocorrelation	τ	0.422	-	2
	Variance in recruitment deviates within spawning populations	σ_v^2	1.28	-	2
	Correlation among spawning populations in recruitment deviates	ρ	0.46	-	2
	Average proportions for age-at-maturity	$\overline{p}_g$	$\overline{p}_3 = 0.23$ $\overline{p}_4 = 0.64$ $\overline{p}_5 = 0.13$	-	3
	Interannual variability in age-at-maturity	$\overline{\omega}$	0.8	-	4
	Maximum target harvest rate	h'_{MAX}	0.42	-	5
	Shape parameter for that harvest rule	m	1.13×10^{-5}		5
	Standard deviation in outcome uncertainty around harvest rate	σ_h	0.13	-	5
Observation	Lognormal observation error of **spawners**	$\bar{\delta}$	- 0.4	-1.6 to 0.0	6
		σ_δ^2	0.25	-	4
		$\bar{\chi}$	0	-1.0 to 1.0	

	Lognormal observation error of **catch**	σ_{χ}^{2}	0.04	-	4
	Variability in observed age-at-return	$\overline{\omega}_{r}$	0.1	-	4

References:

1. Based on the range of indicator and non-indicator streams reported in the Pacific Salmon Explorer (www.salmonexplorer.ca) for the eight central coast chum CUs.

2. Calculated from river-level stock-recruitment data for central coast chum CUs. See Online Supplement for details.

3. From the NCCDBV2 (Challenger et al. 2018).

4. Same as assumed in Holt et al. (2018) for south-coast chum salmon.

5. Calculated from CU-level harvest rates and total return size, from the Salmon Watersheds Data Library (Salmon Watersheds Program - Pacific Salmon Foundation 2019). See Online Supplement for details.

6. Based on expert opinion. Expansion Factor of F’’’ = 1.5 in Table A3-A4 of English et al. (2016).