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Article

Linking hierarchical population models with habitat data improves assessment of data-limited salmon stocks

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ABSTRACT

Objective: Managing data-limited populations is a challenge to the sustainability of fisheries globally. Meta-analytic approaches, where insights from data-rich populations are drawn on to inform data-limited ones, along with the use of habitat-based information, have each been proposed as ways to overcome data-limited assessment challenges, but the two approaches have rarely been combined. Sockeye Salmon *Oncorhynchus nerka* spawn and rear in many remote coastal watersheds of British Columbia, Canada, challenging comprehensive population assessments. Estimating conservation and management reference points for such populations is particularly relevant given their importance to Indigenous and commercial fisheries. Most Sockeye Salmon have obligate lake-rearing as juveniles, and total abundance is typically limited by production in nursery lakes. Although methods have been developed to estimate population capacity based on the photosynthetic rate of nursery lakes and lake area or volume, they have not yet been widely incorporated into spawner–recruitment analyses.

Methods: We tested the value of combining these lake-based capacity estimates with various hierarchical structures in spawner–recruitment analyses to assess population status using a set of Bayesian spawner–recruitment models for 69 populations across coastal British Columbia, many of which were data limited.

Results: Our analysis revealed regional variation in the population productivity of Sockeye Salmon, with coastal populations exhibiting slightly lower mean productivity than those in interior watersheds. Hierarchical spawner–recruitment models with and without informative lake habitat-based priors greatly improved predictive ability across all populations.

Conclusions: These findings reveal opportunities to integrate spatial analyses of habitat characteristics with population models to inform the conservation and management of exploited species and their natal habitats, particularly where populations are data limited.

KEYWORDS: Bayesian, data-limited fisheries, habitat-based model, hierarchical models, population assessment, Sockeye Salmon

LAY SUMMARY

Evaluating the status of data limited fish populations to inform fisheries management is a core challenge for the sustainability of fisheries around the world. In Canada's remote North and Central Coast region, hundreds of salmon populations are lacking in formal assessment to define management benchmarks. One opportunity to improve the available information about population status and inform sustainable fisheries management is to integrate habitat-based insights with traditional spawner–recruit modeling to estimate stock status and management benchmarks for data-limited populations. Most Sockeye Salmon rear in freshwater lakes for 1–2 years prior to their seaward migration, and maximum population sizes are limited by the size and productivity of their rearing lake. Using a Bayesian-hierarchical modeling

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approach, we integrated information on lake size and productivity into a Ricker spawner–recruit model as prior information for 69 Sockeye Salmon populations on the remote North and Central Coast of British Columbia. We further evaluated the benefits incorporating regional biogeographic differences in productivity—the number of offspring produced at low spawner abundance—into models that we used to estimate the status of Sockeye Salmon populations. Overall, we found that this Bayesian-hierarchical approach greatly reduced uncertainty in the estimated population parameters that are used to inform assessments of stock status, particularly for the most data-limited populations that we evaluated.

INTRODUCTION

Assessing population status and estimating conservation or management targets for data-limited fish populations is a major challenge to the sustainability of fisheries. In the absence of information to support management, many small, unassessed fisheries around the world are depressed due to overfishing (Costello et al., 2012). Overfishing has resulted in the loss of billions of metric tons in potential fisheries yields per year (Ding et al., 2017), creating economic hardship and undermining food security in coastal communities (Golden et al., 2016). Given this challenge, a variety of approaches have been proposed for setting management targets without lengthy time series of population abundance and thus limited data. These range from management that relies on local knowledge rather than stock-assessment data (Johannes, 1998) to quantitative approaches such as meta-analyses that combine information from multiple sources to reduce the uncertainty that is associated with sparse time series of abundance within populations (Myers & Mertz, 1998; Punt et al., 2011).

Meta-analytic approaches allow researchers to combine insights from multiple populations and are a valuable tool for understanding and managing populations with limited data (Myers & Mertz, 1998). These analyses rely on the assumption that population parameters are drawn from a shared underlying distribution. Under this assumption, population parameters can be readily estimated for data-limited populations by borrowing information from populations with more robust time series (Gelman, 2006; Thorson & Minto, 2015). Similarly, researchers now routinely share information across populations using hierarchical-Bayesian methods, which assume that some population parameters are drawn from common hyperdistributions (Punt & Hilborn, 1997). These approaches have been used to examine spawner–recruitment relationships (e.g., Liermann & Hilborn, 1997; Michielsens & McAllister, 2004) and understand the effects of climate on recruitment across multiple populations (e.g., Mueter et al., 2002).

Another potential approach to inform management in data-limited fisheries involves predicting management-relevant parameters based on habitat information when habitat limits production (e.g., Sundblad et al., 2014). For fish populations where density-dependent dynamics occur in well-delineated habitats, such as the use of freshwater habitat by juvenile salmon, habitat quantity and the productivity and structure of food webs can impose constraints on the carrying capacity of fish populations (Shortreed et al., 2001). For example, the amount and gradient of available stream-rearing habitat has been used to predict Coho Salmon *Oncorhynchus kisutch* production (Bocking & Peacock, 2004; Bradford et al., 1997) and accessible watershed area has been used to inform estimation of population parameters in data-limited Chinook Salmon *O. tshawytscha* populations (Liermann et al., 2010; Parken et al., 2006). Hume et al. (1996) used data from several populations with juvenile enumeration (i.e., fall fry or smolt) and limnological monitoring (including photosynthetic rate [PR]) to model the empirical relationship between optimal smolt biomass outputs and total autotrophic production. This relationship has subsequently been used to predict the carrying capacity for approximately 60 lakes in coastal British Columbia and most interior nursery lake systems (e.g., Shortreed et al., 1998, 2001, 2007). Although spawner–recruitment modeling is data intensive, often requiring decades-long time series, these habitat-based models may improve the fit of shorter spawner recruitment time series (e.g., Korman & English, 2013; Liermann et al., 2010) and only require information on available habitat that could be estimated remotely using geospatial analysis or with as little as a single year of field sampling. By coupling data from populations with intensive population monitoring and known habitat constraints for the species of interest, researchers can model the underlying relationship between habitat conditions and population parameters that are estimated from spawner–recruitment time series (e.g., Hume et al., 1996; Parken et al., 2006). This relationship is then extended to estimate biological reference points such as carrying capacity or maximum sustainable yield (MSY) for fish populations. These habitat-based estimates of capacity can be merged with spawner–recruitment analyses in a Bayesian framework, either through their inclusion in the model as a covariate modifying the unfished equilibrium population size (e.g., Liermann et al., 2010) or as a population-specific prior on the spawner abundance that produces maximum recruitment, S_{Max} (Korman & English, 2013).

Sockeye Salmon *O. nerka* are a primary target of commercial, Indigenous subsistence, and recreational fisheries in coastal British Columbia and Alaska. Understanding the status and capacity of remote Sockeye Salmon populations is particularly important to coastal First Nations in British Columbia. The food security, culture, and livelihoods of these communities are intimately linked to Pacific salmon, and Indigenous Nations are increasingly assuming leadership of resource monitoring and management within their traditional territories. Managing Sockeye Salmon fisheries for sustainable economic and cultural benefits is a primary goal (e.g., Atlas et al., 2017). Thus, methods that integrate multiple sources of information on populations and their habitats are needed to inform the management of data-limited Sockeye Salmon populations for sustainable social–ecological benefits. Most Sockeye Salmon have an obligate juvenile lake-rearing phase of 1 or 2 years prior to their seaward migration, during which time they feed on zooplankton and invertebrates (Groot & Margolis, 1991). Given this dependence on rearing habitat in lakes, lake size and the transfer of energy through food webs can control the carrying capacity of Sockeye Salmon populations (Hyatt & Stockner, 1985; Juday et al., 1932; Shortreed et al., 2001). Smolt-to-adult

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survival during the marine phase of the Sockeye Salmon life cycle is also a main driver of population productivity, with major regime shifts in ocean climate implicated in interannual and decadal changes in the productivity of wild salmon populations (Mantua et al., 1997; Mueter et al., 2002; Peterman & Dorner, 2012).

Canada's Wild Salmon Policy calls for the establishment of biological benchmarks for evaluating population status and implementing management and recovery efforts. Although Sockeye Salmon are relatively well studied in many parts of their range, time series of spawner abundance and recruitment are often sparse in more remote regions and for smaller populations, creating challenges for setting management goals and conservation benchmarks. Conservation benchmarks, which rely solely on biological information, differ from management targets, which consider socioeconomic factors (Holt & Irvine, 2013). The North and Central Coast (NCC) of British Columbia is a region where the development of such benchmarks has proven a challenge but is of timely importance. The NCC is remote and vast, covering more than 175,000 km^2, and there are more than 120 genetically and demographically distinct populations of lake-type Sockeye Salmon, designated as Conservation Units under the Wild Salmon Policy. A few well-studied populations, which historically supported large commercial fisheries, have been assessed as currently depressed (Connors et al., 2019; McKinnell et al., 2001; Price et al., 2019), but most watersheds in the NCC region are remote and only accessible by boat or air, making consistent population monitoring logistically challenging and costly. Furthermore, many of these populations are small, with average run sizes of fewer than 10,000 fish, and monitoring efforts have historically been focused on the largest and most commercially important populations.

Here we integrate habitat-based and hierarchical population-dynamic based approaches to characterize the dynamics of 69 populations of Sockeye Salmon in coastal British Columbia. Specifically, we developed hierarchical-Bayesian models of spawner–recruit dynamics for Sockeye Salmon, integrating information on lake water clarity (clear, stained, glacial), biogeography (interior, fjord, coastal), productivity (PR), and surface area through the inclusion of habitat-based estimates of carrying capacity as prior information to ask how informative habitat priors and hierarchical modeling approaches can support improved precision and accuracy of biological benchmarks for data-limited freshwater-rearing salmonids.

METHODS

Overview

For each of 69 Sockeye Salmon populations, we fit spawner–recruitment models to time series of spawner abundance and catch to estimate productivity, carrying capacity, and S_{MSY}. We then compared four model structures to evaluate the potential advantages of incorporating hierarchical grouping structures across populations and applying informed priors that we derived from PR models. For most populations with age data, average broodyear age composition was used to estimate recruitment per spawner across these time series, except in the Babine, Meziadin, Owikeno, and Long Lake populations, where annual age data were available for some or all years, allowing more precise estimates of broodyear recruitment (English et al., 2018; Supplement 1 [see online Supplementary Material]). These spawner–recruit models incorporated habitat-based priors that were drawn from 66 limnological assessments across 28 years that were conducted by the Fisheries and Oceans Canada (DFO) Lakes Research Program in Sockeye Salmon-bearing lakes of the NCC (e.g., Shortreed et al., 1998, 2001, 2007). These data were then combined in a series of models to evaluate the degree to which information on the location and productivity of rearing habitats could inform hierarchical model structure and provide prior information on the spawner abundance to maximize recruitment (i.e., S_{Max}, the inverse of the Ricker β parameter, Equation 1, which is the spawner abundance that produces maximum recruitment, S_{Max}). We assessed the advantages of hierarchical groupings and habitat-based priors by comparing the predictive accuracy of each model form for recruits per spawner.

Escapement and catch data

We used spawner abundance and harvest data from 69 populations on the NCC that have been collected since the 1950s by DFO. Following English et al. (2018), we assumed that neighboring populations within management areas have similar run timing and distribution and are therefore similarly vulnerable to coastal fisheries. As a result, in cases where harvest data were not available for a specific population, we used the average harvest rate for other populations in the same DFO statistical area to reconstruct catch (e.g., Pacific Salmon Foundation, 2022; $n = 49$). These data represent the best available information on harvest rates over time but should be interpreted with caution when neighboring populations diverge in their respective vulnerability to fisheries. Harvest rates ranged from more than 70% in the early part of the time series for some populations to less than 10% in more recent years. The quality and availability of age data were highly variable across populations. We used annual or average population-specific empirical estimates of age composition where they existed ($n = 5$ high quality, $n = 19$ lower quality). For populations lacking age composition data ($n = 45$), we predicted average brood-year age composition using a multinomial Dirichlet regression technique, as described in Supplement 1.

We then used the available age data and the model estimates of age composition to construct brood tables that were used to assign recruits to previous parent cohorts to estimate the relationship between spawner abundance and recruitment. We examined each population time series individually, identifying and removing years that produced unreasonably high estimates of per capita recruitment that exceeded the observed maximum productivity for Sockeye Salmon populations around their northeast Pacific range (more than 20 adult recruits per spawner; Cunningham et al., 2015; Dorner et al., 2008; McPherson & Woodey, 2009). These outliers were likely attributable to poor data quality or extrapolated estimates of harvest that inflated per capita recruitment. We also dropped data points of fewer than 100 spawners, as population sizes that small are rare and are likely a reflection of poor data quality (English et al., 2018). This process resulted in the elimination of 73 data points out of a possible 1,850 spawner–recruit pairs. Data richness varied widely across the 69 populations of interest, with the number

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of spawner–recruit pairs ranging from 4 to 57 (Supplement 1). For the purposes of our analysis, populations with fewer than 20 spawner–recruit pairs were classified as data poor, those with 20–39 spawner–recruit pairs were classified as moderate in data richness, and populations with more than 40 spawner–recruit pairs were classified as data rich.

Ricker model of spawner–recruit dynamics

We modeled density-dependent population dynamics for each time series of spawner abundance (S) and recruitment (R) for populations (i) using a Ricker model (Ricker, 1954) with lognormally distributed error, ε, where α is per capita productivity (slope) at the origin and β dictates the strength of density-dependence (Equation 1).

$$\ln(R_{i,t}/S_{i,t}) = \ln(\alpha_i) - \beta_i S_{i,t} + \varepsilon_{i,t}. \qquad (1)$$

$$S_{Max_i} = 1/\beta_i.$$

$$\varepsilon_{i,t} \sim \text{normal}(0, \sigma^2{}_i).$$

This equation has been widely used for stock assessment of Sockeye Salmon, in part because it can be transformed into a linear relationship by taking the natural log of the number of recruits per spawner at a given population size (e.g., Connors et al., 2019; Cunningham et al., 2015; Korman & English, 2013). The spawner abundance that maximizes recruitment (S_{Max}) is estimated as the reciprocal of β.

The common biological reference point, S_{MSY}, was calculated using the exact solution proposed by Scheuerell (2016):

$$S_{\text{MSY}_i} = \frac{1 - W(e^{1-\alpha_i})}{\beta_i}, \qquad (2)$$

where W is the Lambert function (Equation 2). More details of the Lambert function are provided in Scheuerell (2016).

Photosynthetic rate model

To provide prior information on the spawner abundance that maximizes recruitment (S_{Max}), we used empirical and predicted model estimates derived from the PR model developed by Hume et al. (1996) and refined by Shortreed et al. (2000; $S_{Max_{\text{PR}}}$). Hourly and daily PRs were estimated in situ to measure autotrophic uptake of inoculated ^{14}C isotopes (see Shortreed et al., 1998 for detailed methods). These hourly estimates of PR were typically made multiple times over a growing season and temporally expanded to daily rates and seasonal mean PRs by previous limnological researchers using an assumed growing season length (May 1–October 31) and lake surface area to estimate total carbon attenuation by primary producers per annual growing season (Shortreed et al., 2000).

The PR model assumes that Sockeye Salmon populations are limited by lake productivity and area, and previous research found that in most cases, this assumption is valid (Shortreed et al., 2001). Hume et al. (1996) used the correlation between empirically derived estimates of S_{Max} and total annual primary production (PR_{Total}) to estimate S_{Max} for lakes using only PR data ($S_{Max_{\text{PR}}}$). This effort yielded a relationship between annual lake productivity and Sockeye Salmon population capacity that has subsequently been used to estimate carrying capacity in lakes across the NCC (Shortreed et al., 1998, 2001, 2007). The model assumes a fixed relationship between lake productivity and maximum smolt output, thus PR_{Total} (metric tons of carbon per year) can be multiplied by the constant 187 (spawners per metric ton of carbon) to yield an estimate of the number of adult spawners required to maximize smolt production (Equation 3; Shortreed et al., 2000):

$$S_{Max_{\text{PR}}} = 187 \times \text{PR}_{Total}. \qquad (3)$$

In most applications, PR measurements are made throughout the growing season, accounting for seasonality in primary production (see Shortreed et al., 2001 for a summary). However, across the numerous remote NCC lakes, access is difficult and assessment costs can be high. Thus, as a preliminary approach, single estimates of PR made in late August or early September have been related to seasonal mean PR values via linear regression, demonstrating correlations between single late-season PR values and with seasonal mean values ($R^2 = 0.604$), with single late-season PR values typically producing estimates within 8% (1 SD) of the seasonal mean (Cox-Rogers et al., 2004). We compiled estimated annual PR values and associated $S_{Max_{\text{PR}}}$ values for 55 Sockeye Salmon rearing lakes across the NCC from DFO reports (Supplement 1). The PR data that were used in our analysis therefore include estimates that were derived from repeated sampling during the growing season ($n = 18$) and from late-season PR measurements that were converted by the DFO lakes assessment program to an estimate of growing season PR using the regression-based approach ($n = 37$). When estimates of annual primary production (PR_{Total}) were available for multiple years (n lakes = 8, see Table S1 and Figure S2 in Atlas et al., 2020), we used the average of these estimates as our prior. In other cases, multiple lakes support rearing Sockeye Salmon within a single population (e.g., Elbow, Lonesome, and Rainbow lakes for Atnarko Sockeye Salmon), and the priors reflected the sum of productivity of all lakes that are known to support Sockeye Salmon rearing.

Although empirical field measurements of PR were only available for 41 of 69 populations in our study, recent modeling efforts have led to the creation of a landscape-scale predictive model for lake PR across the NCC (Atlas et al., 2020). These efforts found that the lake productivity (PR) of Sockeye Salmon was reasonably well predicted by whether the lake is clear, humic stained, or glacially turbid and by a suite of other landscape-scale factors. Therefore, we used predicted $S_{Max_{\text{PR}}}$ values from this landscape model as mean priors for S_{Max} in populations where the rearing lakes were unsampled for PR. For all lakes, we inferred uncertainty in $S_{Max_{\text{PR}}}$ from the empirical estimates of the standard deviation of lake variation in $S_{Max_{\text{PR}}}$, by water clarity group, which we assumed coarsely approximated the true uncertainty arising from measurement error and year-to-year variation in lake productivity, expressed as $\sigma_{S_{Max_{\text{PR}}}}$. For more information on data sources and methods, see Supplement 1.

Spawner–recruit statistical models

To evaluate the effects of estimating productivity (α) hierarchically and using $S_{Max_{\text{PR}}}$ as an informative prior, we estimated

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Ricker spawner–recruitment parameters for each population (i) using six models with increasing complexity. First, a simple status quo model was fit to each population; then, two hierarchical models were fit that structure productivity: one from a single shared distribution among all populations and another by three regional groupings. Another model was fit where each population had independent productivity estimates, with an informative capacity prior based on S_{MaxPR}, and a final set of two models included both forms of hierarchical productivity and informative capacity priors. Full model specifications and associated code are available in Supplement 2 (see online Supplemental Material).

General descriptions of the models are as follows:

Model 1. All parameters were estimated independently for each of the 69 populations following Equation (1). This was the simplest or status-quo model. Priors were weakly informative to constrain parameter estimates to be biologically plausible with

$$\ln(\alpha_i) \sim \text{normal}(1.5, 2), \tag{4}$$

$$\beta_i \sim \text{lognormal}(-12, 5),$$

and

$$\varepsilon_i \sim \text{normal}(1, 1),$$

where ε_i and variance parameters henceforth had a lower bound of 0.

Model 2a. Productivity (α_i) and error (σ_i) were estimated hierarchically, where population-specific deviations were drawn from a shared or global distribution (α_0, σ_0), to evaluate the benefits of the hierarchical model structure for improved precision and reduced uncertainty in the estimates of S_{MSY}. As in model 1, an uninformative prior was used for β_i (Equation 5).

$$\ln(\alpha_i) \sim \text{normal}\ [\ln(\alpha_0), \sigma^2{}_{\alpha_i}]. \tag{5}$$

$$\ln(\alpha_0) \sim \text{normal}(1.5, 2).$$

$$\sigma^2{}_{\alpha_i} \sim \text{gamma}(2, 3).$$

$$\varepsilon_{i,t} \sim \text{normal}(0, \sigma^2{}_i).$$

$$\sigma^2{}_i \sim \text{normal}(\sigma^2{}_0, \sigma^2{}_{\sigma_i}).$$

$$\sigma^2{}_0 \sim \text{normal}(1, 1).$$

$$\sigma^2{}_{\sigma_i} \sim \text{normal}(0, 1).$$

Model 2b. The Sockeye salmon bearing watersheds of the NCC span broad hydrological and climatological gradients, from low elevation coastal bog forest through deep mountainous fjords and into the interior plateau. Given the potential differences in environmental conditions influencing Sockeye Salmon productivity across these three regions, we also evaluated whether there was support for including three regional groupings of productivity, by fitting the model with region-specific deviations from the global α_0 (Z_r) that correspond to the biogeoclimatic regions defined by Holtby and Ciruna (2007) for Pacific salmon (i.e., coastal, fjord, interior). Model 2b (Equation 6) followed the structure and weakly informative priors in model 2a, with the exception of the structure and new priors of productivity (α_i):

$$\ln(\alpha_i) \sim \text{normal}(\ln(\alpha_r), \sigma^2_{\alpha_i}), \tag{6}$$

$$\ln(\alpha_r) \sim \text{normal}(\ln(\alpha_0), \sigma^2{}_{\alpha_r}),$$

and

$$\sigma_{\alpha_r} \sim \text{gamma}(2, 3),$$

where $\ln(\alpha_r)$ is a regional estimate of productivity and σ_{α_r} is the variance in productivity among regions, with other priors for $\ln(\alpha_0)$ and $\ln(\alpha_0)$ following Equation 5.

Model 3. We used informative priors for β_i based on S_{MaxPR} to evaluate the potential for the inclusion of habitat-based priors to improve the accuracy and reduce uncertainty in the spawner–recruitment fits. Productivity (α_i) and error (σ_i) were estimated independently for each population as in Equation 1, but the model (Equation 7) used an informative prior on β_i:

$$\beta_i \sim \text{lognormal}(1/S_{MaxPR_i}, 1/\sigma_{S_{MaxPR_i}}). \tag{7}$$

A lognormal bias correction (Quan & Zhang, 2003) was applied when converting beta priors into log space.

Models 4a and 4b. Productivity (α_i) and error (σ_i) were estimated hierarchically as in models 2a and 2b, paired with an informative prior for β_i as in model 3. These models leveraged both hierarchical structure and informative priors to evaluate the benefits of merging these approaches. We tried both hierarchical structures laid out in models 2a and 2b to see which performed better and whether any problems arose from having a habitat-based metric inform both the hierarchical structure and act as a prior.

Model fitting and diagnostics

All the models were fit to the data in a Bayesian estimation framework with Stan (Carpenter et al., 2017; Stan Development Team, 2020) using the *rstan* R package (Stan Development Team, 2020), which implements the no-U-turn Hamiltonian Markov chain–Monte Carlo algorithm (Hoffman & Gelman, 2014). We generated a joint posterior probability distribution of all unknown parameters in each model. The models sampled 16,000 iterations over four chains and discarded the first half as warm-up (8,000 iterations total). We assessed chain convergence visually via trace plots and by ensuring that $\hat{R}$ (potential scale reduction factor; Vehtari et al., 2021) was less than 1.05 and that the effective sample sizes of all parameters were greater than 800, or 10% or the iterations. Posterior predictive checks were used to make sure that the model returned predictions similar to the observations.

Predictive performance

We assessed model performance using cross validation, whereby we randomly sampled half of each population's

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Table 1. Model predictive performance as ranked by stacked model weights from out-of-sample cross validation, including change in exact log-posterior density from the top model (Δelpd) and change in standard error from the top model (ΔSE). The Note column contains any model warnings (i.e., divergent transitions) or issues that were flagged during model diagnostics, which are available in Supplement 2.

Model	Description	Stacked weight	Δelpd	ΔSE	Note
m4b	Regional-hierarchical productivity and informative capacity	0.6099	0	0	35 divergent transitions
m2b	Regional-hierarchical productivity	0.3246	−39.64	18.99	4 divergent transitions, maximum R-hat = 1.14, low minimum effective sample size
m1	Status quo	0.0654	−173.38	22.91	Maximum R-hat = 1.09, low minimum effective sample size
m4a	Hierarchical productivity and informative capacity	0.0001	−11.09	2.72	
m2a	Hierarchical productivity	0	−34.86	17.02	Low minimum effective sample size
m3	Informative capacity only	0	−159.41	16.51	Low minimum effective sample size

spawner–recruit observations, which were removed for model fitting and reserved to score predictive accuracy. Each model was refit to the remaining observations, and the likelihood was computed for each out-of-sample observation based on the model predictions. Observations within a time series were randomly thinned because the models are static, assuming no temporal trends in productivity or capacity. This (computationally intensive) cross-validation procedure was repeated five times to account for variability in the inferences when randomly sampling observations. Both the population-specific and aggregate (including all populations) out-of-sample likelihoods among the five randomization sets were converted into model weights to compare general model predictive performance. We used Bayesian stacking weights to evaluate relative model support (Yao et al., 2018), implemented in the R package *loo* (Vehtari et al., 2017), as this method is ideal for comparing predictions from nested model forms.

Stock status

Although the focus of this article is primarily methodological, we used our estimates of S_{MSY} from the aggregated top model to illustrate how stock status can be estimated among Sockeye Salmon populations in the NCC region. We evaluated stock status by dividing the mean of the past 10 years of spawner estimates, when available, to our estimate of S_{MSY} to calculate a common metric of status: S/S_{MSY}.

RESULTS

The model diagnostics and convergence varied by model type, and there appeared to be difficulties with estimating the β parameters in models 1, 2a, and 2b with uninformative priors. The posterior predictive checks showed that the model returned data that fit the model reasonably well; rather than omitting data poor populations or removing models, we kept these issues in mind and continued with our analysis for assessing predictive performance. Diagnostic statistics are available in Supplement 2.

Across populations, model 4b, which included regional-hierarchical productivity and an informative $S_{Max_{\mathrm{PR}}}$ prior, had the best predictive performance, carrying 61% of the model weight (Table 1). Next was model 2b, with regional-hierarchical productivity and uninformative capacity priors, carrying 32% of the weight, and then model 1, or the status quo model, carrying 0.07% of the model weight. This demonstrates the utility of combining hierarchical structure informed by biogeographic differences in habitat productivity, and informative habitat-based priors on S_{Max}, as these models greatly outperformed nonhierarchical models even when they contained informative priors, as in model 3, or in hierarchical models that did not consider regional differences in habitat (for example, as in the ungrouped structure in model 2a). In data-limited populations, productivity posteriors generally shrunk toward the mean among all populations as the models gained complexity (Figure 1, left column,), although this was not as pronounced in populations with more data (Figure 1, middle and right columns). Including an informative prior only (model 3) sometimes had the effect of pulling the posterior away from other models, but this was mediated when including a hierarchical component in models 4a and 4b (e.g., Johnston et al.; Figure 1). The populations in Figure 1 are a random, illustrative subset of populations across data amounts and regions; full posterior distributions of productivity, capacity, and S_{MSY} are available for all models and populations in Supplement 2.

The data-limited populations generally had reduced uncertainty in the parameter estimates when including regional-hierarchical productivity, particularly for the more data-limited populations (Figure 2; Supplement 2). On average, the precision of estimates of S_{MSY} from model 4b were much lower (by an average of 11 CV units) than they were for the next most parsimonious model (2b) model. The regional-hierarchical model tended to reduce the magnitude of expected recruitment at high spawner abundances relative to the shape of the status quo relationship in some populations (e.g., Owikeno, Atnarko; Figure 2), potentially due to the uninformative prior allowing for much higher estimates of S_{Max} to be explored in the status quo model (See beta posteriors in Supplement 2 for these populations). When looking at the fits from the top model (4b), the interior populations had slightly higher productivity than both the coastal fjord and low coastal populations (Figure 3).

We compared population-specific stacked out-of-sample likelihood weights between models 4b and 1 to explore

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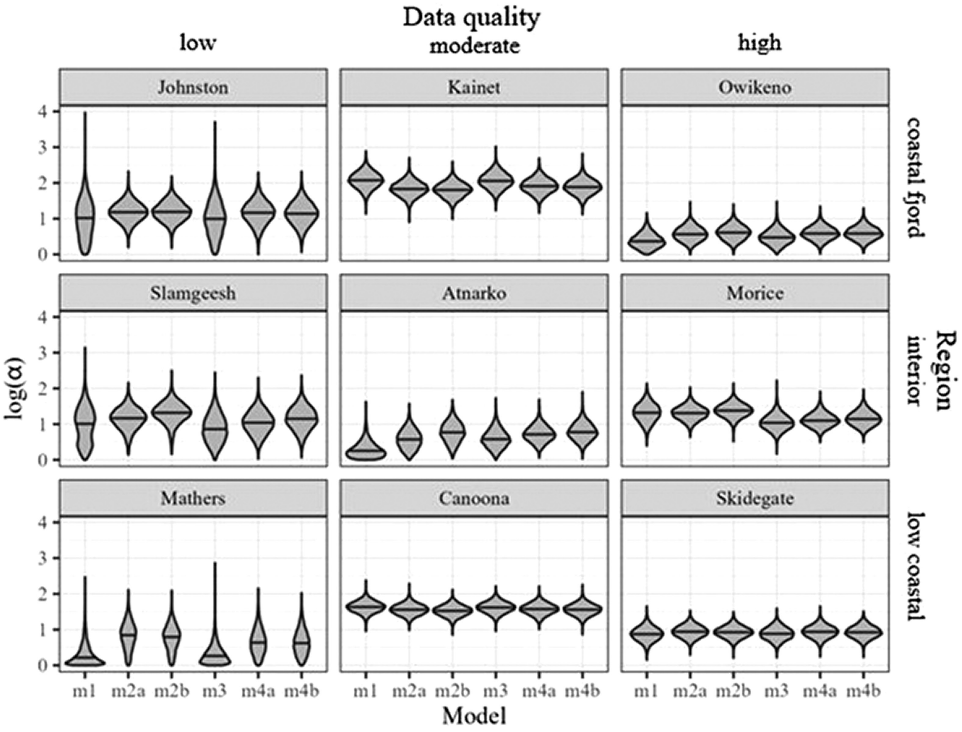

Figure 1. Estimated values for the natural log of α (population productivity) by model type. A subset of populations (inset labels) is shown and organized by amount of data (columns) and region (rows). Populations were randomly selected and are illustrative; the distributions from all populations, models, β, and S_{MSY} parameters are available in Supplement 2.

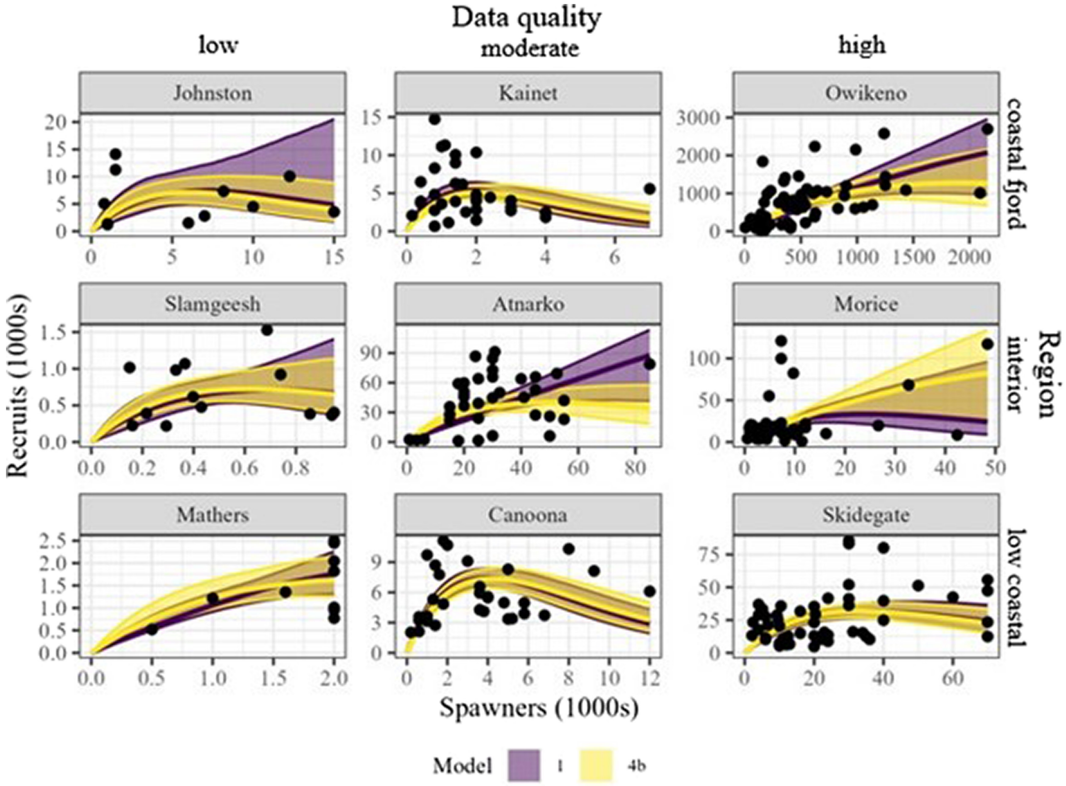

Figure 2. Estimated Ricker spawner–recruit fits and uncertainty for spawner–recruit dynamics in nine populations, where the columns represent data richness (low, medium, high; left to right) and the rows are regions (coastal fjord, interior, and low coastal; top to bottom). The purple line depicts the median Ricker model fit for each population independently (model 1) and the shaded area is the 80th percentile of this model fit. The yellow line and shaded area depict the median Ricker model fit for each population when we included regional hierarchical estimation of productivity (α) and photosynthetic-rate-based priors on S_{Max} (model 4b).

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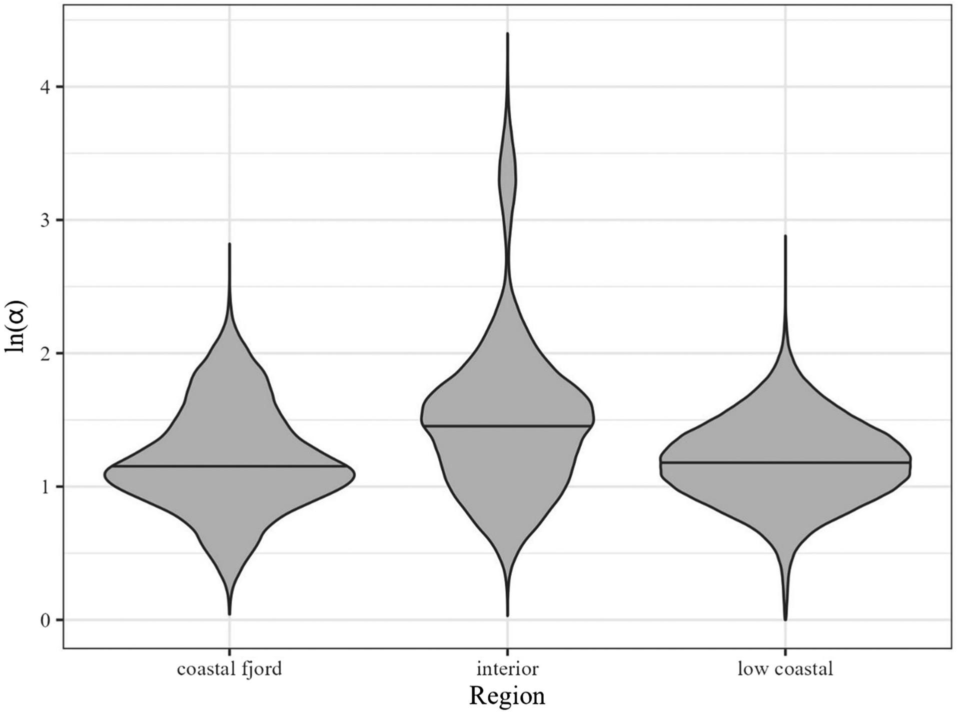

Figure 3. Estimates of productivity from all populations in the top model, model 4b, grouped by region.

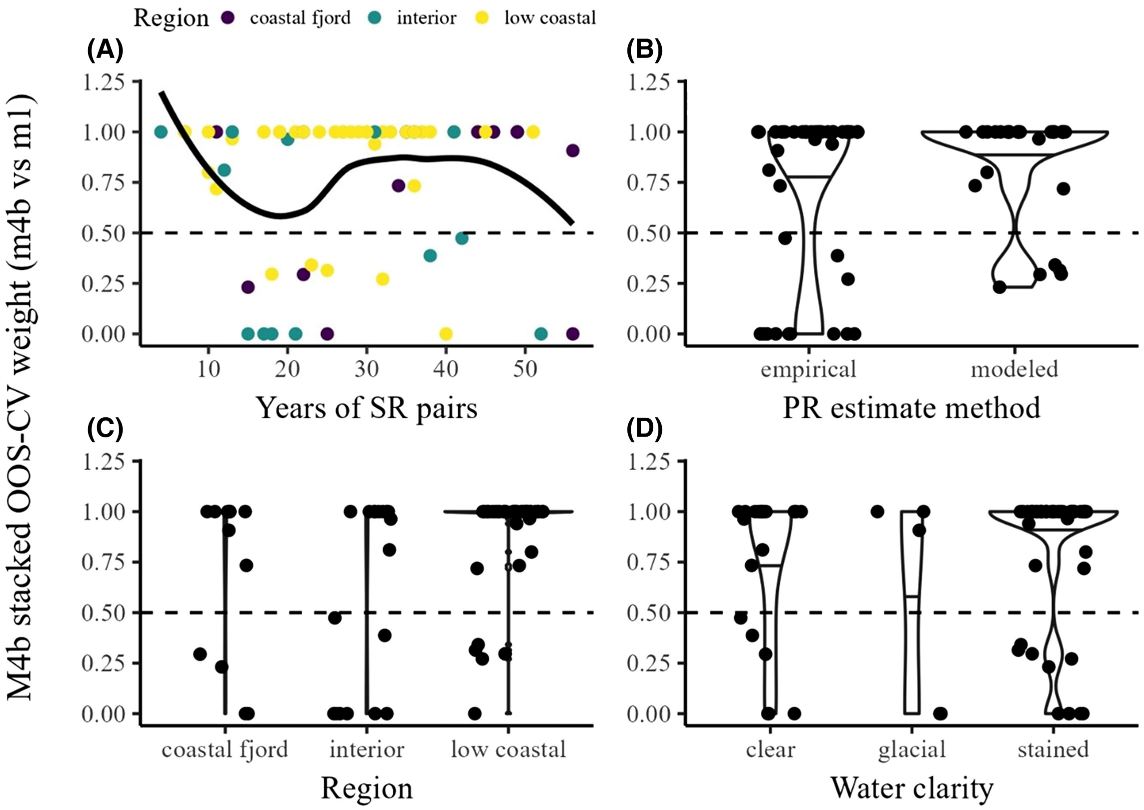

Figure 4. Relative stacked out-of-sample likelihood weight of the top model relative to the status quo (i.e., models 4b and 1) by population, where LOOIC (leave one out information criterion) stacking weights are calculated on five runs of randomly selected out-of-sample data: Panel (A) shows the weight for the top model relative to the number of stock–recruitment pairs and region with a simple LOESS (locally estimated scatterplot smoothing) smoother to aid visualization, panel (B) compares support by the $S_{Max_{PR}}$ estimation method, panel (C) compares support by region, and panel (D) compares support by lake water clarity group. OOS-CV = out of sample coefficient of variation; SR = spawner-recruit.

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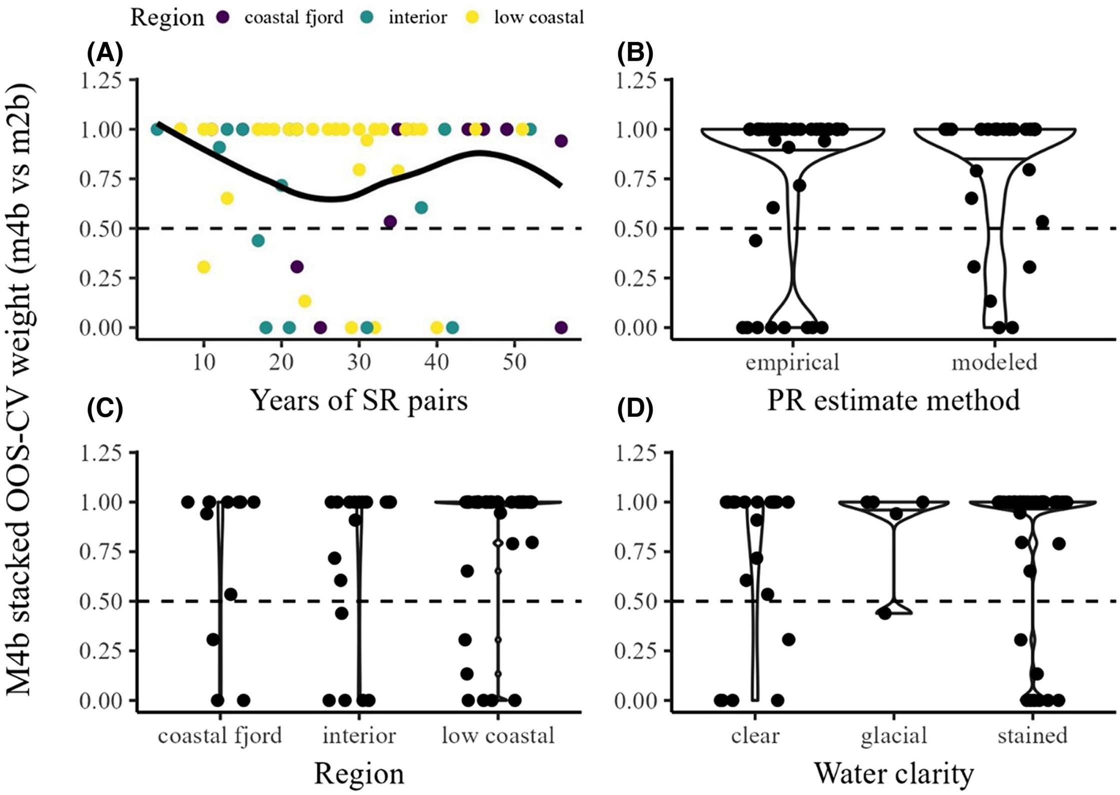

Figure 5. Relative stacked out-of-sample likelihood weight of top models with (4b) and without (2b) informative priors: (A) shows the weight for the top model relative to the number of stock–recruitment pairs and region with a simple LOESS (locally estimated scatterplot smoothing) smoother to aid visualization, (B) compares support by the $S_{Max_{PR}}$ estimation method, (C) compares support by region, and (D) compares support by lake water clarity group. PR = photosynthetic rate.

the performance of the top model relative to the status quo approach (model 1) by amount of data, PR estimate method, region, or lake water clarity group. Strong trends did not emerge when making these comparisons, but there was some weak support for including the added complexity when data were limited (Figure 4A); most populations favored model 4b over model 1 when compared directly. We repeated this exercise by comparing models 4b and 2b to look more closely at where including the informative prior helped (Figure 5). Inference was similar to the comparisons between models 4b and 1, with some evidence for the more complex model (model 4b) being particularly helpful for data-limited populations.

Assessment of population status

Recent estimates of spawner abundance (since 2014) were only available for 48 of the 69 populations. We assessed population status using the median estimate of S_{MSY} from the model with the highest predictive performance (4b). Of these populations with recent data, one-third had mean spawner escapements above S_{MSY} and the remaining two-thirds were below S_{MSY} (Figure 6). Population status relative to S_{MSY} exhibited substantial variability across NCC Sockeye Salmon populations (max = 4.01 in Mathers Lake; min = 0.11 in Swan Lake). No clear regional pattern in status was apparent for the Sockeye Salmon populations across the NCC; however, the level of population monitoring and our ability to evaluate population status did differ across biogeographic regions. The interior populations were most likely to be assessed, with 15 of 19 populations having sufficient monitoring data to evaluate status, and coastal fjord populations were reasonably well assessed, with 8 of 12 populations having recent escapement data with which to evaluate status. The low coastal populations were far less likely to be monitored in the past decade, with only 20 of 38 populations having recent data with which to assess status.

DISCUSSION

We developed and applied spawner–recruitment models that incorporate habitat information to assess the conservation status of Sockeye Salmon populations across the NCC of British Columbia. The results for model selection revealed support for the use of a hierarchical Bayesian spawner–recruitment model that combines a regional-hierarchical grouping of stock productivity with lake habitat information to estimate population productivity (α) and spawner abundance at carrying capacity (S_{Max}) for 69 populations. Model weights that were derived from out-of-sample likelihoods first supported using a regional-hierarchical grouping of stock productivity and lake-based PR estimates as a prior for S_{Max} in the spawner–recruitment models. This regional-hierarchical model revealed new management-relevant insight into regional differences in productivity (α), with populations spawning in interior watersheds exhibiting the highest average productivities and populations spawning in low elevation coastal watersheds exhibiting the lowest average productivities.

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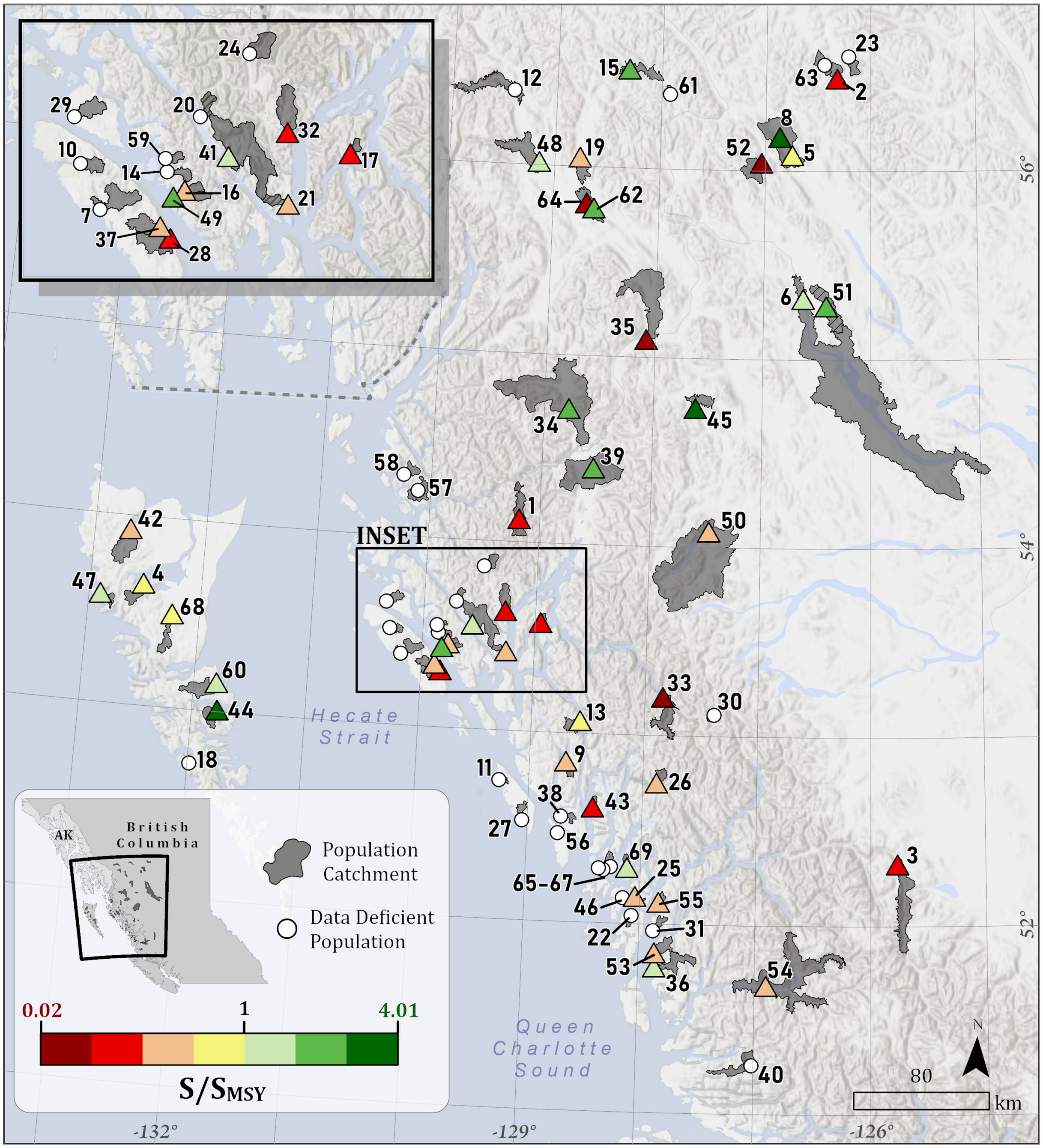

1	Alastair	10	Bonilla	19	Fred Wright	28	Keecha	37	Kooryet	46	Mcloughlin	55	Port John	64	Swan
2	Asitika	11	Borrowman	20	Freeda Lakes	29	Keswar	38	Kwakwa	47	Mercer	56	Price	65	Tankeeah
3	Atnarko	12	Bowser	21	Hartley Bay	30	Kimsquit	39	Lakelse	48	Meziadin	57	Prudhomme	66	Tuno East
4	Awun	13	Canoona	22	Hauyat	31	Kisameet	40	Long	49	Mikado	58	Shawaltan	67	Tuno West
5	Azuklotz	14	Curtis Inlet	23	Johanson	32	Kitkiata	41	Lowe	50	Morice	59	Sheneeza	68	Yakoun
6	Babine	15	Damdochax	24	Johnston	33	Kitlope	42	Marian Eden	51	Morrison	60	Skidegate	69	Yeo
7	Banks	16	Devon	25	Kadjusdis	34	Kitsumkalum	43	Mary Cove	52	Motase	61	Slamgeesh		
8	Bear	17	Evelyn	26	Kainet	35	Kitwancool	44	Mathers	53	Namu	62	Stephens		
9	Bloomfield	18	Fairfax	27	Kdelmashan	36	Koeye	45	Mcdonell	54	Owikeno	63	Sustut		

Figure 6. Mean estimates of spawning escapement since 2014 (S) divided by the median estimate of S_{MSY} from model 4b.

The added complexity of the top model seemed to benefit the data-limited populations the most. The top model (model 4b) produced estimates of biological benchmarks that were more robust to data limitations and provided stronger predictive performance than alternatives. When data were available (i.e., 48 of 69 populations), we found that 66% of NCC Sockeye Salmon populations had average annual spawner escapements that were below their estimated S_{MSY} in the past two generations (i.e., since 2014). Our analysis extends recent work to synthesize existing data and assess the status of NCC salmon by incorporating habitat-based priors for carrying capacity (Connors et al., 2018). These results demonstrate the utility of combining

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spawner–recruitment-based population assessments with habitat information to bolster that spawner–recruitment model estimates of population parameters that underlie management and recovery planning for Sockeye Salmon and other freshwater-rearing salmon. Given the dearth of stock assessment data for many NCC Sockeye Salmon populations, there is an opportunity to link existing data on spawner and recruit abundance with habitat-derived estimates of lake capacity to generate conservation benchmarks and management targets for data-limited populations across the region.

In recent decades, hierarchical models assuming a common distribution for productivity (α) have become commonplace in fisheries stock assessment (Thorson & Minto, 2015), as populations of the same species often face the same biophysical constraints on their productivity (Myers & Mertz, 1998). Reduced uncertainty and shrinkage toward the population mean are relevant from a conservation and management standpoint because productivity has a direct influence on estimates of sustainable harvest rates and the expected rate of population recovery from low population sizes—as is presently the case for Sockeye Salmon in the NCC regions. In general, this shrinkage toward population mean productivity (α) will result in more biologically conservative estimates of sustainable harvest rates in populations with high productivity but less biologically conservative harvest management in populations with low productivity. For example, the estimated productivity (α) of Kainet Sockeye Salmon is higher when it is estimated independently (model 1), with shrinkage toward the regional average productivity in the regional-hierarchical model (model 2b). In contrast, for Atnarko and Owikeno, two collapsed but culturally and economically important Sockeye Salmon populations, the regional-hierarchical productivity estimates are higher than those that were estimated independently for each population.

Our work demonstrates the potential utility of consistent limnological assessments of Sockeye Salmon nursery lakes to inform conservation and management targets. Estimates of capacity based on PR can typically be made with data from one or a few years (Hume et al., 1996; Shortreed et al., 2000), whereas producing reliable estimates of capacity with spawner–recruitment modeling requires decades of continuous monitoring of abundance. Given the fundamental constraints that are imposed by lake productivity and size for most lake-rearing Sockeye Salmon populations (Groot & Margolis, 1991; Shortreed et al., 2001), inclusion of this information through the specification of priors is a logical way to narrow the range of possible values for S_{Max} in a population. Our estimates of S_{MSY} from our hierarchical habitat-based model (model 4b) were consistent with previous escapement targets that were derived from a variety of spawner–recruitment- and habitat-based approaches in well-studied populations like the one in Meziadin Lake (Bocking et al., 2002), suggesting that these approaches can add to and strengthen the scientific basis of management, reducing uncertainty in data-limited salmon fisheries.

The management targets that were estimated with lake-PR priors should be implemented with sufficient precaution and understood through each nursery lake's specific ecological and data context. In some populations where the posterior estimates of S_{Max} far exceeded their habitat-based priors, reliance on strongly informative $S_{Max_{\mathrm{PR}}}$ priors may lead fishery managers to forego sustainable harvest opportunities by overestimating the biological benchmarks that are necessary for conservation. Lake productivity can also change over time, owing to a variety of natural and anthropogenic processes (e.g., climate warming, land use changes, reduced glacial inputs), making the recency of both PR and stock–recruitment data important for interpreting model results. Notably, all PR data included in our analysis was >10 years old, highlighting the need for increased investment in lake assessments within the NCC region of British Columbia. Insights into changing limnological conditions from updated field surveys could improve the applicability of $S_{Max_{\mathrm{PR}}}$ as a source of prior information, elevating the long-term management value of standardized and extensive limnological monitoring of Canada's Sockeye Salmon nursery lakes.

Cases where $S_{Max_{\mathrm{PR}}}$ diverges substantially from the spawner–recruitment-based estimates of capacity may also provide important clues about the factors limiting population size and productivity. As the PR model primarily characterizes autotrophic energy pathways, it does not capture the energy flows that support Sockeye Salmon in lakes, where microbial processing or allochthonous sources contribute a high proportion of total production (Atlas et al., 2020; Stocker & Shortreed, 1989). Thus, PR model estimates will most accurately reflect lake carrying capacity in watersheds, where most primary production flows through pelagic autotrophic pathways. In other cases, zooplanktivorous competitors such as Threespine Stickleback *Gasterosteus aculeatus* may limit food availability for juvenile Sockeye Salmon and reduce carrying capacity relative to the overall primary productivity of a given lake (O'Neill & Hyatt, 1987; Shortreed et al., 2001)—for example, in Alastair Lake and many other coastal lake systems. Efforts have been made by some investigators to account for competitor biomass in PR-based capacity estimates (Cox-Rogers et al., 2004); however, given the broad geographic scope of our study and the lack of data on the composition of the fish community for most of the lakes, we did not incorporate competitor biomass. Finally, population growth may be limited by the amount of available spawning habitat rather than the size and productivity of the rearing lake (Shortreed et al., 1998). In these instances, the PR model will fail to capture the habitat processes that limit population growth, potentially leading to higher estimates of S_{Max} when PR-based capacity values are integrated with spawner–recruitment models as prior information.

The survival and productivity of Sockeye Salmon populations in coastal BC has fluctuated over time, and in recent decades, smolt-to-adult survival is believed to have declined for many populations (Peterman & Dorner, 2012). Population capacity (S_{Max}) can vary in relation to survival, and recent declines in smolt-to-adult survival are likely reflected in contemporary S_{Max} values that may be lower than they were historically when survival was higher. This temporal variability in spawner–recruitment dynamics also creates the possibility of autocorrelation among the recruitment residuals and population size that can introduce negative bias in the estimates of S_{Max} and positive bias in estimates for productivity (α; Walters, 1987). This bias will be greatest for unproductive populations with temporal autocorrelation in stochastic natural mortality (Korman et al., 1995; Myers & Barrowman, 1995). Ideally,

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spawner–recruitment models would be fit with temporal autocorrelation in the residuals or with time-varying productivity to account for the temporal trends in recruitment variation (e.g., Liermann et al., 2010). However, given the frequency of missing data for many populations in our study and already highly parameterized models, we opted to treat productivity as time invariant, modeling spawner–recruitment dynamics across the entire six decades of population-monitoring data, reflecting both current and historic recruitment dynamics. Although the approach we have taken is valuable for evaluating population status relative to historic conditions and quantifying the benefits of using habitat-based priors in model specification, models that incorporate temporal variability in productivity should be considered for harvest planning, a critical next step for data limited Sockeye Salmon populations in the NCC region.

The integration of hierarchical-Bayesian spawner–recruitment models with prior information on lake rearing capacity or regional hierarchically grouped productivity is a promising avenue toward more informed management of Sockeye Salmon in the NCC and elsewhere across their range. However, understanding the limitations and potential biases that are associated with the data set and modeling approaches are important if model outputs are to be used to guide management. For most populations—except for Babine, Atnarko, Owikeno, Long, and Meziadin—only average age structure was available, and we assumed that age structure was fixed across brood years. Zabel and Levin (2002) have cautioned against the use of fixed age structure in spawner–recruitment models, as it will tend to smooth recruitment variability, resulting in underestimates of S_{Max} and overestimates of productivity. The $S_{Max_{\mathrm{PR}}}$ estimates had their own limitations, as we had to infer some of them based on models and empirical estimates that were dated, deterministic, and based on an assumed constant (i.e., 187 spawners·ton·C^{-1}). When empirical $S_{Max_{\mathrm{PR}}}$ estimates were available, they did not have estimates of sampling uncertainty and we had to assume error based on water clarity groupings. This level of complexity can be best addressed while conducting assessments at the population or stock management unit level, where a more thorough examination of data inputs and system biology can be considered, ideally with the guidance of local First Nations and biologists.

The models we developed can serve as a guide for future efforts to estimate conservation and management goals for data-limited salmon populations and provide insights into where habitat-based priors or habitat-informed hierarchical structures are appropriate. This modeling approach provides a foundation for conservation and fisheries management under the Wild Salmon Policy (DFO, 2005) and the Fisheries Act. Our analysis demonstrates the utility of merging hierarchical spawner–recruitment analysis with information that is derived from habitat-based models. Hierarchical models are a powerful tool for estimating spawner–recruitment parameters in populations with variable data quality or quantity, and the inclusion of habitat-based priors for carrying capacity provides a logical and biologically grounded means of defining the priors for S_{Max}. Combining insights from habitat-based models of population capacity with spawner–recruitment analyses in a Bayesian framework can reduce the uncertainty that is associated with estimates of population parameters and management targets resulting from highly stochastic adult-to-adult recruitment data. Although we advise caution in setting management targets for fisheries with limited data, habitat-based models are a useful starting point for evaluating population status and setting precautionary harvest goals, even with limited spawner–recruitment data. Together these approaches provide useful tools for managers of fisheries in developing economies or remote regions where a lack of population data currently hinders scientific decision making.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

DATA AVAILABILITY

The data and model code used in this analysis are available on the project GitHub page: https://github.com/DylanMG/DL-CC-sockeye?tab=readme-ov-file.

ETHICS STATEMENT

All the time series data on Sockeye Salmon abundance were obtained from Fisheries and Oceans Canada and were used with appropriate permissions. Data were not manipulated or changed to accurately reflect the status of the Sockeye Salmon populations that we evaluated. We are committed to promoting conservation efforts and advancing scientific knowledge while respecting the rights of all rightsholders and stakeholders involved.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to report related to this research.

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