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A Bayesian life-cycle model to estimate escapement at maximum sustained yield in salmon based on limited information

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Abstract: Life-cycle models combine several strengths for estimating population parameters and biological reference points of harvested species and are particularly useful for those exhibiting distinct habitat shifts and experiencing contrasting environments. Unfortunately, time series data are often limited to counts of adult abundance and harvest. By incorporating data from other populations and by dynamically linking the life-history stages, Bayesian life-cycle models can be used to estimate stage-specific productivities and capacities as well as abundance of breeders that produce maximum sustained yield (MSY). Using coho salmon (*Oncorhynchus kisutch*) as our case study, we show that incorporating information on marine survival variability from nearby populations can improve model estimates and affect management parameters such as escapement at MSY. We further show that the expected long-term average yield of a fishery managed for a spawner escapement target that produces MSY strongly depends on the average marine survival. Our results illustrate the usefulness of incorporating information from other sources and highlight the importance of accounting for variation in marine survival when making inferences about the management of Pacific salmon.

Résumé : Les modèles de cycle biologique combinent plusieurs forces pour estimer des paramètres démographiques et des points de référence biologiques d'espèces exploitées et sont particulièrement utiles pour les espèces présentant des changements d'habitat distincts et exposés à différents milieux. Malheureusement, les données de séries chronologiques se limitent souvent à des dénombrements d'abondance et de prises d'adultes. En incorporant les données d'autres populations et en reliant dynamiquement les étapes du cycle biologique, les modèles de cycle biologique bayésiens peuvent être utilisés pour estimer les productivités et capacités de différentes étapes du cycle biologique, ainsi que l'abondance de géniteurs qui produisent un rendement équilibré maximal (REM). En utilisant le saumon coho (*Oncorhynchus kisutch*) comme étude de cas, nous démontrons que l'intégration d'information sur la variabilité de la survie en mer pour des populations avoisinantes peut améliorer les estimations découlant des modèles et avoir une incidence sur des paramètres de gestion comme l'échappement au REM. Nous démontrons en outre que le rendement moyen à long terme prévu d'une pêche gérée en fonction d'une cible d'échappement de géniteurs qui produit le REM dépend fortement de la survie en mer moyenne. Nos résultats illustrent l'utilité d'intégrer de l'information d'autres sources et soulignent l'importance de tenir compte de la variabilité de la survie en mer au moment de faire des inférences concernant la gestion de saumons du Pacifique. [Traduit par la Rédaction]

Introduction

Life-cycle models discretize an aggregate stock–recruitment model into a number of distinct life-history stages. Such models dynamically link the different life stages and propagate information about intrinsic and extrinsic factors that affect survival probabilities at different times during the life cycle, such as density dependence, environmental impacts, and harvesting. In a management context, life-cycle models can be used to calculate the stock size and harvest rate that produce maximum sustained yield (MSY) (Moussalli and Hilborn 1986). Using a Bayesian approach for estimating model parameters also allows the contribution of different sources of uncertainty in derived parameters such as stock size at MSY to be quantified, facilitating a nuanced decision process when setting management goals. In addition, information from independent sources can easily be incorporated, for instance from geographically proximate populations, to improve estimates of process uncertainty and biological reference points.

Models that distinguish life-history stages are particularly useful for anadromous species such as Pacific salmon (*Oncorhynchus* spp.) that exhibit distinct ontogenetic habitat shifts and experience contrasting environments during their lives (Scheuerell et al. 2006). Because density dependence in salmonid populations is believed to be strongest during the freshwater phase due to limited food and space (Bradford et al. 1997; Achord et al. 2003; Quinn 2005), estimates of carrying capacity during the early life stages may be crucial for evaluating management objectives. Stock-specific information on marine survival rates might also be critically important because marine survival varies greatly at interannual and

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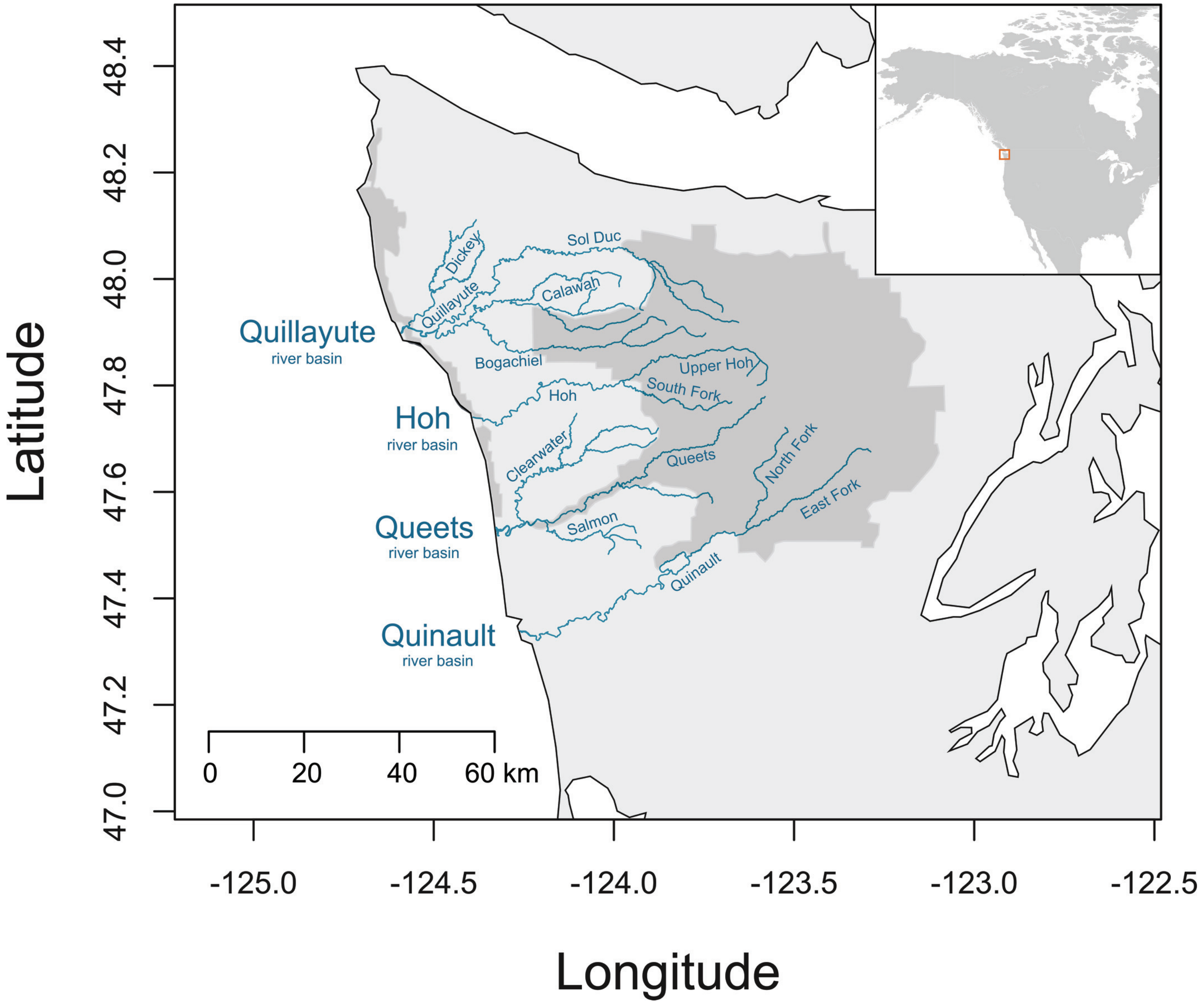
Fig. 1. Map of study area. Shown is the Olympic Peninsula in western Washington State with four major river systems that sustain naturally spawning fall-run coho salmon (*Oncorhynchus kisutch*) populations, the Quillayute, Hoh, Queets, and Quinault basins. Olympic National Park is shown in dark gray. [Colour online.]



interdecadal time scales (Mantua et al. 1997; Hare et al. 1999; Quinn et al. 2005; Zimmerman et al. 2015), yet appropriate stock-specific time series data are often missing. Environmental conditions in freshwater and marine habitats, which vary at different spatial and temporal scales, are key determinants of population productivity (Quinn 2005; Jonsson and Jonsson 2011) and affect sustainable harvest rates of salmonid populations. This is important because a major obstacle in setting management goals for salmonids is that populations often fluctuate in abundance and productivity in response to changing environmental conditions.

Harvest management of Pacific salmonids is usually governed by the principle of MSY, including populations in Washington State, as established by the Boldt Decision in 1974. Similarly, the Magnuson–Stevens Fishery Conservation and Management Act requires that optimum yield be the goal for fisheries managed under the Act, and this is often defined as MSY (for populations not listed under the Endangered Species Act). Management objectives are typically expressed in terms of escapement goals, i.e., the number of adult fish surviving to spawn that are required to produce such MSY.

The Olympic National Park on the Olympic Peninsula in western Washington is a World Heritage Site and designated Biosphere Reserve offering largely pristine habitat for diverse wildlife. The park encompasses spawning and rearing habitats for distinct populations of Pacific salmonids, including coho salmon (*Oncorhynchus kisutch*). The salmonids that inhabit the park's rivers are of high ecological, recreational, and cultural importance and contribute to commercial, sport, ceremonial, and subsistence fisheries (National Park Service 2010). Current management goals for salmonid populations that spawn in the Olympic National Park were originally established decades ago based on the data and scientific methods available at that time.

Here, we develop a Bayesian life-cycle model for coho salmon populations that spawn and rear in rivers that drain from the western Olympic Peninsula, which are not Endangered Species Act listed, based on stock-specific information on escapements and total harvest rates. The model distinguishes a density-dependent freshwater phase and a density-independent marine phase and incorporates estimates of smolt capacity in the river systems. It reflects the life-history characteristics of coho salmon, but the general approach can easily be adopted to other Pacific salmonids. We test whether including estimates of marine survival from nearby populations improves the life-cycle models by improving estimates of process uncertainty, and we evaluate the use of these improved models for the management of the populations. We then compare model-derived estimates of escapement at MSY to existing management (escapement) goals. Finally, because fisheries managers are rarely able to achieve desired escapement goals precisely, we perform a simulation analysis of the expected long-term average yield of a fishery that incurs implementation error. This analysis quantified the expected yield under different escapement targets and the expected changes in fisheries yield in response to persistent changes in average marine survival due to long-term shifts in ocean conditions (e.g., regime shifts in the Pacific Ocean).

Methods

We used data on coho salmon populations from four major river basins on the Olympic Peninsula (Fig. 1): (*i*) the Quillayute basin including the Quillayute, Bogachiel, Calawah, Sol Duc, and Dickey rivers, (*ii*) the Hoh basin including the upper and south forks of the river, (*iii*) the Queets basin containing the Queets, Clearwater, and Salmon rivers, and (*iv*) the Quinault basin including the Quinault River and its east and north forks. The coho salmon of the Quillayute, Hoh, and Queets river systems are managed for wild spawning escapement and we focused our analysis on the wild components of these populations. However, hatchery releases of coho salmon also occur in these river systems (see Discussion).

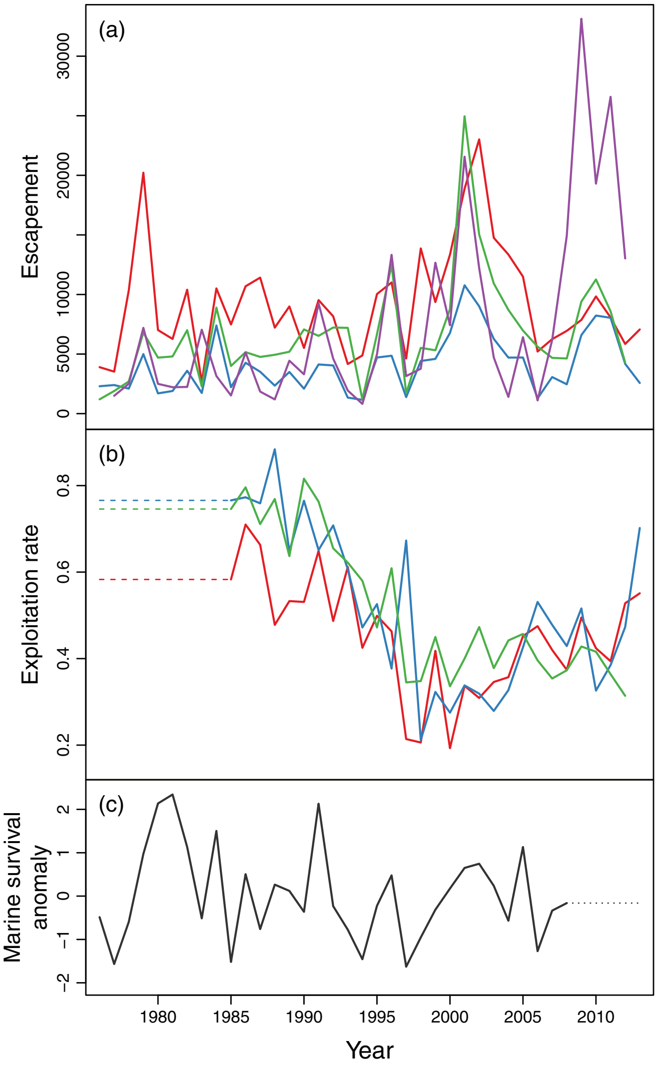
Time series data

We used stock-specific time series data on spawning escapements and total exploitation rates as well as a time series of marine survival rates for Washington coastal coho (Fig. 2). Escapement data were obtained from the Washington Department of Fish and Wildlife, Treaty Tribes, and annual reports by the Pacific Salmon Commission. Escapement estimates used in this study were derived from redd counts or area-under-the-curve counts of live spawners (i.e., by dividing the integral over the escapement curve by the average residence time of spawners in the survey area) that were subsequently expanded to account for unsurveyed areas and times. Escapements were analyzed for the years 1976–2013 for the Quillayute and Hoh, 1976–2012 for the Queets, and 1977–2012 for the Quinault (Table S1[1]).

Exploitation rates were taken from periodic and annual reports of the Pacific Salmon Commission Joint Coho Technical Committee (Pacific Salmon Commission 2013) and were available for all years since 1986 for the Quillayute, Hoh, and Queets (Table S1). Reported exploitation rates (Pacific Salmon Commission 2013) were derived from the Coho Fisheries Regulation Assessment Model based on coded wire tag recoveries of indicator stocks. We used exploitation rate data from the Queets River as a surrogate for the nearby Quinault River. Exploitation rates prior to 1986 were estimated in the model based on the mean of the years 1986–1990 because limited earlier data suggest that exploitation rates during the decade prior to 1986 were similar to rates observed in the late 1980s (Pacific Salmon Commission 1987).

We used a time series of average marine survival rates of Washington coastal coho salmon for the years 1976–2007 (Beetz 2009). These data were derived from coded wire tag recoveries obtained from the coded wire tag database of the Pacific States Marine Fisheries Commission (www.psmfc.org). The marine survival time series for Washington coastal coho was based on seven hatchery populations (Sooes, Sol Duc, Salmon, Quinault, and Humptulips rivers as well as Bingham and Forks creeks) and one wild population (Bingham Creek). Marine survival rate after 2007 was set to the mean of the years 2003–2007 because marine survival of Washington coho populations has been relatively constant since the early 2000s (Zimmerman et al. 2015). Wild coho salmon typically experience higher survival than hatchery coho but show similar trends, interannual variability, and spatial distributions (Labelle et al. 1997; Coronado and Hilborn 1998; Zimmerman et al. 2015). Furthermore, marine survival is strongly influenced by environmental conditions during the early ocean phase such that covariability in survival among populations is high at the regional scale (<150–200 km), e.g., among populations along the northern

Fig. 2. Historical escapements, exploitation rates, and marine survival anomaly. (*a*) Time series of spawner escapements for all rivers systems (red: Quillayute, blue: Hoh, green: Queets, purple: Quinault), (*b*) time series of total exploitation rates for all river systems except the Quinault, and (*c*) marine survival anomaly of Washington coastal coho stocks. Marine survival is shown for the same year as escapements and harvests, i.e., the year of smolt return (ocean entry year +1). Dotted lines for marine survival indicate years with constant values (see text for details). Dashed lines for exploitation rates indicate years for which exploitation rates were estimated in the model (see Fig. S3). [Color online.]



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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0382.

Washington coast (Hobday and Boehlert 2001; Teo et al. 2009; Zimmerman et al. 2015).

Coho salmon life cycle

The populations examined are fall-run coho salmon whose adults enter the rivers in late summer and fall to reproduce between October and December of a given brood year, primarily in small creeks but also in main river channels. The embryos incubate in the gravel over the winter and fry emerge from the gravel a few months later (brood year + 1). The majority of the fish from these large rivers spend about 1 year in freshwater and emigrate to the ocean as smolts in late spring of the following year (brood year + 2), from early April to early June. Some juvenile coho salmon migrate downstream and enter marine waters during the first summer in coastal streams (Quinn et al. 2013) but the proportion doing so declines with distance upriver (Roni et al. 2012), and scale analyses suggest that this life history does not contribute substantially to adult returns in most Washington river systems (Washington Department of Fish and Wildlife, unpublished data). Coho salmon usually return to the rivers in the fall of the following year (brood year + 3) after having spent two summers at sea. We assumed that all fish follow this "typical" life cycle and return to their natal rivers at age 3 (Coronado and Hilborn 1998; Quinn 2005). We thus implicitly assume that the number of fish that return as "jacks" after one summer (males only) or spend additional years in the ocean (both sexes) is small and does not substantially alter brood year recruitment (Quinn 2005).

We considered a life-history model based on two life stages. The model divided the life cycle into freshwater and ocean phases, whereby survival during the freshwater phase is assumed to be regulated by density according to an asymptotic (Beverton–Holt) relationship. Hence, we assumed that the carrying capacity of the freshwater environment is limiting, whereas carrying capacity of the ocean is unlimited. There is evidence for density-dependent growth and, to some extent, survival in large stock complexes of Pacific salmon during their ocean phase (e.g., Ruggerone and Connors 2015). However, density dependence during the ocean phase tends to be observed in the much more abundant species such as sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) and in areas where salmon are more numerous than they are along the Washington coast (Pyper and Peterman 1999; Ruggerone and Nielsen 2004; Ruggerone and Connors 2015). Additionally, such density dependence is generally associated with the abundance of large stock aggregates, rather than the abundance of individual populations, which was the subject of our modeling.

Life-cycle model

In each population, the numbers of smolts (s) produced in a given year (y) ($N_{\mathrm{s},y}$) depend on the number of adults (a) returning to spawn in the previous generation ($N_{\mathrm{a},y-2}$), adult-to-smolt productivity ($p_{\mathrm{a}\to\mathrm{s}}$), which is the maximum per capita recruitment, and the carrying capacity for smolts in the freshwater environment (c_s):

$$(1) \qquad N_{\mathrm{s},y} = \frac{N_{\mathrm{a},y-2}}{\dfrac{1}{p_{\mathrm{a}\to\mathrm{s}}} + \dfrac{1}{c_\mathrm{s}} N_{\mathrm{a},y-2}}$$

The carrying capacity is related to the amount of available habitat in the natal watershed and was assumed to be constant among years. The number of adults returning to spawn ($N_{\mathrm{a},y}$) depends on the number of smolts in the previous year, smolt-to-adult productivity ($p_{\mathrm{s}\to\mathrm{a},y}$), total exploitation rate (ER_y) in the year of return, and an error term ($e^{\varepsilon_\mathrm{p}}$) that captures unexplained variation in smolt survival, which may arise from either observation error or stochasticity in the recruitment process:

$$(2) \qquad N_{\mathrm{a},y} = N_{\mathrm{s},y-1}\, p_{\mathrm{s}\to\mathrm{a},y}\, (1 - \mathrm{ER}_y) e^{\varepsilon_\mathrm{p}}$$

The error term $\varepsilon_\mathrm{p} \sim \mathrm{N}(-0.5\sigma_\mathrm{p}^2, \sigma_\mathrm{p})$ has a mean of $-0.5\sigma_\mathrm{p}^2$ to bias correct its expected value to zero based on its lognormal error variance (Quinn and Deriso 1999). Unknown exploitation rates during the early part of the time series were estimated in the model as $\mathrm{logit}(\mathrm{ER}_y) \sim \mathrm{N}(\mu_{\mathrm{ER}}, \sigma_{\mathrm{ER}})$, where μ_{ER} is the mean exploitation rate during the reference period (see above).

Because we assumed no density dependence during residence at sea, smolt-to-adult productivity is equal to the survival from the smolt to the adult stage. Smolt-to-adult productivity ($p_{\mathrm{s}\to\mathrm{a},y}$) in a given year was modeled using mean productivity ($\bar{p}_{\mathrm{s}\to\mathrm{a}}$) and interannual variability about this mean, which was estimated from a time series of average marine survival of Washington coastal coho (Beetz 2009). Because the survival estimates included hatchery-origin fish, which tend to have lower average survival than wild stocks but similar year-to-year variability (Coronado and Hilborn 1998; Zimmerman et al. 2015), we standardized the marine survival time series (MS_y) to mean zero and unit standard deviation and estimated the degree (γ) to which the stock-specific productivity follows the variability of the aggregate marine survival of the indicator stocks (i.e., a linear relationship with intercept $\bar{p}_{\mathrm{s}\to\mathrm{a}}$ and slope γ):

$$(3) \qquad p_{\mathrm{s}\to\mathrm{a},y} = \bar{p}_{\mathrm{s}\to\mathrm{a}} + \gamma\, \mathrm{MS}_y$$

We therefore assumed that the variability pattern, i.e., the survival anomaly, but not mean survival, was well represented by a mix of wild and hatchery stocks from that region. As part of our analysis, we ran the same model with and without inclusion of the marine survival time series to assess whether incorporating interannual variability in marine survival resulted in a decrease in process error variance. We further compared models with and without the marine survival term using the widely applicable information criterion (WAIC, a generalized version of the Akaike information criterion) as implemented in the R package loo (v.1.1.0) (Vehtari et al. 2017).

Management parameters

The life-cycle model can be used to estimate the spawner escapement (and harvest rate) that produce MSY (Moussalli and Hilborn 1986). Total population productivity (P_n), an index of survival across life stages without effects of density dependence, was calculated as the product of the life-stage-specific productivities as $P_n = \Pi_{i=1}^{n} p_i$, where n denotes the number of life stages in the model (i.e., in our model, P_n is the product of the smolt-to-adult and adult-to-smolt productivities). The cumulative capacity (C_n) of a population is then $C_n = P_n / \sum_{i=1}^{n} \dfrac{P_i}{c_i}$. Based on these population-level parameters, the spawner escapement at MSY can be calculated as

$$(4) \qquad S_{\mathrm{MSY}} = \frac{C_n}{P_n}\left(P_n^{0.5} - 1\right)$$

Uncertainty in S_{MSY} and cross-correlations between parameters was accounted for by drawing parameter values from the joint posterior distribution on a sample-by-sample basis.

Expected yield

In addition to the above-described life-cycle model, we simulated the long-term average catch of a fishery that incurs implementation error under different escapement targets. We thereby assumed that management goals are not always achieved precisely such that escapement in a given year can be higher or lower than the target. In this yield analysis, the process error variance in the stock–recruitment relationship was the same as the error variance estimated in the life-cycle model.

Total recruitment to the fishery in a given year (Rec_y) was calculated for each sample of the joint posterior distribution based on the estimated capacity and total population productivity:

$$\text{(5)} \qquad \mathrm{Rec}_y = \frac{S_y}{\dfrac{1}{P_n} + \dfrac{1}{C_n}S_y} e^{\varepsilon_\mathrm{p}}$$

Given recruitment and the management target (T), spawner escapement (S_{y+1}) is then given by

$$\text{(6)} \qquad S_{y+1} = \begin{cases} T(1 + \varepsilon_\mathrm{i}), & T(1 + \varepsilon_\mathrm{i}) < \mathrm{Rec}_y \\ \mathrm{Rec}_y, & T(1 + \varepsilon_\mathrm{i}) \geq \mathrm{Rec}_y \end{cases}$$

Here, ε_i is the implementation error, assumed to be normally distributed with $\varepsilon_\mathrm{i} \sim \mathrm{N}(0, \sigma_\mathrm{i})$. Despite evidence of correlations between historical run sizes and spawner escapements in a given year, i.e., the tendency toward overfishing small runs and overescaping large runs, we chose not to include a correlation between process error and implementation error in our simulations to avoid implicit assumptions about the nature of future management. The observed correlations apply to current escapement goals and may not hold for all other target levels that were simulated in the analysis.

Total catch is calculated as the difference between recruitment and the actual spawner escapement:

$$\text{(7)} \qquad C_y = \mathrm{Rec}_y - S_{y+1}$$

For each target escapement, we simulated fishery yield over 50 years for all posterior samples by drawing random process errors (stock-specific σ_p estimated in models) and random implementation errors (σ_i = 0.2). The latter value was set to reflect a realistic amount of implementation error (increasing σ_i increases uncertainty in the simulated yield but decreases the long-term average yield). We repeated this procedure 100 times. Finally, we simulated the expected long-term average yield for different values of smolt-to-adult productivity to quantify the change in the expected maximum yield at different levels of marine survival. The expected yield was evaluated at the escapement target that produced MSY (Fig. S2).

Bayesian parameter estimation

We used a Bayesian approach for parameter estimation to incorporate prior knowledge and accurately account for uncertainty in the estimated parameters. Here, the priors are confronted with the observational data to estimate the joint posterior distribution of the model parameters. The analysis was performed using the program JAGS (Plummer 2012), which uses Gibbs sampling as a Markov chain Monte Carlo (MCMC) algorithm, via the package R2jags (Su and Yajima 2013) from within R (ver. 3.2.2) (R Core Team 2015). MCMC runs consisted of three chains, each of which contained 500 000 iterations, of which 100 000 were discarded as burn-in. We retained one iteration out of every 1000 to reduce autocorrelation in the chains. The posterior distributions thus consisted of 1200 samples (400 samples per chain). We ensured convergence of the MCMC chains visually by using autocorrelation, cross-correlation, and trace plots as well as common diagnostics such as tests of heterogeneity among chains (Gelman and Rubin 1992) and convergence of individual chains (Geweke 1992).

Priors and parameter values

We used informative priors for the stage-specific productivity and capacity based on survey data and previous studies, including meta-analyses of other coho salmon populations, in line with the recommendation to use prior information derived from meta-analytical approaches in fisheries science (Thorson et al. 2015). The prior for mean adult-to-smolt productivity ($\bar{p}_{\mathrm{s}\rightarrow\mathrm{a}}$) was set as lognormally distributed with a mode of 60 and a standard deviation of 0.33 (Barrowman et al. 2003; Quinn 2005; Korman and Tompkins 2014). The prior for smolt-to-adult productivity ($\bar{p}_{\mathrm{s}\rightarrow\mathrm{a}}$) was set as logit-normally distributed with a mean of 0.075 and a standard deviation of 0.25 (Bradford 1995; Quinn 2005; Shaul et al. 2007; Zimmerman et al. 2015). Capacity priors (c_s) were based on estimates of maximum smolt density per unit river length, which were derived from an extensive survey of late-summer parr in 2003 in the Calawah River of the Quillayute system following the year with the highest escapement in the past four decades (McMillan et al. 2013). While smolt capacity is expected to be lower than parr capacity due to overwinter mortality (Quinn and Peterson 1996), the survey was assumed to underestimate parr density due to imperfect detection such that the survey-based estimates per unit river length were used as priors for smolt carrying capacity. The average density used was 756 smolts/km in the main stem and 1548 smolts/km in the tributaries. Similar smolt densities have been reported previously for coastal coho populations (Bradford et al. 1997; Sharma and Hilborn 2001; Barrowman et al. 2003; Korman and Tompkins 2014). The accessible habitat used was 578 km in the Quillayute basin, 210 km in the Hoh basin, 361 km in the Queets basin, and 255 km in the Quinault basin. For the Quillayute basin, we assumed that the Sol Duc River, roughly one third of the total habitat in this basin, was shared between fall-run coho (75%) and summer-run coho (25%). The resulting modes of the capacity priors were 0.528, 0.247, 0.436, and 0.313 million coho salmon smolts in the Quillayute, Hoh, Queets, and Quinault basins, respectively. The smolt capacity priors were lognormally distributed with a standard deviation of 0.5, i.e., priors were assumed to be less certain for smolt capacity than for productivity. The standard deviation of the exploitation rates in early years (σ_ER) was set to 0.25 in logit space to reflect the variance during the reference period. We used uniform priors for the coefficient of the marine survival anomaly (γ) [–0.5,0.5] and the standard deviation of the error term (σ_p) [0,2]. The limits of the uniform priors were set such that they were not approached during the sampling process. An overview of all prior distributions is provided in Table S4.

Results

For the Quillayute, Hoh, Queets, and Quinault rivers, the median estimates of capacity were 0.327, 0.186, 0.330, and 0.304 million smolts, median estimates of adult-to-smolt productivity were 90, 113, 109, and 114, and median estimates of smolt-to-adult productivity were 0.087, 0.089, 0.090, and 0.100, respectively. The latter estimates translate into average marine survival rates of 8.7%–10% across stocks. The credible intervals and full posterior distributions of the stock-specific productivity and capacity parameters are provided in the supplementary information (Fig. S1; Table S2). Median estimated exploitation rates during 1978–1985 were in the range 0.54–0.62, 0.74–0.78, and 0.72–0.75 for the Quillayute, Hoh, and Queets rivers, respectively (Fig. S3).

Inclusion of the marine survival time series was supported based on the following criteria. First, the gamma parameters (γ), i.e., the regression coefficients of marine survival variability, were all positive (median estimates 0.026–0.041) and significantly different from zero (Fig. 3*a*). Second, incorporating interannual variability in marine survival considerably decreased the process error standard deviation (Fig. 3*b*). The median value of the process error standard deviation decreased by 17%, 17%, 23%, and 11% in the Quillayute, Hoh, Queets, and Quinault rivers, respectively. Third, the more complex models were supported by the widely applicable information criterion (Table S5). Incorporating the marine

Fig. 3. Accounting for interannual variability in marine survival. (*a*) Marine survival regression coefficient: median estimates (circles) and 95% credible intervals (lines) of the regression coefficient (γ) of marine survival anomaly in all river systems. (*b*) Process error standard deviation: median estimates (circles) and 95% credible intervals (lines) of the standard deviation of the process error (σ_p) for models including time series of marine survival anomalies (black) and models not accounting for interannual variability in marine survival (gray). (*c*) Escapement at MSY comparison: median estimates (circles) and 95% credible intervals (lines) of the escapement at MSY for models including time series of marine survival anomalies (black) and models not accounting for interannual variability in marine survival (gray).

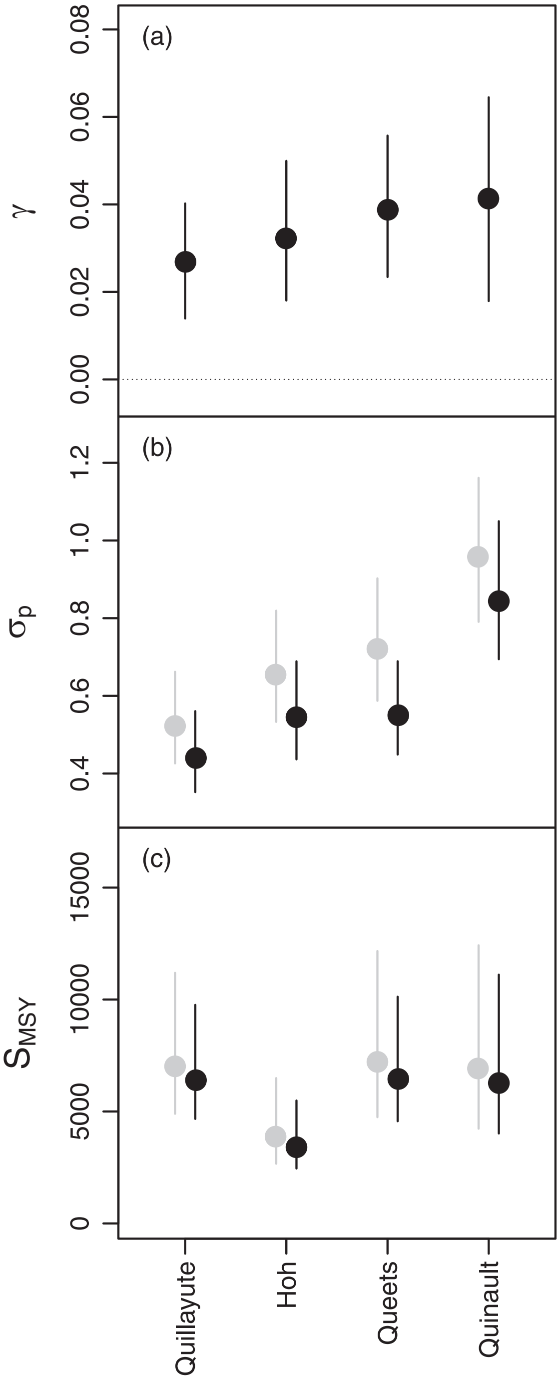
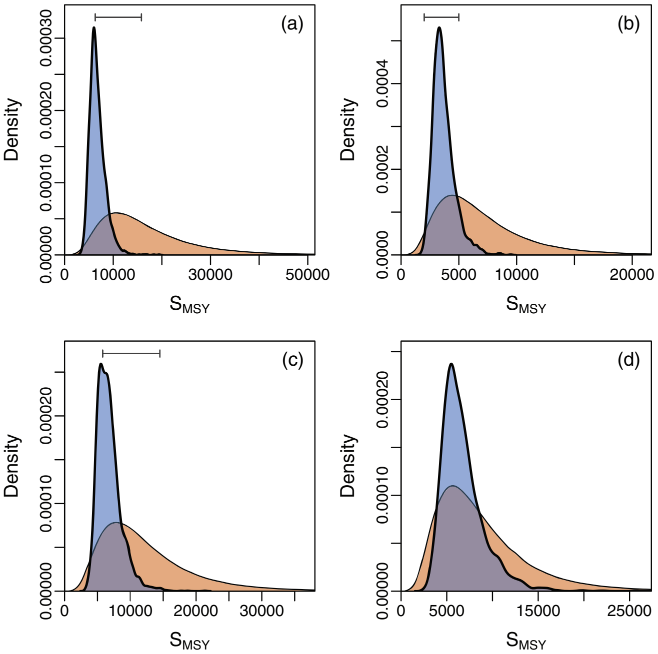


Fig. 4. Escapement at MSY. Prior (orange, thin line) and posterior (blue, thick line) probability density distributions of the escapement at MSY for each stock: (*a*) Quillayute, (*b*) Hoh, (*c*) Queets, and (*d*) Quinault. The range of established escapement goals is shown at the top (gray). [Color online.]

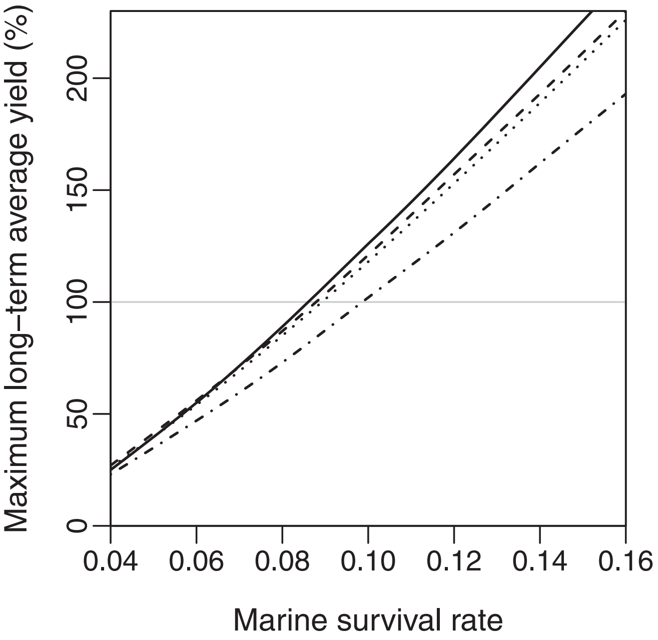


survival anomaly time series further led to consistently lower median values and lower uncertainties in the estimates of the escapement at MSY. Median S_{MSY} estimates were up to 11% lower compared to models that did not account for variability in marine survival (Fig. 3*c*), decreasing by 8%, 11%, 11%, and 9% in the Quillayute, Hoh, Queets, and Quinault rivers, respectively. The coefficient of variation (i.e., the standard deviation divided by the mean), as a measure of the uncertainty in the S_{MSY} estimates, decreases by 5%–19%.

The posterior distributions of the escapement at MSY were narrower than the prior distributions (Fig. 4). The median estimates of the escapement at MSY were 6438 fish in the Quillayute, 3505 fish in the Hoh, 6443 fish in the Queets, and 6252 fish in the Quinault rivers. Credible intervals of the stock-specific S_{MSY} estimates are provided in the supplementary information (Table S3). Previously established escapement goals for fall-run coho salmon in the coastal streams of the Olympic Peninsula were defined as conservation goal ranges (Quillayute: 6300–15 800 fish, Hoh: 2000–5000 fish, Queets: 5800–14 500 fish). No escapement goals currently exist for fall-run coho salmon in the Quinault River. Median estimates of the escapement at MSY are slightly higher than the established minimum conservation goals in the Quillayute, Hoh, and Queets rivers (Fig. 4). As expected, the long-term average yield of a fishery that incurs implementation error was highest at the model-estimated escapement at MSY. The reduction in the expected yield at other escapement targets, however, is highly asymmetric (Fig. S2). A close-to-maximum yield can be achieved for a larger range of above-optimal levels of escapements compared to below-optimal escapements.

Finally, simulating different marine survival rates showed that the maximum average yield of a fishery that incurs implementation error and is managed for the target escapement that produces MSY is expected to decline rapidly with decreasing average marine survival (Fig. 5). For instance, a reduction in average marine survival of the Queets River stock from 9% (the estimated

Fig. 5. Expected yield as a function of marine survival. Expected long-term average yield as a function of marine survival rate for all stocks: Quillayute (dot-dashed line), Hoh (dotted line), Queets (dashed line), and Quinault (solid line). The expected yield for a given marine survival rate was evaluated at the escapement target that produces maximum long-term average yield and is expressed in percent of the maximum yield achieved at the estimated average marine survival rate, i.e., the median value of smolt-to-adult productivity. The estimated median for each stock can thus be found where the yield curve equals 100% (horizontal gray line).



median smolt-to-adult productivity) to 6% causes a decline in the expected yield of about 50%, with similar reductions in the expected maximum yield for the other three stocks.

Discussion

We showed that incorporating estimates of marine survival rates can improve life-cycle models and affect management parameters such as the escapement at MSY. Inclusion of estimates of marine survival anomaly from nearby populations was supported, as it decreased the standard deviation of the process errors and thus increased the variance explained by the models in all four river basins that we modeled. The reason for the relatively small reduction in error variance in the Quinault River model is likely that stock-specific exploitation rates were not available for this stock. Furthermore, median estimates of the escapement at MSY, the quantity that can be used to update or establish escapement goals for the stocks, decreased upon inclusion of the marine survival anomalies, and uncertainty in the escapement at MSY estimates declined due to the reduction in process error variance. Finally, we showed that the expected average yield of a fishery that is managed for the escapement that produces maximum yield strongly depends on the average marine survival rate. Taken together, our results highlight the benefit of incorporating time series of marine survival variability as well as good estimates of average marine survival when making inferences about the productivity and management of Pacific salmon. Ideally, this should be done in a dynamic model that estimates the joint likelihood of processes occurring throughout the life cycle of a species, as done in the present study.

Decisions about the management and conservation of natural resources often need to be made under substantial uncertainty. Failure to account for uncertainty can lead to poor decisions with potentially serious consequences (Ludwig et al. 1993; Regan et al. 2005). Our model estimates of the escapement at MSY are associated with considerable uncertainty. The median estimates are higher than the established minimum conservation goals, yet the lower bound of the credible intervals is close to or lower than the established goals in all cases. This begs the question about the level of confidence that managers should use when setting escapement goals. Because the Bayesian approach quantifies uncertainty in the estimated parameters (given the data at hand and the prior knowledge incorporated into the models), probability distributions of escapement at MSY can be used to choose a desired level of confidence or precaution when setting management goals. Compared to using point estimates, this framework allows for a more nuanced decision process when setting management objectives, guided by the desired level of precaution, i.e., accepted level of risk.

The expected long-term average yield of an imprecisely managed fishery was shown to be highly asymmetric around the escapement target that is expected to produce MSY. Targets above S_{MSY} would result in relatively minor losses in the expected yield compared to targets below S_{MSY} due to the strong adverse effects of underescaping a stock on future stock production. In addition, adopting a precautionary approach by setting higher than "optimal" escapement targets can also facilitate ecological function at relatively minor losses in expected yield. This is particularly relevant for anadromous, semelparous species such as Pacific salmonids because adults transport marine-derived nutrients into lakes and streams and their eggs, fry, and juveniles often provide critical food sources for other aquatic and terrestrial predators (Helfield and Naiman 2001; Gende et al. 2002). Specifically, potential ecological benefits of higher abundances of spawners include increases in algal productivity (Schindler et al. 2005), terrestrial vegetation growth (Helfield and Naiman 2001), macroinvertebrate abundances (Janetski et al. 2009), and resident fish growth (Scheuerell et al. 2007). This added ecological value for the freshwater ecosystems used as nursery habitat by salmonids is not considered under the paradigm of MSY, but should be taken into account when making management decisions.

While the Bayesian approach allows for the quantification of uncertainty given the available data and prior knowledge, the parameter estimates are associated with additional uncertainty that was not quantified in the models. Most importantly, we make the simplifying assumption that the escapements and exploitation rates represent true values. However, these types of data can be associated with uncertainty due to sampling and estimation error (Walters and Ludwig 1981). In addition, escapements may be biased, as they are typically derived from spawner or redd surveys conducted at limited spatial and temporal scales, which need to be extrapolated to construct estimates of escapement. Reported exploitation rates may be biased due to misreporting of harvest or illegal fishing. Another potential source of bias can result from hatchery fish that spawn in the natural habitat and are counted as wild spawners. While hatchery-origin coho salmon exist in some of the examined rivers, we assumed that hatchery fish spawning in the wild have minor effects on productivity estimates in the studied systems due to substantial wild runs. Finally, models are a simplification of the true life history and ecological complexity of a species, and the presented model does not account for life-history variants such as jacks or time-varying freshwater productivity, e.g., due to variability in environmental temperature or river flow.

Some of the additional uncertainties that are not quantified in the models could be reduced by gathering additional information on the stocks under consideration. Specifically, the life-cycle approach presented here would greatly benefit from reliable estimates of smolt capacity in the different river systems as well as efforts to evaluate the potential error and bias associated with estimates of escapements and reported exploitation rates. Quantifying bias in fishery mortality rates and spawner counts would be crucial for understanding its potential impacts on the management of salmon fisheries. Efforts should thus be made to accurately document the methods used to estimate harvest rates and escapements, quantify associated uncertainties where possible, and provide estimates of unreported fishing mortality.

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