

Development and application of an integrated population model for
Chinook salmon in the Willamette River basin

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Prepared by

Mark D. Scheuerell¹

Fish Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Seattle, WA

¹mark.scheuerell@noaa.gov

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1 Summary

This report describes the development and application of an integrated population model for natural-origin Chinook salmon (*Oncorhynchus tshawytscha*) from the Willamette River basin. The model was developed with the intent of investigating the possible effects of present-day river flows and temperature on the recruitment of adults, in the hope of informing future consequences to fish and wildlife owing to possible changes in reservoir operations. Unfortunately, temperature records were incomplete across several consecutive years, which precluded their use in the model. Flow metrics were generated through a collaborative process with the Science of Willamette Instream Flows Team (SWIFT), and focused on effects of flow during particular life stages based on first principles (*e.g.*, decreased flows during the summer may negatively affect parr survival). SWIFT derived 32 different flow scenarios that included the following periods/life stages: prespawning, egg incubation, rearing of age-1 parr, age-1 outmigrants, and age-2 outmigrants.

The model involves two primary components: process models governing population dynamics, and observation models to account for imperfect information. Using fish and flow data from 1999-2017, a model based upon the maximum flow during the period when age-2 smolts were outmigrating had the greatest predictive accuracy. Results from that model indicated relatively strong density-dependent population dynamics. The median intrinsic productivity was about 1.6 recruits per spawner at low spawner abundance, and the carrying capacity was approximately 9000 adults. This time period was also marked by rather poor recruitment overall; after accounting for the negative effect of flows and spawner density, only four years were at or above replacement. In addition, because the chosen set of flow metrics had such high covariance among them, many models had relatively similar predictive accuracy. Thus, care should be exercised when interpreting the importance of any one flow metric over another.

2 Introduction

Life cycle models are commonly used in the Pacific Northwest to evaluate the potential responses of salmon populations to possible future management actions (*e.g.*, changes in reservoir operations) or environmental conditions (*e.g.*, climate change). These models are typically constructed by first synthesizing available demographic information (*e.g.*, age, fecundity, survival rates), which may be derived from different species and locations. Next, the estimated parameters and available data are used as inputs into population models and projections are made via repeated resampling from amongst the stochastic elements (*e.g.*, Scheuerell et al. 2006; Honea et al. 2009). However, this general approach suffers from several shortcomings. First, information is lost when data are summarized to calculate demographic rates, which creates problems for determining the appropriate likelihood functions and evaluating model diagnostics. Second, there is no formal treatment of the variance and covariance within and among model parameters, which results in a false sense of precision as the model is iterated through time. Third, some data types (*e.g.*, age structure) contain information about multiple aspects of population dynamics (*e.g.*, recruitment and survival), which can lead to biased parameter estimates when not explicitly acknowledging their trade-offs.

More recently, integrated population models (IPMs) have been developed to address these limitations (Schaub and Abadi 2011; Maunders and Punt 2013). Because IPMs are based on a joint likelihood constructed from each of the individual data components, they capture the full uncertainty in the data to improve the precision and accuracy of parameter estimates (Tavecchia et al. 2009; Johnson et al. 2010). IPMs are closely related to state-space models (de Valpine and Hilborn 2005), which consist of a process model used to describe the true but unobservable population dynamics, and an observation model to address errors in the data that arise due to incomplete sampling, misidentification, etc. IPMs have been used in studies of birds (Schaub et al. 2007; Oppel et al. 2014), mammals (Tavecchia et al. 2009; Johnson et al. 2010), and marine fishes (Ianelli 2002; Punt et al. 2010), but they are less familiar in salmonid management and conservation (*c.f.* Buhle et al. 2018).

Chinook salmon (*Oncorhynchus tshawytscha*) from the Willamette River basin were listed as threatened under the Endangered Species Act in 1999, and the recovery plan developed by the Oregon Department of Fish and Wildlife (ODFW) and the National Marine Fisheries Service (NMFS) called for protecting existing high-quality habitats while restoring deteriorated locations (ODFW and NMFS 2011). The goal of this project was to develop an IPM for Chinook salmon from the Willamette River basin and investigate whether there were detectable flow effects on the production and survival of offspring (recruits) from their spawning parents. There was a secondary goal of also evaluating the effects of water temperature as well, but the data were incomplete across several years in the middle of the time series, which precluded their inclusion in the model.

3 Methods

3.1 Fish data

I obtained estimates of the number of spawning Chinook salmon and their age composition for calendar years 1999-2017 from the Oregon Department of Fish and Wildlife (T. Friesen and M. Lewis, *pers. comm.*). Details on the sampling methodology and extrapolation to total counts can be

found elsewhere. Because the numbers of spawning adults are estimates and not exhaustive counts, I used an observation model to account for their uncertainty (see below).

Importantly, the model described below relies on the actual number of adult fish in each age class in each year, rather than the more typically reported proportion-by-age. Adult Chinook salmon in the Willamette River basin return at ages 3 through 6, and the median number of observed fish of ages 3, 4, 5, and 6 was 21, 231, 199, and 7, respectively. As with the spawner data, the incomplete census of ages required an observation model to account for their uncertainty (see below).

Here I assume the harvest of natural-origin adults to be zero due to legal restrictions on retaining them in the sport fishery. Nevertheless, estimates do not account for errors in reporting by anglers (*e.g.*, incorrect species, wrong area code) or concerted illegal harvest. Additionally, estimates of catch do not account for any possible incidental impacts on wild fish in mixed-stock fisheries directed at hatchery fish. Thus, estimates of recruitment will be biased downward to the extent that natural-origin fish were retained in a fishery.

Due to difficulties in assessing whether or not fish of specific age were of natural or hatchery origin, I only consider the production of natural-origin fish by natural-origin parents. Thus, estimates of recruitment will be biased upward to the extent that hatchery-origin spawners contribute to natural production.

3.2 Flow covariates

During a series of workshops, the Science of Willamette Instream Flows Team (SWIFT) developed a set of 32 possible flow covariates to include in the model as possible drivers of productivity. The set included summaries of river flows over different months and year that were focused on a specific life stage (*e.g.*, minimum flows from July through September might affect the survival of parr).

Specifically, I retrieved the raw flow data, as measured at Salem, OR, from the US Geological Service National Water Information System using the **EGRET** package for **R** (Hirsch and De Cicco 2015). I then summarized the data according to each of the specific flow metrics. Please see Appendix S1 for a detailed workflow describing the retrieval and summarization of the flow covariates.

Importantly, many of the covariates were highly correlated due to the nature of the statistics used to summarize them (*e.g.*, min/max/range) and the time periods over which they were calculated (Figure S1). Thus, I included only one covariate in the model at a time to prevent problems from collinearity. Accordingly, one should expect that estimates of the parameters and states should be quite similar from those models with closely related flow metrics.

3.3 Process models

3.3.1 Total recruits

The IPM for Pacific salmon that I describe here shares several features with those of Su and Peterman (2012), Fleischman et al. (2013), and Winship et al. (2014). I begin with the process model that describes the true, but unknown production of offspring from their parents. In any given year t , spawning adults (S_t) produce some number of surviving recruits (R_t) according to a general Ricker model (Figure 1), such that

$$R_t = \frac{\alpha S_t}{e^{\beta S_t}}, \quad (1)$$

and α and β are the intrinsic productivity and *per capita* strength of density dependence, respectively.

In this case I make two modifications to the traditional model form in Eqn (1): *i*) I allow the intrinsic productivity to vary over time, and *ii*) I allow for additional unexplained annual variation. Specifically, the log-linear model is

$$\log(R_t) = \log(S_t) + \log(\alpha_t) - \beta S_t + w_t, \quad (2)$$

where $\log(\alpha_t)$ is the log of the annual density-independent productivity. Here w_t is an autocorrelated process error, which accounts for unknown and unmeasured environmental drivers of Chinook productivity; $w_t \sim N(\phi w_{t-1}, q_a)$. Previous applications of time-varying productivity (e.g., Peterman et al. 2003; Dorner et al. 2008) have used a Markov form where $\log(\alpha_t) \sim N(\log(\alpha_{t-1}), \sigma_\alpha)$, but I model $\log(\alpha_t)$ as a function of time-varying covariates. Specifically,

$$\log \alpha_t = \mu_a + \gamma F_{t+h}, \quad (3)$$

μ_a is the underlying mean productivity, and γ is the effect of the appropriately lagged flow covariate, F_{t+h} .

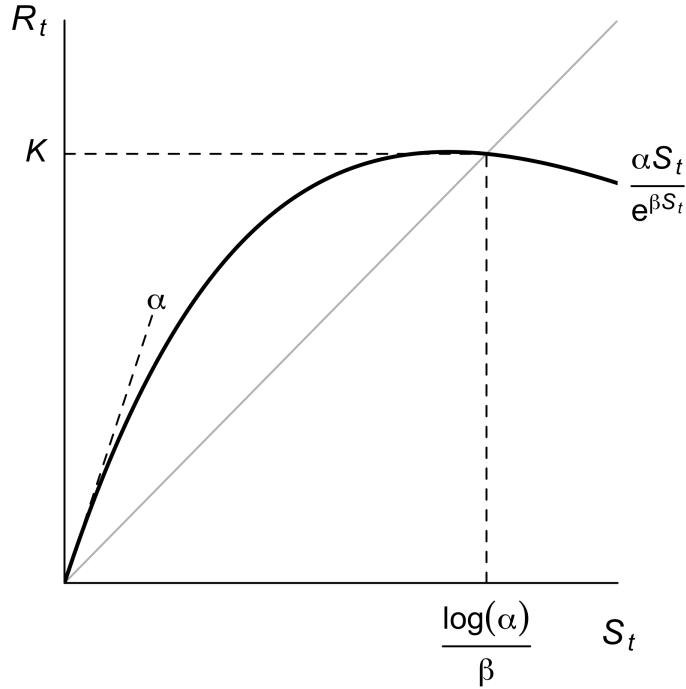


Figure 1. Deterministic form of the Ricker model used in the analysis. The parameter α is the slope at the origin and the derived parameter K is the carrying capacity. The gray line is where $R_t = S_t$.

3.3.2 Age-specific survival & maturation

The estimated number of fish of age a returning in year t ($N_{a,t}$) is the product of the total number of brood-year recruits in year $t - a$ and the proportion of mature fish from that brood year returning to spawn at age a ($p_{a,t-a}$), such that

$$N_{a,t} = R_{t-a} p_{a,t-a}. \quad (4)$$

The vector of age-specific return rates for brood year t , $\mathbf{p}_t = [p_{3,t-3} \ p_{4,t-4} \ p_{5,t-5} \ p_{6,t-6}]$, is a combination of the probability of surviving to, and maturing in years $t + a_{\min}$ to $t + a_{\max}$ (*i.e.*, $t + 3$ to $t + 6$). I modeled (\mathbf{p}_t) as a random effect using a hierarchical form of the Dirichlet distribution, where

$$\mathbf{p}_t \sim \text{Dirichlet}(\boldsymbol{\mu}, \pi). \quad (5)$$

In this formulation, the mean vector $\boldsymbol{\mu}$ is itself distributed as a Dirichlet, and therefore has a total of A elements that are all greater than zero. The precision parameter π affects each of the elements in $\boldsymbol{\mu}$, such that large values of π results in values of \mathbf{p}_t that are very close to $\boldsymbol{\mu}$.

3.4 Observation models

3.4.1 Spawners

Estimates of the number of spawning adults necessarily contain some sampling or observation errors due to incomplete censuses, mis-identification, etc. Therefore, I assume that the estimates of escapement (E_t) are log-normally distributed about the true number of spawners (S_t), such that

$$\log(E_t) \sim \text{Normal}(\log(S_t), r_s). \quad (6)$$

There is no harvest of natural-origin fish within the freshwater portion of the basin, so the total number of spawners equals the sum of the age-specific totals from Eqn (4), such that

$$S_t = \sum_{a=3}^6 N_{a,t}. \quad (7)$$

3.4.2 Age composition

The age composition data include the number of fish in each age class a in year t ($O_{a,t}$). The vector of age data $\mathbf{O}_t = [O_{3,t} \ O_{4,t} \ O_{5,t} \ O_{6,t}]$ is then modeled as a multinomial process with order Y_t and proportion vector $\mathbf{d}_t = [d_{3,t} \ d_{4,t} \ d_{5,t} \ d_{6,t}]$, such that

$$\mathbf{O}_t \sim \text{Multinomial}(Y_t, \mathbf{d}_t). \quad (8)$$

The order of the multinomial is simply the sum of the observed numbers of fish across all ages returning in year t

$$Y_t = \sum_{a=3}^6 O_{a,t}. \quad (9)$$

The proportion vector \mathbf{d}_t for the multinomial is based on the age-specific, model-derived estimates of adult returns in year t ($N_{a,t}$) and the true number of total spawners (S_t), such that

$$d_{a,t} = \frac{N_{a,t}}{S_t}. \quad (10)$$

3.5 Model fitting & evaluation

I used Bayesian inference to estimate all model parameters and the unobserved true numbers of spawners and recruits over time. I used version 3.5 of the **R** software (R Core Team 2018) for data retrieval, data processing, and summarizing model results, and version 4.2 of the **JAGS** software (Plummer 2003) for Markov chain Monte Carlo (MCMC) simulation. Specifically, I used 4 chains with 1.3×10^5 iterations each. Following a burn-in period of 5×10^4 , I retained every 100th sample for a total of 5000 samples from the posterior distributions.

I assessed convergence and diagnostic statistics via the **CODA** package in **R** (Plummer et al. 2006). Specifically, I used visual inspection of trace plots and density plots, and verified that Gelman and Rubin’s (1992) potential scale reduction factor was less than 1.1, to ensure adequate chain mixing and parameter convergence.

I evaluated the out-of-sample prediction accuracy for each model via leave-one-out cross-validation (LOO) as estimated in the **loo** package for **R** (Vehtari et al. 2018). LOO is more appropriate for Bayesian model selection than the more common deviance information criterion (DIC), especially for hierarchical models such as that used here (Vehtari et al. 2017). Traditionally, differences in DIC are considered fixed and known, but the estimation of the LOO information criterion (LOOIC) allows one to evaluate its uncertainty. That is, point-estimates of the difference between any two models may suggest a difference in their prediction accuracy, but the standard errors of the LOOIC values may be large enough to preclude any conclusion about which of the models is superior.

Appendix S2 contains a detailed workflow that will allow anyone to reproduce the model fitting and evaluation phases described here. Appendix S3 contains all of the code to replicate the figures in this report.

4 Results

The model incorporating flow during the smolt outmigration period had the most data support and lowest LOOIC (Table 1), so the following results are based on that model. However, the relative large standard errors in the model-specific LOOIC values indicates very little difference in the predictive accuracy among the various models. That said, there is some evidence suggesting that the models with flow covariates offer an improvement in predictive accuracy over the base model containing no flow covariate.

Table 1. Table of model selection results with models ranked from greatest to least data support. Columns correspond to the life stage at which the flow effect would be expected to manifest itself (Life stage); the statistic used to summarize flow (Stat); the beginning and ending dates over which the flow was summarized expressed as month-day (Begin, End); the number of years by which the flow covariate was lagged relative to the brood year (Lag); the number of effective parameters (p_e); the leave-one-out information criterion (LOOIC) and its standard error (se LOOIC); and the difference in LOOIC among models (Δ LOOIC). The model where “Life stage = base” does not contain any effect of flow.

Life stage	Stat	Begin	End	Lag	p_e	LOOIC	se LOOIC	Δ LOOIC
2+ outmigrants	Max	02-01	04-30	2	53.8	339.4	63.7	0.0
rearing	Max	07-01	09-30	1	53.9	342.2	64.1	2.8
rearing	Range	07-01	09-30	1	53.0	342.4	63.7	3.0
rearing	Min	07-01	09-30	1	55.6	342.6	64.4	3.2
prespawn	Min	04-01	04-30	0	55.3	342.7	63.9	3.2
prespawn	Max	05-01	05-31	0	53.3	343.0	63.5	3.6
1+ outmigrants	Max	05-01	05-31	1	52.9	343.0	63.3	3.6
base	NA	NA	NA	NA	53.4	343.6	63.6	4.2
2+ outmigrants	Range	04-01	04-30	2	54.0	344.0	63.3	4.6
prespawn	Median	11-01	03-31	-1	55.6	344.1	64.0	4.6
prespawn	Range	04-01	06-30	0	57.3	344.1	64.1	4.6
2+ outmigrants	Min	02-01	04-30	2	53.2	344.2	63.0	4.8
1+ outmigrants	Min	04-01	04-30	1	55.3	345.0	63.8	5.6
2+ outmigrants	Max	04-01	04-30	2	55.8	345.8	64.4	6.4
prespawn	Min	04-01	06-30	0	54.9	346.7	63.8	7.2
prespawn	Min	07-01	09-30	0	54.7	347.0	64.1	7.6
1+ outmigrants	Min	05-01	05-31	1	55.3	347.9	63.9	8.6
incubation	Median	11-01	03-31	0	79.4	403.0	55.3	63.6
1+ outmigrants	Range	04-01	06-30	1	84.3	416.4	52.4	77.0
2+ outmigrants	Median	02-01	04-30	2	87.8	421.6	51.0	82.2
1+ outmigrants	Max	04-01	06-30	1	86.9	421.8	49.0	82.4
incubation	Max	11-01	03-31	0	89.5	424.9	48.9	85.4
1+ outmigrants	Min	04-01	06-30	1	89.6	426.1	49.0	86.8
rearing	Median	07-01	09-30	1	90.4	426.2	50.1	86.8
prespawn	Min	05-01	05-31	0	90.5	428.7	48.8	89.4
prespawn	Median	07-01	09-30	0	92.4	430.5	51.7	91.0
2+ outmigrants	Range	02-01	04-30	2	97.4	435.9	52.0	96.6
prespawn	Median	04-01	06-30	0	93.8	448.4	47.1	109.0
prespawn	Max	04-01	06-30	0	101.1	450.1	55.8	110.6
1+ outmigrants	Median	04-01	06-30	1	98.7	459.3	48.7	120.0
2+ outmigrants	Median	04-01	04-30	2	107.2	467.0	58.7	127.6
prespawn	Max	11-01	03-31	-1	107.7	481.8	54.5	142.4
2+ outmigrants	Min	04-01	04-30	2	107.2	481.9	57.1	142.4

4.1 Population size

Estimates of the total population size of spawners over time agreed quite well with the observed data; all of the observations fell within the 95% credible intervals (Figure 2). There was a notable decrease in spawner abundance from 2003 to 2008; the number of spawners during the five years from 1999-2003 was 2-3 times greater than during the period from 2004-2017.

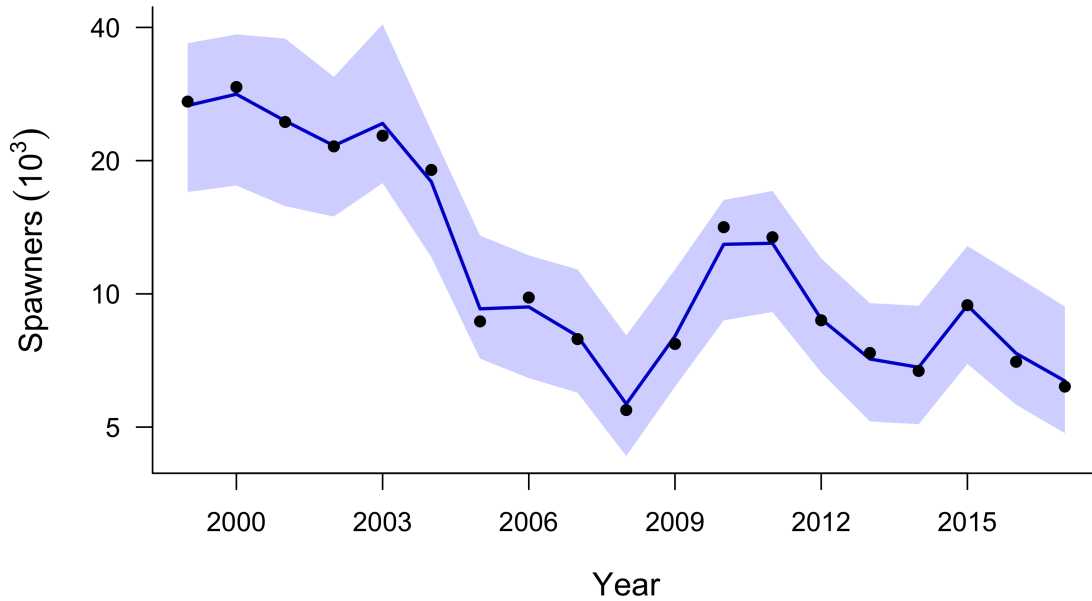


Figure 2. Time series of the estimated total population size. The observed data are the points; the solid line is the median estimate of the true number of spawners and the shaded region indicates the 95% credible interval.

4.2 Spawner-recruit relationship

We estimated considerable uncertainty in not only the numbers of spawning Chinook salmon and their subsequent offspring in the Willamette River basin, but also in the relationship between them (Figure 3a). Across all years, the median of the mean intrinsic productivity (i.e., μ_α the slope at the origin) was 1.6 surviving recruits per spawner (Fig. 3b). The lower bound of the 95% credible interval was 0.91 offspring per parent, which is just below the population replacement level. The upper bound of the 95% credible interval was 3.2 recruits per spawner. The median of the posterior probability distribution for the carrying capacity of the freshwater habitat was about 9000 adults (Fig. 3c). However, the 95% credible interval for the carrying capacity of the Willamette River basin was rather wide, ranging from approximately 1800 to 14,000 Chinook.

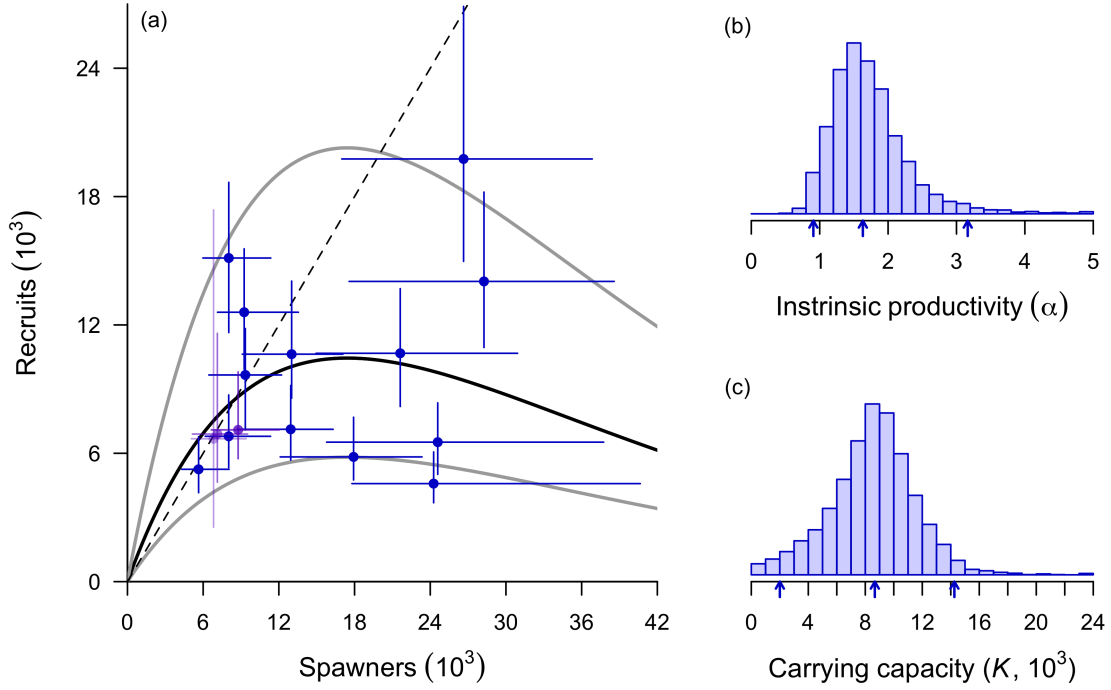


Figure 3. Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming median values for the flow covariate (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the posterior estimates; error bars indicate the 95% credible intervals. Blue points are for estimates with complete broods; purple points are for the most recent years with incomplete broods. The black line in (a) shows the expected relationship based on the median flow value over all years; gray lines indicate the 2.5th and 97.5th credible limits. Note that for plotting purposes only in (b) and (c), the density in the largest bin for each parameter contains counts for a few values greater than or equal to it. Vertical arrows under the x-axes in (b) and (c) indicate the 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

4.3 Recruits per spawner

In only 4 out of the 15 brood years did the population manage to replace itself, as evidenced from the time series of estimated recruits per spawner (Figure 4) and the general decline in spawners from 1999-2017 (Figure 2). There were three consecutive brood years (2005-2007) when overall productivity was good and the estimated recruits per spawner was above one (Figure 4), which resulted in the increase in spawners from 2008-2010 (Figure 2). There are no “recruit data” *per se* with which to compare the model estimates because they in themselves are a model-derived product.

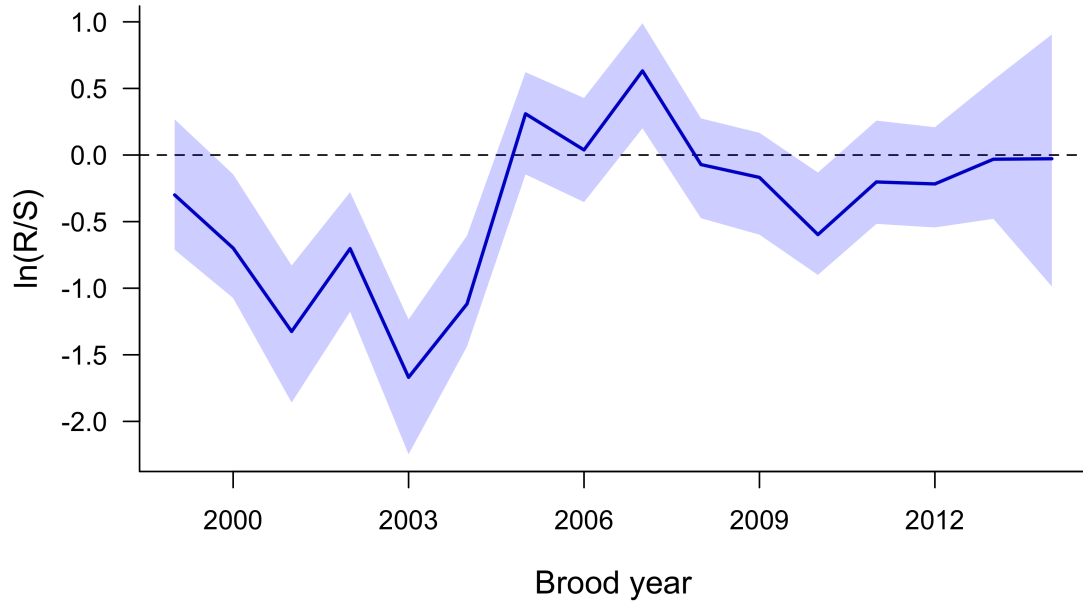


Figure 4. Time series of the estimated recruits per spawner. The solid line is the median estimate and the shaded region indicates the 95% credible interval.

4.4 Flow effects

There was a negative effect of winter-spring flows during the year the smolts would have been migrating to sea on the overall productivity of the population (Figure 5). The median flow effect was $-0.0095 \text{ (1000 cfs)}^{-1}$, and the 95% credible interval spanned from -0.022 to $0.000 \text{ (1000 cfs)}^{-1}$. Thus, an increase in flow of 10^4 cfs would translate into a decrease in productivity of $\sim 12\%$. This means, for example, that a relatively low-flow year like 1999 had ~ 2.4 times greater productivity than the highest flow year of 2012.

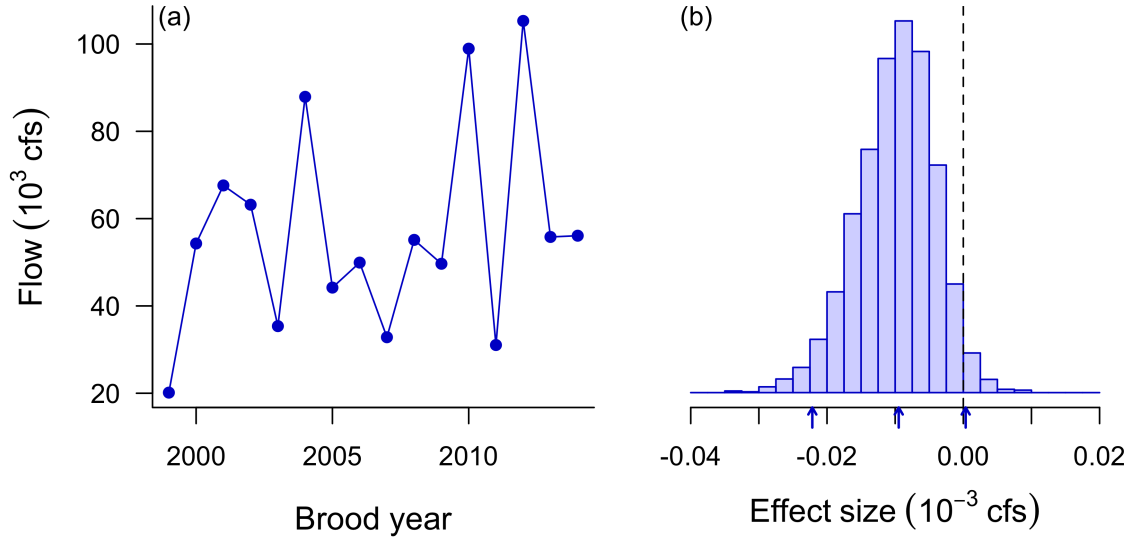


Figure 5. Time series of the maximum of the 7-day mean flow during the months of February through April (a), and its estimated effect on population productivity (b). Small arrows under the histogram in (b) denote 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

4.5 Process errors

The process errors (w_t in Eqn 2) showed very little autocorrelation from year to year (Figure 6), indicating that interannual autocorrelation in both flows and spawners was sufficient to explain autocorrelation in recruitment.

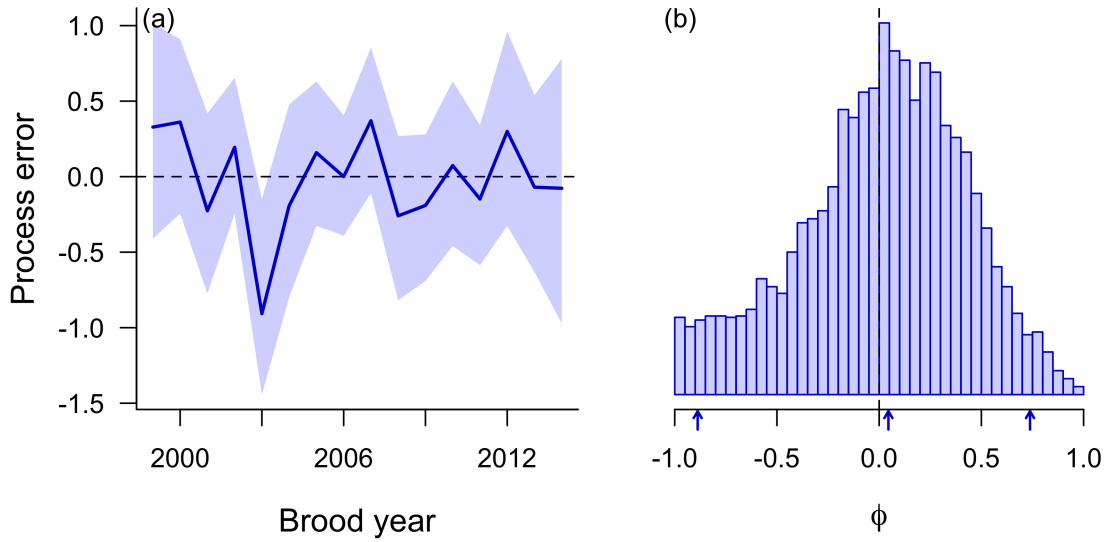


Figure 6. Time series of the estimated process errors (a), which represent the population's productivity after accounting for the effects of density dependence and environmental covariates, and the posterior distribution of the autocorrelation parameter ϕ (b). The solid line in (a) is the

median estimate and the shaded region indicates the 95% credible interval. Small arrows under the histogram in (b) denote 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

5 Discussion

The reconstruction of true spawner counts from the data demonstrates a clear downward trend since the turn of the century, which is rather disconcerting given the rather low intrinsic productivity of this stock. From 2005 onward, spawner numbers have varied around the estimated carrying capacity of about 9000 adults. However, this analysis was focused solely on the effects of flow on productivity, and cannot speak to possible causes of the relatively low capacity. Nevertheless, in addition to obvious losses of habitat, possible competition from hatchery-origin fish may be decreasing capacity for wild fish (Buhle et al. 2009; Chilcote et al. 2011; ODFW and NMFS 2011).

The negative effect of high flows during the spring when age-2 smolts are outmigrating is somewhat puzzling, as one would generally expect that higher flows would be beneficial. Perhaps particularly high flows in spring may push smolts downstream and into the estuary before they have adequate time to undergo the necessary physiological changes necessary for life at sea. In addition, the increased precipitation and runoff that leads to high flows may increase the transport of contaminants from terrestrial to aquatic environments, which have known negative effects on juvenile salmon in this region (Lundin et al. 2019).

The IPM developed here differs in several ways from other life-cycle models created for Chinook salmon in the Willamette River basin. To date, those efforts have focused on developing highly detailed descriptions of the life-cycle and then filling in the necessary information from disparate sources. In contrast, this IPM was based solely upon the available data, and thus focuses on adult-to-adult transitions without any intermediate life stages. Although that lack of detail may be disappointing to some, it does present *i)* an open and direct treatment of the data, and *ii)* a full accounting of the uncertainty in the input data and estimated parameters and states. One of the advantages of the IPM is that it treats possible covariates just any other source of information. That is, any effect of flow is estimated directly within the same model framework that governs population dynamics rather than being prescribed *a priori*.

The results of several models based upon the various flow metrics were largely equivocal, and the ability to discriminate among the predictive accuracy of the varying model forms was influenced by three things. First, high correlation among the flow covariates necessarily means we should expect similar outcomes. Second, the relatively short duration of the time series does not provide for as much contrast in both fish abundance and flow regimes to tease apart any important effects. Third, uncertainty within the age composition data across years and ages can create regions of statistically low-likelihood (*i.e.*, the model predicts a proportion of relatively rare age-3 or age-6 fish that is inconsistent with the observations). The importance of data weighting and its influence on model outputs has been widely addressed in marine stock assessments (Maunder and Punt 2013), but is relatively uncommon in the evaluation of salmon models (Buhle et al. 2018), and should therefore be considered explicitly in the future.

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