

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

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Contents

Summary	3
1 Introduction	3
2 Methods	3
2.1 Fish data	3
2.2 Flow covariates	4
2.3 Process models	4
2.3.1 Total recruits	4
2.3.2 Age-specific survival & maturation	5
2.4 Observation models	6
2.4.1 Spawners	6
2.4.2 Age composition	7
2.5 Model fitting & evaluation	7
3 Results	8
3.1 Population size	8
3.2 Spawner-recruit relationship	8
3.3 Recruits per spawner	9
3.4 Flow effects	10
3.5 Process errors	11
4 Discussion	14
5 References	14

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Summary

1 Introduction

Life cycle models are commonly used in the Pacific Northwest to evaluate the potential responses of salmon populations to possible future management actions 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 even 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 (Schaub and Abadi 2011; Maunder and Punt 2013). However, this general approach suffers from several shortcomings. First, information is lost when 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. 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 (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).

The goal of this project was to develop an IPM for Chinook salmon (*Oncorhynchus tshawytscha*) from the Willamette River basin and investigate whether there were detectible flow effects on the production and survival of offspring (recruits) from their spawning parents. 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). 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.

2 Methods

2.1 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).

Adult Chinook salmon in the Willamette River basin return at ages 3 through 6. 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. 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.

2.2 Flow covariates

During a series of workshops, the Science of Willamette Instream Flows Team (SWIFT) developed a set of 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 from models with closely related flow metrics should be quite similar.

2.3 Process models

2.3.1 Total recruits

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, however, 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} .

2.3.2 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 $\boldsymbol{\mu}$.

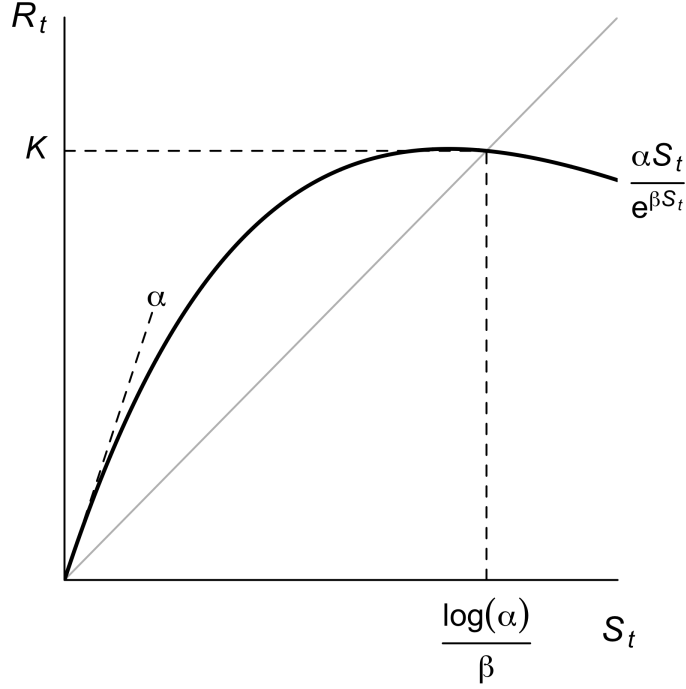


Figure 1. Deterministic form of the Ricker model used in the analysis. The parameter α is the slope at the origin and the derived parameter K is the carrying capacity. The gray line is where $R_t = S_t$.

2.4 Observation models

2.4.1 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, such that

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

2.4.2 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

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

2.5 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** (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 real 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. Appendix S3 contains all of the code to replicate the figures in this report.

3 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.

3.1 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.

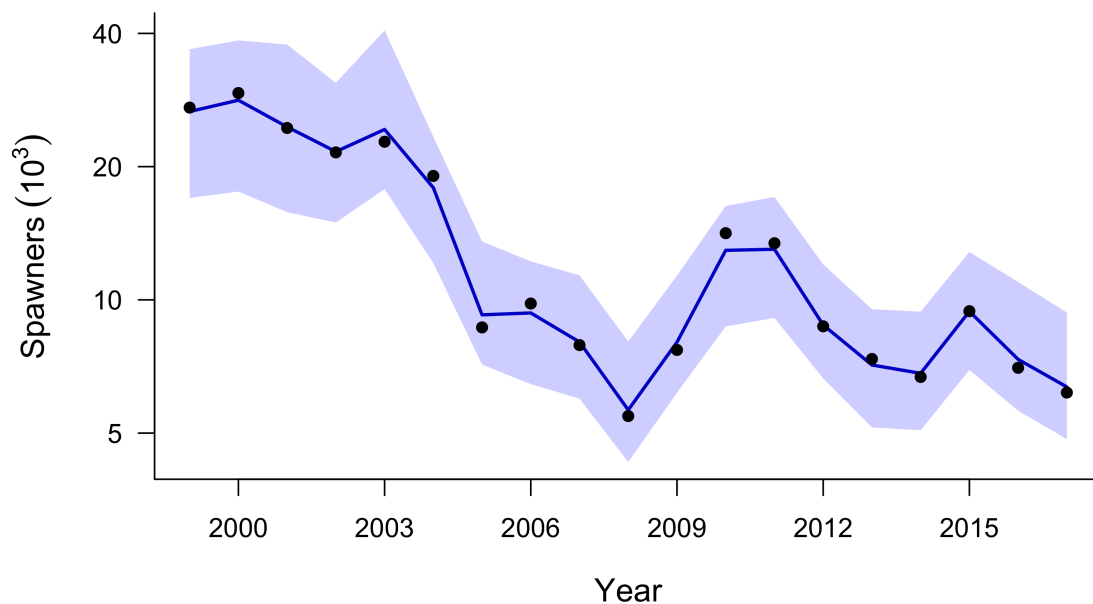


Figure 2. Time series of the estimated total population size. The observed data are the points; the solid line is the median estimate of the true number of spawners and the shaded region indicates the 95% credible interval.

3.2 Spawner-recruit relationship

We estimated considerable uncertainty in not only the numbers of spawning Chinook 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.

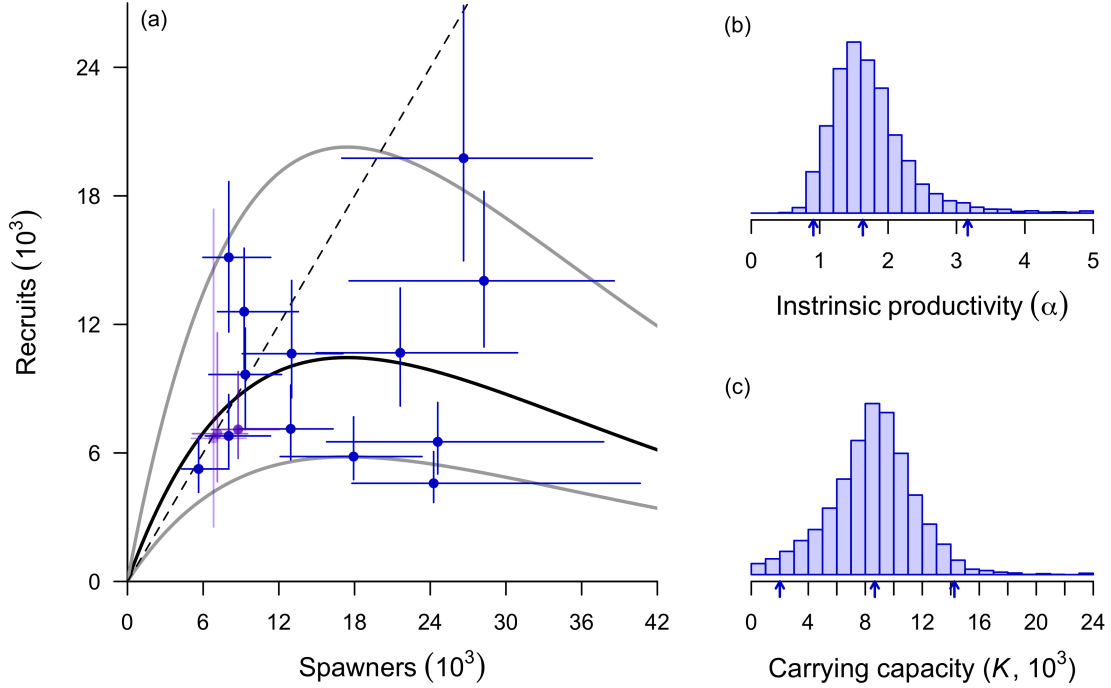


Figure 3. Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming median values for the flow covariate (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the 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 all 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.

3.3 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).

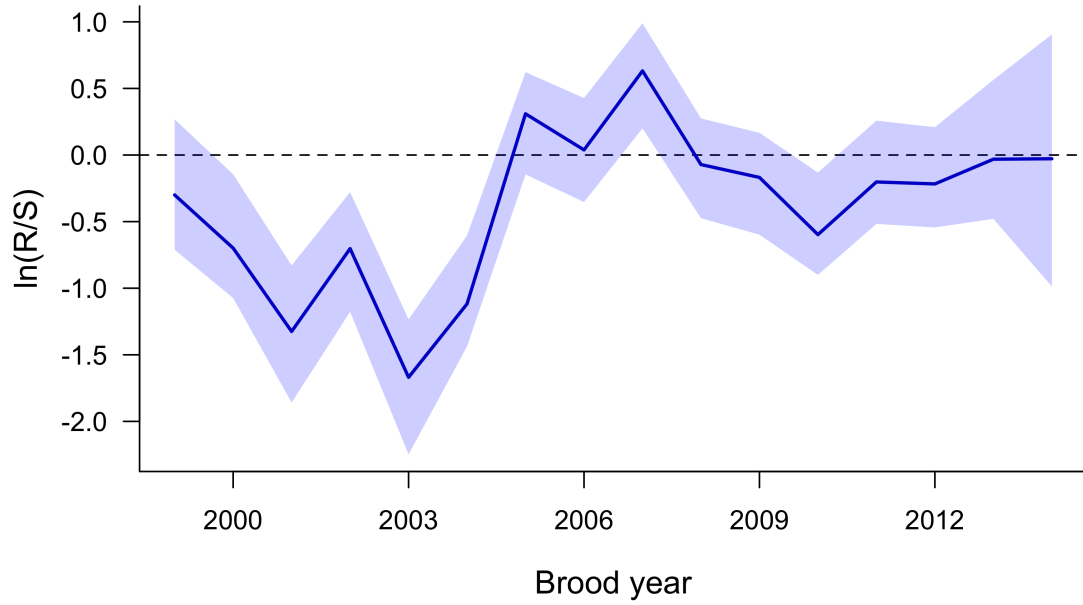


Figure 4. Time series of the estimated recruits per spawner. The solid line is the median estimate and the shaded region indicates the 95% credible interval.

3.4 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.

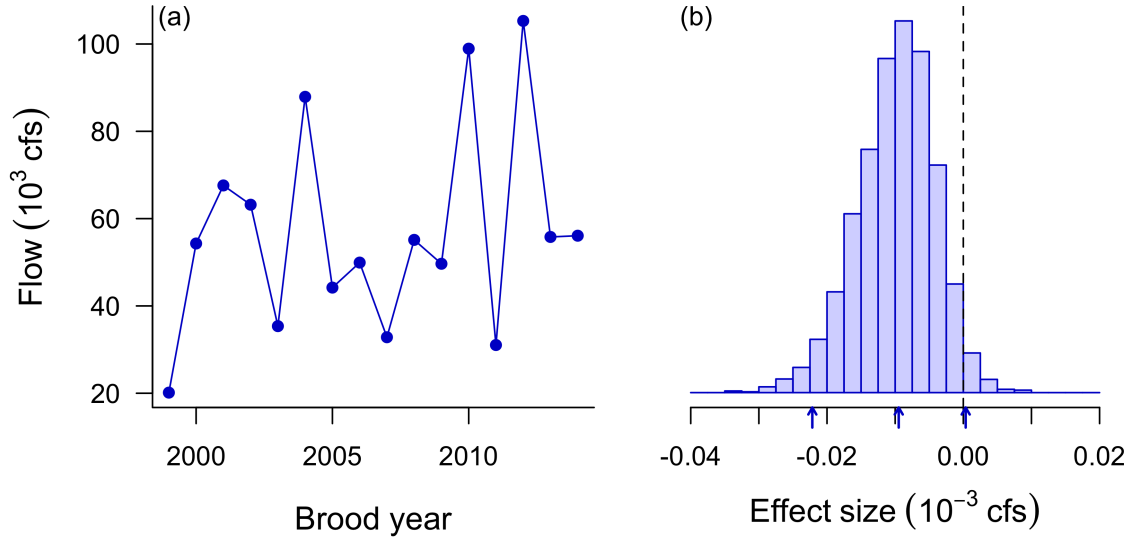


Figure 5. Time series of the maximum of the 7-day mean flow during the months of February through April (a), and its estimated effect on population productivity (b). Small arrows under the histogram in (b) denote 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

3.5 Process errors

The process errors (Figure 6a) showed very little autocorrelation in recruitment after accounting for the effects of spawners and flow on productivity (Figure 6b).

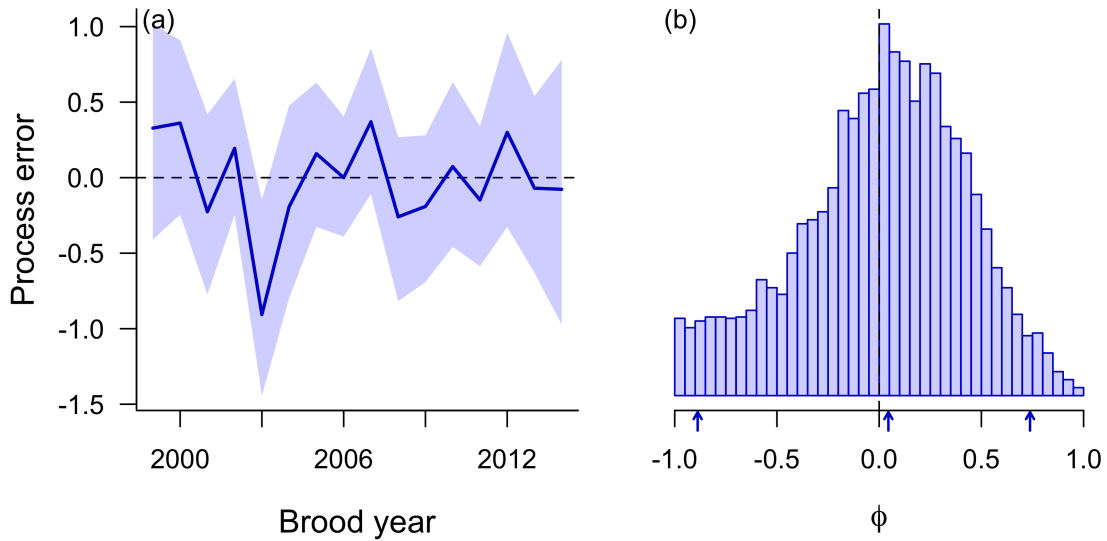


Figure 6. Time series of the estimated process errors (a), which represent the population's productivity after accounting for the effects of density dependence and environmental covariates, and the posterior distribution of the autocorrelation parameter ϕ (b). The solid line in (a) is the median estimate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

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 Discussion

Flow covariates were highly correlated so results should be equivocal.

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