Characterizing the strength of density dependence in at-risk species through Bayesian model averaging

Guillaume Bal[1,2], Mark D. Scheuerell[3] and Eric J. Ward[4]

[1]National Research Council, under contract to Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E, Seattle WA, 98112, USA

[2] Marine Institute, Oranmore, Co. Galway, Ireland

[3] Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Association, Seattle, WA 98112, USA

[4] Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Association, Seattle, WA 98112, USA

Corresponding author: G. Bal, Marine Institute, Oranmore, Co. Galway, Ireland. (E-mail: guillaume.bal.pro@gmail.com, Phone: +353 85 835 1670, Fax: +353 91 387 201)

ABSTRACT

Developing effective conservation plans for at-risk species requires an understanding of the relationship between numbers of breeding adults and their subsequent offspring. In particular, establishing the degree to which density-dependent effects limit population size can be difficult due to errors in the data themselves, uncertainty in model parameters, and possible misspecification of model structure. Here we develop a Bayesian model averaging framework to fit four simple models of adult-offspring production and estimate the probabilities that negative (i.e., decreasing survival with increasing density) and positive (i.e., Allee effects) density dependence exists. As an example, we analyzed 48 at-risk populations of anadromous Chinook salmon (*Oncorhynchus tshawytscha*) from the northwestern United States. We found strong evidence that more than two-thirds of the populations exhibit negative density-dependent effects of adults. This result was somewhat unexpected given the large reductions in adult numbers relative to historical benchmarks, indicating that carrying capacity of spawning habitat has been reduced considerably. Approximately two thirds of the populations also had non-zero probabilities of positive density-dependent effects of adults, which could suggest that cumulative losses of spawning adults over the past century has led to decreased nutrient and energy subsidies from semelparous carcasses, and diminished bio-physical disturbance from nest-digging activity. Importantly, our analysis highlights the utility of Bayesian model averaging in a conservation context wherein errors in choosing the best model may have more severe consequences than errors in estimating model parameters themselves.

Keywords: density dependence, bayesian model averaging, management strategies, Allee effect, compensation, depensation, salmon.

1 INTRODUCTION

One of the cornerstones of conservation biology is establishing the relationship between the numbers of parents and the offspring they produce. In particular, the degree to which organisms are affected by population density has important implications for individual fitness and population growth. Negative density dependence (NDD) occurs when density is relatively high and any further increases in density lead to increased competition for resources (e.g., food, breeding locations) or transmission of diseases, ultimately causing reductions in per capita survival (Hixon et al. 2002, Brook and Bradshaw 2006). Conversely, positive density dependence (PDD), or the “Allee effect”, arises when density is relatively low and the loss of more individuals causes decreased per capita survival because of cooperative foraging or defensive behaviors, decreased probability of finding a mate, or combinations of these factors (Courchamp et al. 1999, Berec et al. 2007, Gregory et al. 2010a). The strength of both NDD and PDD in wild populations has practical management implications. For example, the presence of NDD could indicate limited habitat availability (i.e., insufficient total area) whereas the existence of PDD might suggest a high degree of habitat fragmentation; rectifying those two types of habitat deficiencies could require rather different actions. When combined with historical knowledge about the population, insights about the combined roles of NDD and PDD are also useful for reintroduction planning (Anderson et al. 2014). Understanding whether NDD and PDD occur and if so, to what extent, is thus particularly valuable for determining the best options for population management and the conservation of at-risk species.

Density-dependence has been studied extensively in fish populations because of its importance to both the management of healthy and economically valuable stocks and the conservation of imperiled populations (Liermann and Hilborn 1997, Barrowman and Myers

2000, Barrowman et al. 2003). In classical fisheries management, NDD within a stock implies parental biomass should be harvested to the point where the surplus production of new recruits to the fishery is maximized relative to replacement (Hilborn and Walters 1992). Conversely, the degree of PDD mortality will determine the rate at which overfished stocks will recover when harvest is reduced. Most conservation practitioners concentrate on the possible existence of PDD. However, NDD at relatively low abundance can exist, implying diminished carrying capacity from factors like habitat loss/modification or the presence of non-native species (Achord et al. 2003), but this is often ignored in conservation contexts.

Models of population dynamics offer a formal means for estimating both positive and negative density dependence (Boyce 1992). For example, Beverton-Holt (1957) and Ricker (1954) models of density dependence have been used to estimate the relationships between parents and offspring for decades. Approaches allowing for flexibility in curves shapes but not process based, such as splines or Gaussian model, have also been developed (Bravington et al. 2000, Munch et al. 2005). Meanwhile Barrowman and Myers (2000) introduced a form of piecewise regression model known as the “hockey stick” (HS) model, which is similar to the Ricker and Beverton-Holt curves. The HS model offers potential advantages over these other models in a conservation context because it provides more conservative estimates of the maximum density-independent survival (i.e., slope at the origin) and carrying capacity (Barrowman and Myers 2000). In addition, the breakpoints in the HS segments may provide natural reference points for management decisions. However, the HS model does not allow for PDD.

Although statistical modeling is a powerful tool, three main types of uncertainties can hinder our ability to infer the true underlying relationship between parents and their offspring.

First, observation errors arise in the form of sampling and measurement errors. Second, model parameters are rarely known without error and instead must be estimated from the data. Third, uncertainty about the structure of the model itself affects inference about the form of the parent-offspring relationship. The first two concerns are often addressed through appropriate sampling designs and explicit consideration of both process and observation/sampling errors. However, possible misspecification of a particular model is typically ignored and instead the “best” model is chosen based on some model selection measure such as Akaike’s Information Criterion (Burnham and Anderson 2002). In such cases, two models with nearly identical support from the data could produce widely divergent predictions, especially when confronted with new data (Pascual et al. 1997, Richards 2005). As a guard against this likely possibility, model averaging (MA) offers a formal means for explicitly addressing model-selection uncertainty in problems of inference and prediction (Burnham and Anderson 2002, Wintle et al. 2003). In particular, model averaging can produce more robust estimates by combining results from an ensemble of multiple independent models (Banner and Higgs 2017). As a cautionary note, however, averaging expectations from models that are capable of producing an important spectrum of different results may confuse interpretations (Galipaud et al. 2014, Cade 2015). Thus, the set of models to consider should be carefully considered.

Pacific salmon (*Oncorhynchus* spp.) are important to human economies and the ecology of coastal ecosystems across the northern Pacific rim (Schindler et al. 2003). Fisheries for salmon are worth hundreds of millions of US dollars annually (NMFS, 2013). Salmon also act as ecosystem engineers by modifying benthic habitats through nest-digging activity (Moore 2006) and serve as keystone species in food webs as food for fish, mammals, birds, and insects (Helfield and Naiman 2006). In many coastal watersheds across western Canada and the US, however, Pacific salmon populations have been reduced to mere fractions of their historical abundances due to changes in habitat, hydropower development, overharvest, and changing climate (Ruckelshaus et al. 2006). Literature also suggest that Pacific salmon population are susceptible to Allee effect through predation, disease and decreased mate finding abilities at low densities (Quinn et al. 2014, Godwin et al. 2015) . Thus, obtaining a proper understanding of whether NDD, PDD, or both occur among at-risk salmon populations and estimating related reference points is necessary for determining the best recovery strategies.

Here we examined the strength of NDD and PDD among 48 populations of Chinook salmon (*O. tshawytscha*) from the northwestern USA that are currently listed as "threatened" under the US Endangered Species Act. To do so, we simultaneously considered four different piecewise-linear models to characterize various forms of density dependence (Fig. 1): 1) unrestricted (density-independent); 2) Allee effect only (PDD); 3) carrying capacity only (NDD); and 4) both PDD and NDD. Piecewise-linear models tend to provide better estimates of per capita productivity at low population sizes, and offer more conservative estimates of mortality rates that lead to extinction. In addition, we addressed both parameter and model uncertainty within a unified framework through Bayesian model averaging (BMA), which allowed us to easily combine predictions and uncertainties across all four models.

2 MATERIAL AND METHODS

2.1 Allee Hockey Stick model and nested sub-models

Barrowman and Myers' (2000) hockey stick (HS) model assumes the number of offspring increases linearly up to an asymptote, beyond which it is independent of parental abundance. For a given population, the model is described by two linear functions above and below some threshold level of parental abundance (P_c),

$$O_t = \begin{cases} \beta P_t & if\ P_t < P_c \\ K & if\ P_t \geq P_c \end{cases} \tag{1}$$

where β is the density-independent per-capita reproductive rate, P_t is the number of parents breeding in year *t*. At parental abundance values above P_c , NDD effects dominate and restrain the number of offspring to *K,* the carrying capacity. As P_c approaches infinity, the degree of density-dependence goes to zero and because of exponential growth, there is no limit to population size.

To allow for PDD (Allee effects) at relatively low levels of parental abundance, we modified the original HS model (Barrowman and Myers 2000) to allow for a third linear segment. This new “Allee Hockey Stick” (AHS) model allows growth rates to become depressed when parental abundance is less than some threshold, P_d

$$O_t = \begin{cases} \beta_1 P_t & if\ P_t < P_d \\ \beta_1 P_d + \beta_2 (P_t - P_d) & if\ P_d < P_t < P_c \\ K & if\ P_t \geq P_c \end{cases} \tag{2}$$

where $0 < \beta_1 < 1 < \beta_2$, $K = \beta_1 P_d + \beta_2 (P_c - P_d)$ and P_d and P_c are the breakpoint thresholds respectively. By fixing some parameters at zero or infinity, the AHS model reduces to three less complex models, each with contrasting assumptions about the occurrence of NDD and PDD (Fig. 1). The first is for unrestricted or linear growth (L model) where $\beta_1 = 0,\ P_d = 0$ and $P_c = \infty$), such that

$$O_t = \beta_2 P_t \tag{3}$$

The second is for an Allee effect only (AL model) where $P_c = \infty$ and

$$O_t = \begin{cases} \beta_1 P_t & \text{if } P_t < P_d \\ \beta_1 P_d + \beta_2 (P_t - P_d) & \text{if } P_t > P_d \end{cases}. \tag{4}$$

The third is the original HS model with carrying capacity only, such that $\beta_1 = 0,\ P_d = 0, K = \beta_2\, P_d$, and

$$O_t = \begin{cases} \beta_2 P_t & \text{if } P_t < P_c \\ K & \text{if } P_t \geq P_c \end{cases}. \tag{5}$$

2.2 Parameter estimation and model weighting

Here we used a 2-steps procedure, where each model is first fit independently to data using the Sampling – Importance – Resampling (SIR) algorithm (Rubin 1988), and then results are averaged across models. The SIR algorithm we used to approximate the posterior distribution by using an importance function to resample parameter draws from a proposal distribution is equivalent to Moore (2008) and detailed in Appendix A. For a given model, the marginal likelihood can be expressed as the product of the prior model probability and the likelihood integrated over the entire parameter space. For instance, the corresponding equation for model M_1 is $P(M_1|y) = P(M_1) \int P(\theta|M_1) P(y|\theta, M_1)$. Across models, we normalized the marginal likelihoods so that they could be interpreted as posterior model probabilities $\sum_i P(M_i|x) = 1$ (Rubin 1988). There are several upsides and downsides of Bayesian estimation in SIR versus other techniques, such as MCMC. As a positive, calculating the expected marginal likelihood is straightforward in SIR because the likelihood of each draw can be easily saved which is not possible in software implementing MCMC, such as WinBUGS (Lunn et al. 2000), JAGS (Plummer 2003) or Stan (Stan Development Team 2016). Second, the SIR algorithm does not require a burn-in period or assessment of MCMC diagnostics for convergence. However, the utility of SIR is somewhat limited for complex models, beyond 4-5 parameters, because sampling can be inefficient. For all models presented above, we assumed that the residual error was lognormally distributed. We chose weakly informative uniform priors and that were shared among the four models whenever possible (Table I).

An R package containing functions to fit the 4 models, together with the dataset discussed below, is freely available on GitHub at the following address: https://github.com/GuillaumeBal/bal.et.al.2018.bma.density.dependence

2.3 **Model Application**

For management purposes, Pacific salmon species are grouped into evolutionarily significant units (ESUs), defined as a group of salmon that (1) is reproductively isolated from other conspecific populations, and (2) represents an important component in the evolutionary legacy of the species (Waples 1991). We estimated the strength of density dependence among 48 Chinook salmon populations within 3 distinct ESUs from Washington, Idaho, and Oregon in the northwestern USA (Fig. 2). These ESUs represent different life-history types, allowing us to compare the strength of density dependence across life histories. For example, Chinook salmon within the Puget Sound ESU are “ocean-type”; these juveniles spend less than 1 year in fresh water before migrating to the ocean. In contrast, salmon from the Snake River and Upper Columbia ESUs are “stream-type” and spend 1 full year in fresh water before migrating to sea (Taylor 1990).

We used the total number of spawning adults in a given year as our estimate of parent abundance. Because salmon from the same cohort mature at different ages, our estimates of offspring are then the sum of subsequent adults that were born in a given year, but that vary in age and return over sequential years (e.g., the offspring of Snake River stream-type adults that spawned in 2000 return as 3-6 years later in 2003-2006). All data used here were compiled by the National Marine Fisheries Service. To ensure time series were long enough to potentially detect positive density dependence (Brook and Bradshaw 2006, Gregory et al. 2010b), we restricted our analysis to those populations with at least 20 years of data, and no more than 5 missing values within that period (Table 2). This resulted in time series length ranging from 20 to 54 years.

3 RESULTS

For both life history types across the three ESUs, we found the strong support from the data for a model with only NDD (Fig. 3a); the median posterior model probabilities were 0.65 and 0.45 for ocean and stream-type Chinook salmon, respectively. We found little evidence for models containing only PDD (Allee effects) and models that included both PDD and NDD had median probabilities of being the best equal to 0.13 and 0.011 for ocean and stream-type salmon, respectively.

Among populations within a specific life history type, however, the relative support for the different models varied considerably (Fig. 3b). Although there were a few populations whose model probabilities were rather evenly split among the four model forms (e.g., 4, 16), most populations showed strong support in favor of one particular model. For ocean-type Chinook salmon, most populations showed strong indications of NDD, but a few populations had little evidence for either form of density dependence (e.g., 1, 4, 8, 14, 15). Evidence for NND was rather strong for stream-type Chinook, and notably, the evidence for models with both PDD and NDD was reasonably strong in fewer populations (e.g., 39, 42).

For each population, the model averaged relationship exhibited subtle to rather significant departure from the best model depending of the relative credibility of the models. For example, the best models selected for Big Creek, the South Fork of the Salmon River east fork and the South fork of the Salmon River mainstem (i.e., populations 23, 39, 40 in Table 2) were the L model, HS model, and L model, respectively. Applying BMA to estimate the shape of this curve may yield a result very similar to the single “best” model, but it can also result in more conservative results (Fig. 4). In the case of Big Creek, a simple model selection would select a linear relationship whereas the shape coming from BMA exhibits NDD when the population reaches 409 fish although the departure from the replacement curve is on average weak. In the South fork of the Salmon River East Fork, PDD is highly likely when the population size falls under 27 individuals. For the South fork of the Salmon River mainstream, however, there is very little difference between the best and BMA models.

Although we found no discernable link between the data support for an Allee effect in a population and the length of the corresponding time series, we did observe a positive relationship with the ratio of the observed lowest to highest counts within a time series (i.e., a measure of relative historical stock depletion; Fig. 5).

4 DISCUSSION

Our results reveal two important messages regarding the role of density-dependence in the population dynamics of Chinook salmon in the Pacific Northwest. First, we found that linear relationships between offspring and parents with no density dependence were probable, especially within the Snake River ESU (median model posterior probability = 0.53) whom the rivers have experimented the strongest historical depletions according to the ratio of minimum over maximum spawners abundances (Table 2). This suggests that quite a few populations from the Columbia River watershed have still not recovered from the overall great reduction in parental abundances compared to historical numbers. With a few exceptions, we found strong support for models with NDD (median model posterior probability = 0.65) in populations from the Puget Sound area. Our results further support ongoing efforts in this region to increase carrying capacity through improvements to freshwater spawning and rearing habitats.

Second, the existence of PDD among these Chinook salmon populations is indeed a possibility, which agrees with previous studies of other salmon species (Liermann and Hilborn 1997, Barrowman et al. 2003), but it appears to be low. The time series used in this study have 20 to 54 years of data, which are similar to previous publications attempting to detect the presence of Allee dynamics (Brook and Bradshaw 2006, Gregory et al. 2010b). Although longer time series are always preferable, we found little relationship between time series length and support for Allee dynamics. Furthermore, most of the populations are at the low end of their historical sizes, such that the ratio of the minimum to maximum spawners ranges from 0% to 20%, with about 50% of the populations below 2.5%. Interestingly, we found that the support for Allee effects is positively correlated with this ratio. The support for Allee effects in populations that have been less depleted may result from a lack of data at extremely low abundances, wherein the Allee model produces different estimates from the linear or HS model.

Although support for Allee effects is weak overall and we cannot identify the exact cause, some reasonable hypotheses exist. First, salmon gain about 90% of their adult biomass in the ocean, and therefore act as net importers of marine-derived nutrients and energy to freshwater ecosystems (Schindler et al. 2003), but decades of low adult abundance may have rendered these ecosystems much less productive for juveniles than they were historically (Rinella et al. 2012). In addition, nest-digging activity by female salmon mobilizes fine sediment (Moore et al. 2004) and decreases the probability of stream-bed scour and excavation of buried salmon eggs or embryos (Montgomery et al. 1996). Thus, losses of adult salmon may have crossed a threshold whereby the freshwater ecosystem cannot support the juvenile production it once did (Achord et al. 2003, Schindler et al. 2005).

Absence of observed Allee effects could also indicate that availability of juvenile habitat is more important than direct mortality from predators (Mogensen and Post 2012). For Puget Sound populations, in particular, much of the lowland areas have been converted from forest to agriculture, which has greatly decreased the carrying capacity for juvenile Chinook salmon (Scheuerell et al. 2006). Furthermore, increasing evidence points to NDD among adult life stages during their ocean residency owing to competition with hatchery fish (Ruggerone et al. 2012, Connors et al. 2012). This potentially shifts the focus away from habitat actions and more toward hatchery reforms (Buhle et al. 2009).

The varying degrees of support for different forms of density dependence among the many populations provide some important insights for conservation. Decisions to list Pacific salmon as threatened or endangered under the Endangered Species Act are made collectively at the relatively large ESU level, but recovery plans are developed and implemented at much smaller scales relating to specific populations. Here we have used posterior model probabilities to assess the degree to which PDD, NDD, or a combination thereof exists for each population within an ESU. Managers could potentially use this information to further direct location-specific actions that might decrease the intensity of PDD or NDD.

The SIR algorithm applied in this study uses samples across the prior distributions to calculate marginal likelihood and derive model probabilities. This approach has already been used in fisheries related studies (Punt and Hilborn 1997, McAllister and Kirkwood 1998, Zerbini et al. 2011) as well as for the study of isotopic mixtures (Semmens and Moore 2008, Moore and Semmens 2008). The efficiency of this SIR algorithm is limited to low dimensionality problems (models with few parameters) as the acceptance rate would otherwise drops off very quickly and thus make computation time very long. For this reason, MCMC methods tend to be favored. Because of some recent criticism of Bayesian model selection tools, such as DIC (Spiegelhalter et al. 2014, Gelman et al. 2014) we were interested in the SIR algorithm's ability to perform estimation for these relatively simple models. Computation time was quick, lasting only a few minutes per population. We also compared our results to that of the more widely used DIC and the more recent LOOIC (Leave One Out Information Criterion) Bayesian model selection approaches. When compared to the SIR algorithm, the DIC approach tended to rank the HS model first to the detriment of the L model in a few cases (Appendix C1). The reversed pattern was observed with the LOOIC approach (Appendix C2). In both cases, those shifts were consistent across the two life history types. Although the different methods lead to a few differences on a river by river basis, the general patterns discussed above and based on the SIR approach are robust. These similarities between methods also support the fact that the chosen priors have little influence on the results obtained.

Our analysis highlights the utility of model averaging for estimating relationships among parents and their offspring. Model averaged results were more conservative than the best model alone, and therefore applying model averaging may be particularly important for populations of conservation concern. The use of the HS and AHS models was largely chosen based on the taxa in our analysis; other model sets could be developed for other species (and unlike our analysis, there is no requirement that all candidate models be nested). Although there are a number of ways to implement Bayesian model averaging, the SIR approach is best for relatively simple models like those we used here. Increased model complexity will decrease the speed of the SIR approach exponentially, however. Using other estimation routines such as Markov Chain Monte Carlo (MCMC), the model-averaged procedure could also be constructed hierarchically across populations, to estimate common strengths of density dependence across populations.

5 ACKNOWLEDGMENTS

This research was performed while Dr. Guillaume Bal was a post-doctoral research associate sponsored by the National Research Council. We thank Brian Burke and Kevin See for helpful comments on an earlier draft of the manuscript.

6 TABLES

Table I. Bayesian priors for the parameters in the four competing models described by equation 2 in the methods. P_{max} and O_{max} are the maximum numbers of observed parents and offspring, respectively, for a given population.

Parameter	Linear	Allee	Hockey Stick	Allee Hockey Stick
β_1		Unif(0, 1)		Unif(0, 1)
β_2	Unif(1, 25)	Unif(1, 25)	Unif(1, 100)	Unif(1, 100)
P_d		Unif(0, P_{max} / 3)	Unif(0, P_{max} / 3)	Unif(0, P_{max} / 3)
K			Unif(O_{max} / 3, O_{max})	Unif(O_{max} / 3, O_{max})
SD	Unif(0, 3)	Unif(0, 3)	Unif(0, 3)	Unif(0, 3)

Table 2. Summary of parent and offspring data for Chinook salmon used in the study. PS, S, and UC refer, respectively, to Puget Sound, Snake, and Upper Columbia Evolutionary Significant Units (ESU).

Index	ESU	River name	Time period	Parents range	Offspring range
1	PS	Cascade River	1981-2005	83-625	92-2458
2	PS	Cedar Creek	1965-2005	126-1896	8-9099
3	PS	Dungeness River	1986-2005	43-955	47-1486
4	PS	Duwamish River	1968-2005	2014-11551	657-52907
5	PS	Elwha River	1986-2005	164-5309	418-5485
6	PS	Nisqually River	1968-2005	114-2788	0-32915
7	PS	Nooksack River North fork	1984-2005	10-7473	13-5337
8	PS	Nooksack River South fork	1984-2005	103-625	100-1364
9	PS	Puyallup River	1968-2005	527-5387	74-23354
10	PS	Sammamish River	1983-2005	34-550	20-1708
11	PS	Sauk River lower part	1952-2005	112-3896	321-22021
12	PS	Sauk River upper part	1952-2005	108-3345	57-27343
13	PS	Skagit River lower part	1952-2005	409-9263	577-62260
14	PS	Skagit River upper part	1952-2005	3586-20040	6146-114870
15	PS	Skokomish River	1968-2005	189-3184	39-16734
16	PS	Skykomish River	1965-2005	1681-7703	110-110621
17	PS	Snoqualmie River	1965-2005	324-3603	149-24714
18	PS	Stillaguamish River North fork	1974-2005	330-1849	353-89489
19	PS	Stillaguamish River South fork	1974-2005	73-391	15-14265
20	PS	Suiattle River	1952-2005	167-1804	87-10407
21	PS	White River	1965-2005	7-2131	9-7779

22	S	Bear Valley	1960-2002	17-2376	24-4457
23	S	Big Creek	1957-2002	5-1858	6-3349
24	S	Camas Creek	1964-1998	3-554	1-1611
25	S	Catherine Creek	1955-2002	28-3161	4-6515
26	S	Grand Ronde River upper mainstem	1956-2002	3-1028	2-1991
27	S	Imnaha River	1954-2002	258-6267	197-5361
28	S	Lemhi River	1957-2002	10-3357	13-7633
29	S	Loon River	1964-2002	2-899	0-816
30	S	Lostine River	1959-2002	37-1585	35-3372
31	S	Marsh Creek	1957-2002	13-1845	4-4461
32	S	Minam River	1954-2002	54-4104	26-4068
33	S	Salmon River lower mainstem	1963-2000	11-432	52-636
34	S	Salmon River upper mainstem	1964-2000	18-2047	137-2545
35	S	Secesh River	1957-2002	48-1395	21-1581
36	S	Snake River (east fork)	1960-2002	11-3374	16-4269
37	S	Snake River lower mainstem	1957-2002	11-4888	24-2444
38	S	Snake River upper mainstem	1962-2002	18-3554	41-5267
39	S	South fork Salmon River East fork	1958-2002	23-1257	17-1444
40	S	South fork Salmon River mainstem	1964-1999	224-1515	354-2259
41	S	Sulphur River	1957-2002	2-876	0-2135
42	S	Tucannon River	1979-2002	11-897	11-16050
43	S	Valley Creek	1957-2002	5-1496	0-2605
44	S	Wenaha River	1964-2002	48-2682	46-5838
45	S	Yankee Creek	1961-1999	2-1488	1-3132
46	UC	Entiat River	1962-1998	18-714	35-1111
47	UC	Methow River	1962-1998	43-2813	141-3894

48	UC	Wenatchee River	1960-2000	58-3523	166-6126

7 FIGURES

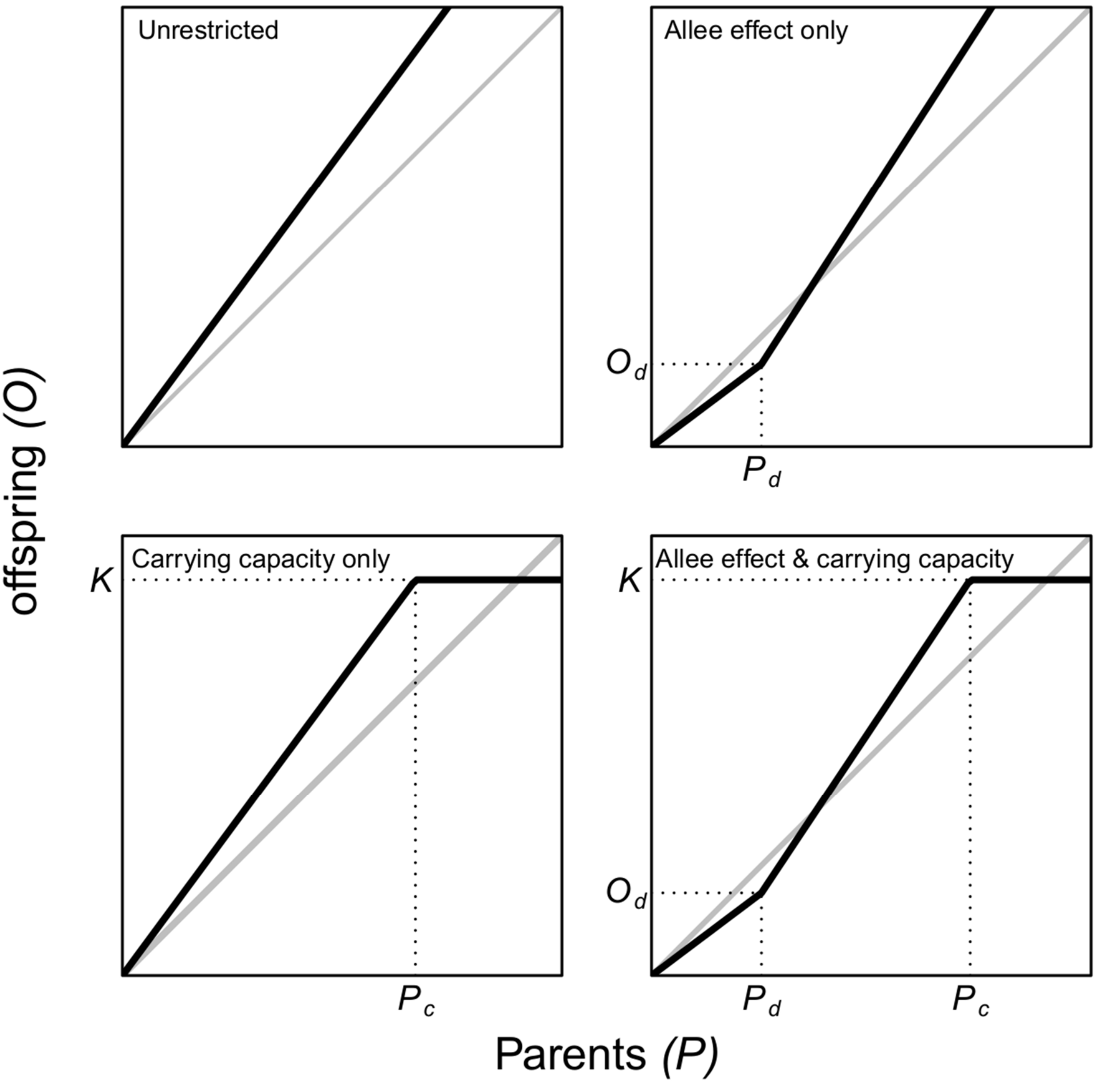

Figure 1: Shape of the four alternative population production models described in the Methods with P_c the number of parents leading to reaching the carrying K and O_d the number of offspring corresponding to the parents depensation breakpoint P_d. Thin grey line is the 1:1 replacement line.

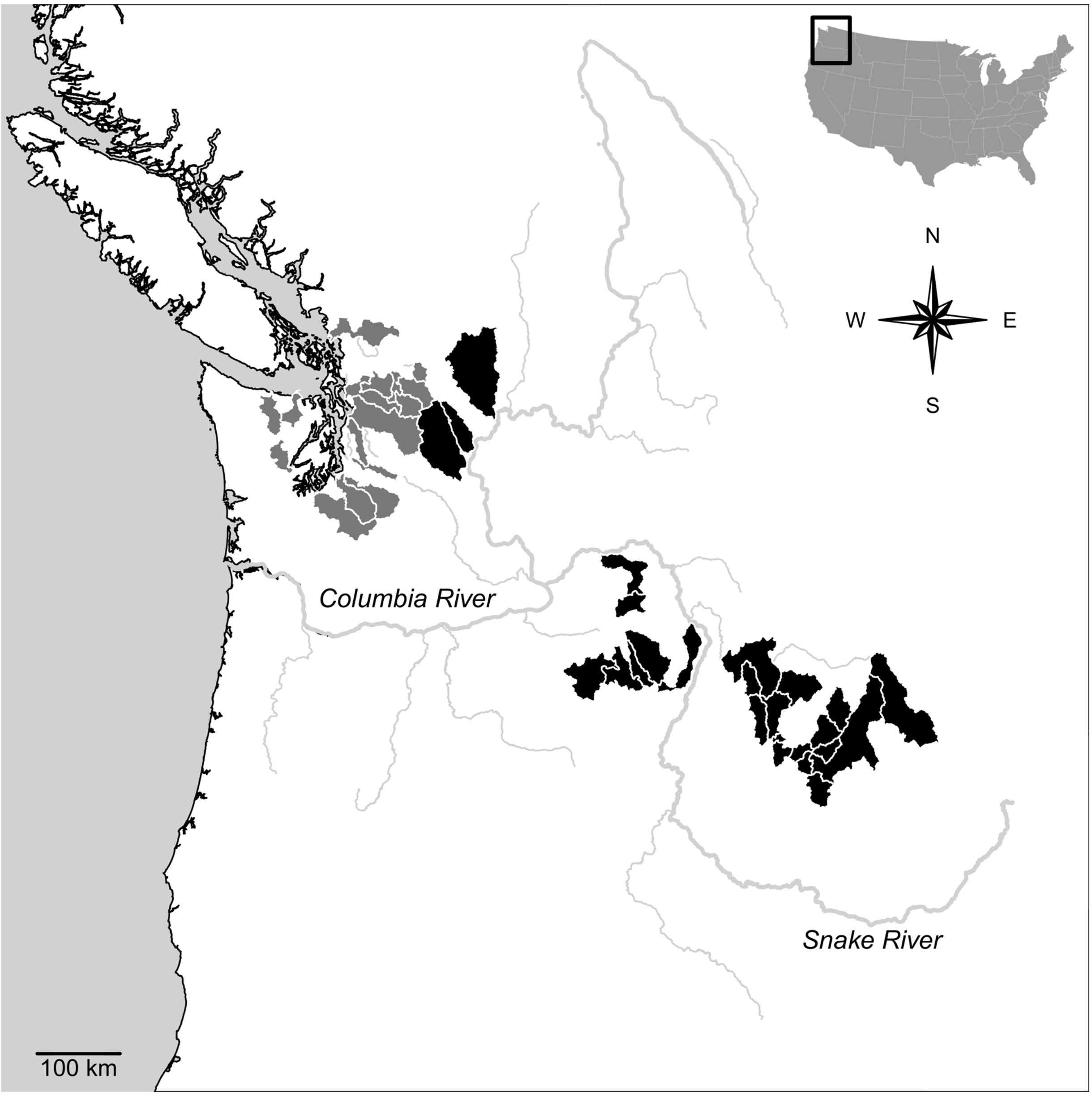

Figure 2. Map of the study area. Grey shading indicates ocean-type populations within the Puget Sound ESU; black shading represents stream-type populations from the Upper Columbia and Snake River ESUs.

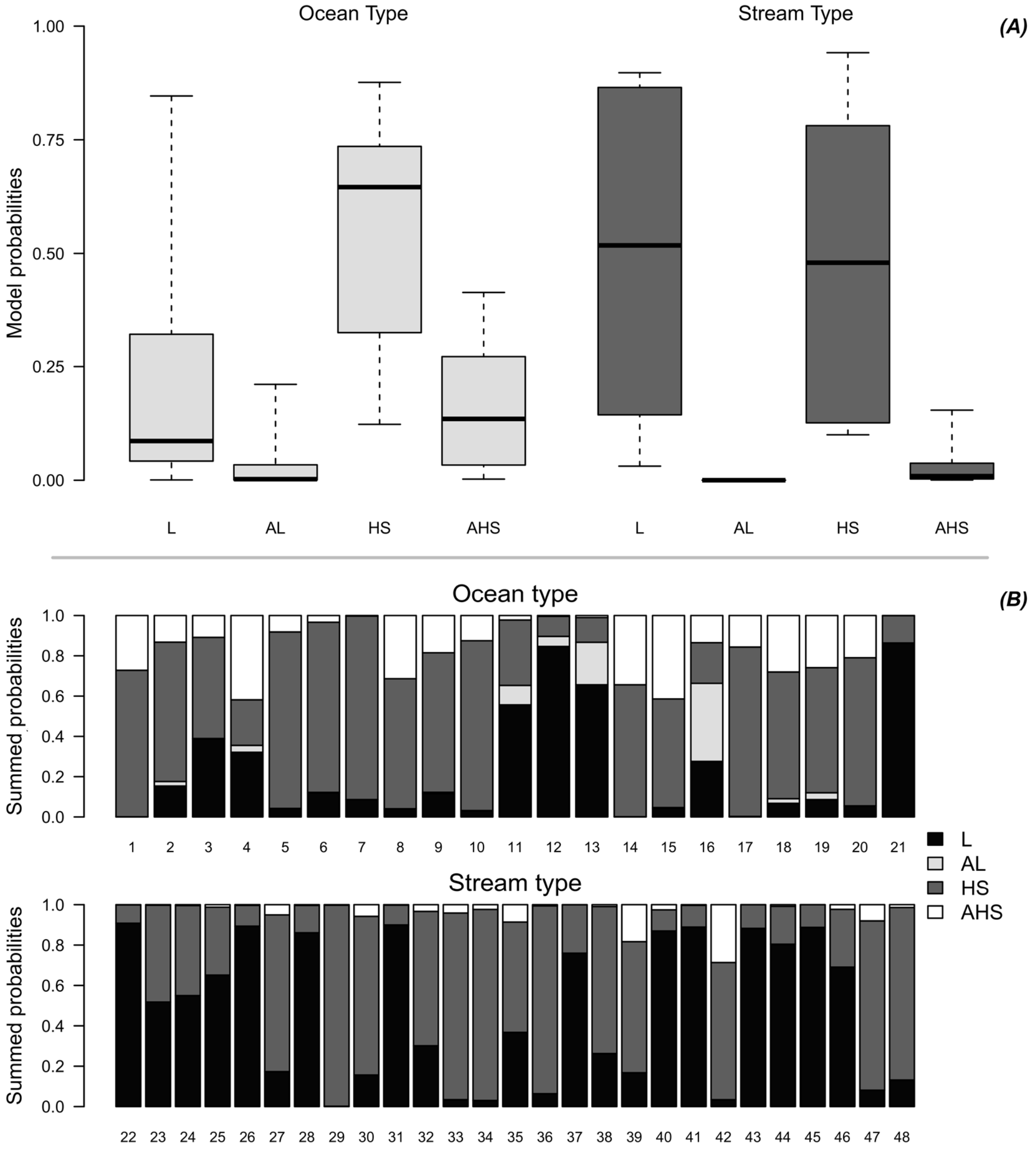

Figure 3. Posterior probabilities for the 4 competing model : linear (L), linear with Allee effect (AL), hockey stick showing compensation (HS), hockey stick with depensation plus Allee Effect (AHS). (A) Boxplots of models probabilities for the two different life-history types of Chinook salmon. Whiskers and hinges indicate the 95% and 50% credible intervals, respectively, around the median. (B) Stacked barplots detailing probabilities for each population. Numbers are indicative of the river index in Table 1.

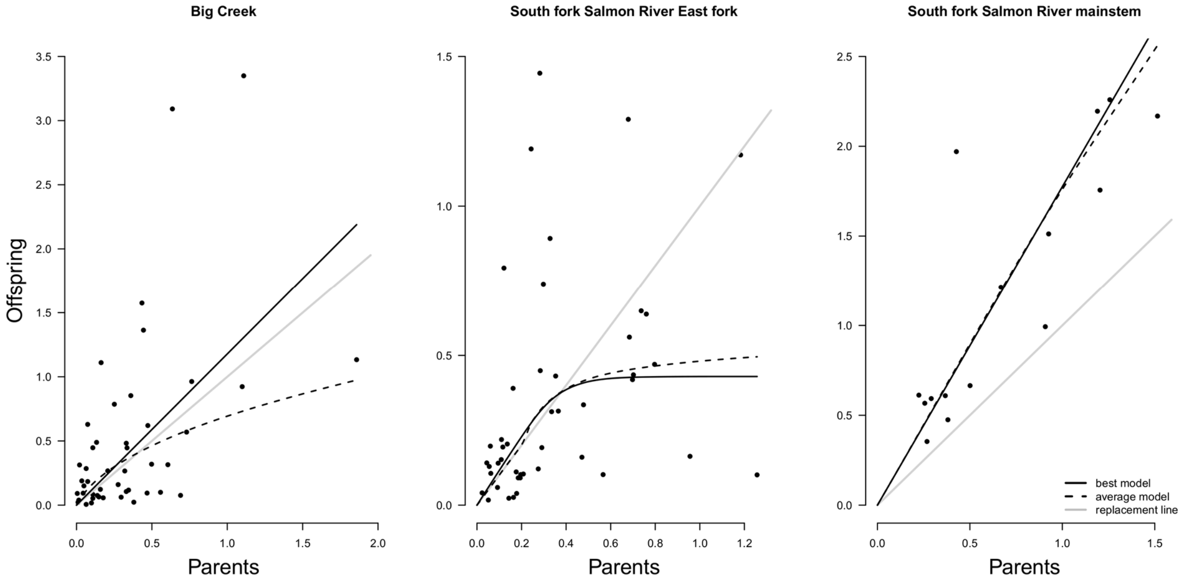

Figure 4. Plot of the stock recruitment data (in thousands) together with the posterior median of predicted values coming from the Bayesian model model averaging and the most credible model only.

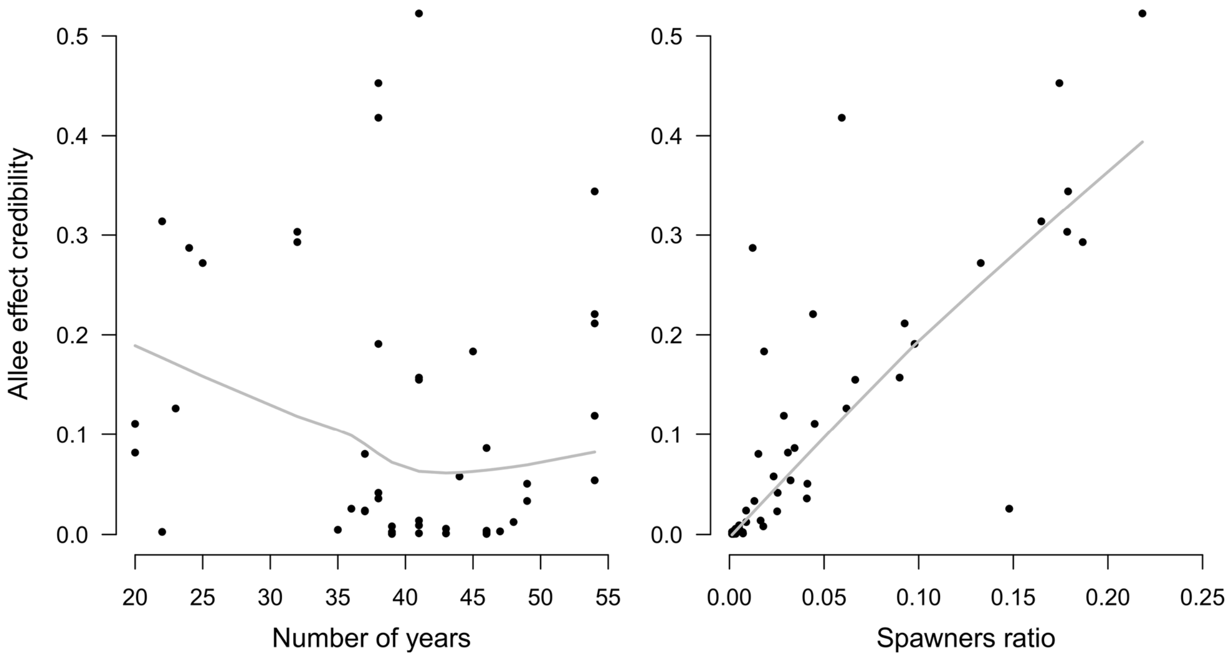

Figure 5. Plot of support for Allee effect in relation to i) time sries length (left panel) and ii) the ratio of minimum over the maximum number of spawners observed (proxy of historical depletion, right panel). Grey curves are non parametric lowess smoothing and highlight relationships between the variables.

8 LITERATURE CITED

Achord, S., Levin, P.S., and Zabel, R.W. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecol. Lett. **6**(4): 335–342. doi:10.1046/J.1461-0248.2003.00438.X.

Anderson, J.H., Pess, G.R., Carmichael, R.W., Ford, M.J., Cooney, T., Baldwin, C., and McClure. 2014. Planning Pacific Salmon and Steelhead Reintroductions Aimed at Long-Term Viability and Recovery. Plan. Pac. Salmon Steelhead Reintroductions **34**(1): 72–93.

Banner, K.M., and Higgs, M.D. 2017. Considerations for assessing model averaging of regression coefficients. Ecol. Appl. **27**(1): 78–93. doi:10.1002/eap.1419.

Barrowman, N.J., and Myers, R.A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Can. J. Fish. Aquat. Sci. **57**(4): 665–676.

Barrowman, N.J., Myers, R.A., Hilborn, R., Kehler, D.G., and Field, C.A. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecol. Appl. **13**(3): 784–793. doi:10.1890/1051-0761(2003)013[0784:tvapoc]2.0.co;2.

Berec, L., Angulo, E., and Courchamp, F. 2007. Multiple Allee effects and population management. Trends Ecol. Evol. **22**(4): 185–191.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations, fishery investigations series II volume XIX, Ministry of Agriculture. Fish. Food **22**.

Boyce, M.S. 1992. Population viability analysis. Annu. Rev. Ecol. Syst. **23**: 481–506. doi:10.1146/annurev.ecolsys.23.1.481.

Bravington, M.V., Stokes, T.K., and O'Brien, C.M. 2000. Sustainable recruitment: the bottom line. Mar. Freshw. Res. **51**(5): 465–475. doi:10.1071/mf99090.

Brook, B.W., and Bradshaw, C.J.A. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology **87**(6): 1445–1451.

Buhle, E.R., Holsman, K.K., Scheuerell, M.D., and Albaugh, A. 2009. Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. Biol. Conserv. **142**(11): 2449–2455. doi:10.1016/j.biocon.2009.05.013.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multi-Model Inference. Springer, New York.

Cade, B.S. 2015. Model averaging and muddled multimodel inferences. Ecology **96**(9): 2370–2382. doi:10.1890/14-1639.1.

Connors, B.M., Braun, D.C., Peterman, R. m., Cooper, A.B., Reynolds, J.D., Dill, L.M., Ruggerone, G.T., and Krkošek, M. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. Conserv. Lett. **5**(4): 304–312. doi:10.1111/j.1755-263X.2012.00244.x.

Courchamp, F., Clutton-Brock, T., and Grenfell, B. 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. **14**(10): 405–410.

Galipaud, M., Gillingham, M.A.F., David, M., and Dechaume-Moncharmont, F.-X. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods Ecol. Evol. **5**(10): 983–991. doi:10.1111/2041-210X.12251.

Gelman, A., Hwang, J., and Vehtari, A. 2014. Understanding predictive information criteria for Bayesian models. Stat. Comput. **24**(6): 997–1016. doi:10.1007/s11222-013-9416-2.

Godwin, S.C., Dill, L.M., Reynolds, J.D., and Krkošek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. Can. J. Fish. Aquat. Sci. **72**(7): 1113–1120. doi:10.1139/cjfas-2014-0284.

Gregory, S.D., Bradshaw, C.J.A., Brook, B.W., and Courchamp, F. 2010a. Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology **91**(7): 2151–2161.

Gregory, S.D., Bradshaw, C.J.A., Brook, B.W., and Courchamp, F. 2010b. Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology **91**(7): 2151–2161. doi:10.1890/09-1128.1.

Helfield, J.M., and Naiman, R.J. 2006. Keystone interactions: Salmon and bear in riparian forests of alaska. Ecosystems **9**(2): 167–180. doi:10.1007/S10021-004-0063-5.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment and management: choice, dynamics, and uncertainty.

Hixon, M.A., Pacala, S.W., and Sandin, S.A. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. Ecology **83**(6): 1490–1508.

Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Can. J. Fish. Aquat. Sci. **54**(9): 1976–1984. doi:10.1139/cjfas-54-9-1976.

McAllister, M.K., and Kirkwood, G.P. 1998. Using Bayesian decision analysis to help achieve a precautionary approach for managing developing fisheries. Can. J. Fish. Aquat. Sci. **55**(12): 2642–2661.

Mogensen, S., and Post, J.R. 2012. Energy allocation strategy modifies growth-survival trade-offs in juvenile fish across ecological and environmental gradients. Oecologia **168**(4): 923–933. doi:10.1007/s00442-011-2164-0.

Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Can. J. Fish. Aquat. Sci. **53**(5): 1061–1070.

Moore, J.W. 2006. Animal ecosystem engineers in streams. BioScience **56**(3): 237–246. doi:10.1641/0006-3568(2006)056[0237:Aeeis]2.0.Co;2.

Moore, J.W., Schindler, D.E., and Scheuerell, M.D. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia **139**(2): 298–308. doi:10.1007/s00442-004-1509-3.

Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecol. Lett. **11**(5): 470–480. doi:10.1111/j.1461-0248.2008.01163.x.

Munch, S.B., Kottas, A., and Mangel, M. 2005. Bayesian nonparametric analysis of stock recruitment relationships. Can. J. Fish. Aquat. Sci. **62**(8): 1808–1821.

NMFS (National Marine Fisheries Service). 2013. Annual Commercial Landing Statistics. Available from http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index [accessed 23 July 2013].

Pascual, M.A., Kareiva, P., and Hilborn, R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conserv. Biol. **11**(4): 966–976. doi:10.1046/J.1523-1739.1997.95437.X.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: The Bayesian approach. Rev. Fish Biol. Fish. **7**(1): 35–63.

Quinn, T.P., Cunningham, C.J., Randall, J., and Hilborn, R. 2014. Can intense predation by bears exert a depensatory effect on recruitment in a Pacific salmon population? Oecologia **176**(2): 445–456. doi:10.1007/s00442-014-3043-2.

Richards, S.A. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology **86**(10): 2805–2814. doi:10.1890/05-0074.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**: 559–623.

Rinella, D.J., Wipfli, M.S., Stricker, C.A., Heintz, R.A., and Rinella, M.J. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Can. J. Fish. Aquat. Sci. **69**(1): 73–84. doi:10.1139/f2011-133.

Ruckelshaus, M.H., Currens, K.P., Graeber, W.H., Fuerstenberg, R.R., Rawson, K., Sands, N.J., and Scott, J.B. 2006. Independent populations of Chinook salmon in Puget Sound.

Ruggerone, G.T., Agler, B.A., and Nielsen, J.L. 2012. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. Environ. Biol. Fishes **94**(1): 149–163. doi:10.1007/s10641-011-9856-5.

Scheuerell, M.D., Hilborn, R., Ruckelshaus, M.H., Bartz, K.K., Lagueux, K.M., Haas, A.D., and Rawson, K. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish?habitat relationships in conservation planning. Can. J. Fish. Aquat. Sci. **63**(7): 1596–1607. doi:10.1139/f06-056.

Schindler, D.E., Rogers, D.E., Scheuerell, M.D., and Abrey, C.A. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. Ecology **86**(1): 198–209.

Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B., and Palen, W.J. 2003. Pacific salmon and the ecology of coastal ecosystems. Front. Ecol. Environ. **1**(1): 31–37.

Semmens, B.X., and Moore, J.W. 2008. Mixsir manual 0.5. Available from https://www.scribd.com/document/73156345/MixSIR-Manual-0-5 [accessed 2 February 2018].

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and van der Linde, A. 2014. The deviance information criterion: 12 years on. J. R. Stat. Soc. Ser. B Stat. Methodol. **76**(3): 485–493. doi:10.1111/rssb.12062.

Taylor, E.B. 1990. Phenotypic Correlates of Life-History Variation in Juvenile Chinook Salmon, Oncorhynchus tshawytscha. J. Anim. Ecol. **59**(2): 455–468. doi:10.2307/4874.

Wintle, B.A., McCarthy, M.A., Volinsky, C.T., and Kavanagh, R.P. 2003. The use of Bayesian model averaging to better represent uncertainty in ecological models. Conserv. Biol. **17**(6): 1579–1590. doi:10.1111/j.1523-1739.2003.00614.x.

Zerbini, A., Ward, E.J., Kinas, P., Engel, M.H., and Andriolo. 2011. A Bayesian assessment of the conservation status of humpback whales (Megaptera novaeangliae) in the western Atlantic Ocean (Breeding Stock A). J. Cetacean Res. Manag. (Special Issue):131–144.