DR MARK D SCHEUERELL (Orcid ID : 0000-0002-8284-1254)

Article type : Research Article

Handling Editor- Hedley Grantham

An integrated population model for estimating the relative effects of natural and anthropogenic factors on a threatened population of steelhead trout

Mark D. Scheuerell[1,5], Casey P. Ruff[2], Joseph H. Anderson[3], Eric M. Beamer[4]

[1] *Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA USA, mark.scheuerell@noaa.gov*

[2] *Skagit River System Cooperative, La Conner, WA USA, cruff@skagitcoop.org*

[3] *Washington Department of Fish and Wildlife, Olympia, WA USA, joseph.anderson@dfw.wa.gov*

[4] *Skagit River System Cooperative, La Conner, WA USA, ebeamer@skagitcoop.org*

[5] **Present address**: *U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA USA, scheuerl@uw.edu*

Corresponding author:

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2664.13789

Mark D. Scheuerell
U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit
School of Aquatic and Fishery Sciences
Box 355020
University of Washington
Seattle, Washington 98195 USA
Telephone: 206.543.5997
Email: scheuerl@uw.edu

Abstract

1. Assessing the degree to which at-risk species are regulated by density dependent versus density independent factors is often complicated by incomplete or biased information. If not addressed in an appropriate manner, errors in the data can affect estimates of population demographics, which may obfuscate the anticipated response of the population to a specific action.

2. We developed a Bayesian integrated population model that accounts explicitly for interannual variability in the number of reproducing adults and their age structure, harvest, and environmental conditions. We apply the model to 41 years of data for a population of threatened steelhead trout *Oncorhynchus mykiss* using freshwater flows, ocean indices, and releases of hatchery-born conspecifics as covariates.

3. We found compelling evidence that the population is under density-dependent regulation, despite being well below its historical population size. In the freshwater portion of the lifecycle, we found a negative relationship between productivity (offspring per parent) and peak winter flows, and a positive relationship with summer flows. We also found a negative relationship between productivity and releases of hatchery conspecifics. In the marine portion of the lifecycle, we found a positive correlation between productivity and the North Pacific Gyre Oscillation.

4. *Synthesis and applications*. The evidence for density dependent population regulation, combined with the substantial loss of juvenile rearing habitat in this river basin, suggests that habitat restoration could benefit this population of at-risk steelhead. Our results also imply that hatchery programs for steelhead need to be considered carefully with respect to habitat availability and recovery goals for wild steelhead. If releases of hatchery steelhead have indeed limited the production potential of wild steelhead, there are likely significant tradeoffs between providing harvest opportunities via hatchery steelhead production, and achieving wild steelhead recovery goals. Furthermore, harvest rates on wild fish have been sufficiently low to ensure very little risk of overfishing.

KEYWORDS

fisheries, management, harvest, hatchery, river, salmon, steelhead, *Oncorhynchus*

INTRODUCTION

Managing at-risk species requires an understanding of the degree to which population dynamics are self-regulated versus driven by external factors. However, the data used to identify potentially important density-dependent and population-environment relationships are rarely, if ever, fully comprehensive or error free. Rather, imperfect detection, misidentification, and non-exhaustive sampling all lead to a somewhat distorted view of the true state of nature. For example, when not addressed in an appropriate manner, errors in population censuses may cause underestimates of recruitment (Sanz-Aguilar *et al.* 2016) or overestimates of the strength of density dependence (Knape & de Valpine 2012). Similarly, imprecision in the estimated age composition of the population also biases the estimated strength of density dependence (Zabel & Levin 2002). In a conservation context, these erroneous conclusions may directly influence the anticipated response of a population to a specific action. Therefore, proper consideration of all sources of uncertainty in the data is necessary to design robust management strategies aimed at protecting at-risk species.

The productivity and carrying capacity of a population may also vary over time and space (Thorson *et al.* 2015), and explicit consideration of external drivers can improve estimates of population dynamics under density dependent conditions (Lebreton & Gimenez 2013). For at-risk species, these exogenous factors can be used to better understand drivers of historical population demographics and help identify possible recovery options. Incorporating covariates into population models can also improve forecasts of future dynamics, especially over shorter time horizons most relevant to natural resource management (Ward *et al.* 2014). Furthermore, accelerated global change will likely create synergistic effects that complicate efforts to make reliable long-term predictions (Schindler & Hilborn 2015). Thus, any reasonable assumptions about future responses of populations should begin with an attempt to fully account for the uncertainty in population-environment relationships based on all of the current information.

Many populations of Pacific salmon (*Oncorhynchus* spp.) throughout the northwestern United States have declined markedly since the early 1900s due to a variety of causes such as habitat alteration, hydropower development, and overharvest (Ruckelshaus *et al.* 2002). For conservation purposes, Pacific salmon species are grouped into evolutionarily significant units (ESU, Waples 1991); 28 of the 49 extant ESUs of Pacific salmon are currently listed as “threatened” or “endangered” under the U.S. Endangered Species Act. As a result, a number of life-cycle models have been developed to evaluate the possible future benefits of conservation actions such as habitat restoration (e.g., Scheuerell *et al.* 2006) and the potentially negative consequences of climate change (e.g., Zabel *et al.* 2006). However, these models were assembled by first obtaining parameter values from the literature, or estimating them from disparate data sources, and then putting all of the pieces together post hoc. Consequently, they do not reflect a comprehensive assessment of the total uncertainty in population demographics.

More recently however, researchers have turned toward integrated population models (IPMs) as a means to convey the combined uncertainty in all of the data sources, which is particularly important in a conservation context (Buhle *et al.* 2018; Zipkin & Saunders 2018). IPMs are similar to state-space models in that they have specific sub-models for 1) describing the stochastic and unobservable population dynamics; and 2) addressing the noisy, incomplete data (Schaub & Abadi 2011; Yen *et al.* 2019). Although IPMs have been widely developed and applied to mammals (e.g., Regehr *et al.* 2018) and birds (e.g., Saunders, Cuthbert & Zipkin 2018), there are very few examples for Pacific salmon (cf., Buhle *et al.* 2018).

Here we combine incomplete data on adult abundance, age composition, and harvest into a Bayesian IPM to answer important questions relevant to management of a threatened population of anadromous steelhead trout *Oncorhynchus mykiss* Walbaum 1792 from the Skagit River basin, which drains ~6900 km^2 in southwestern Canada and northwestern United States. Specifically, we used 39 years of age structured abundance data (1978-2018) to quantify the degree of density dependence and the effects of a specific suite of environmental drivers on intrinsic productivity (ie., recruits per spawner in the absence of density-dependence). We found that although recent population censuses are well below historical estimates, the population still operates under relatively strong density dependence. We also found that streamflow during winter and releases of hatchery-reared juvenile steelhead were negatively related to wild steelhead productivity, but that productivity was positively related to streamflow during summers as juveniles and sea-surface temperatures experienced as adults in the North Pacific. In light of remaining uncertainty in the factors governing the population dynamics of Skagit River steelhead, this modelling framework is an effective tool for setting near term recovery goals and evaluating population level response recovery actions.

MATERIALS AND METHODS

Study species and data

The Skagit River system is predominantly a glacially fed system that consists of a combination of rain, snow-transitional, and snow-dominated tributaries providing approximately 48 km^2 of potential habitat suitable for spawning and rearing by wild steelhead (Hard *et al.* 2015). We use the term “wild” to describe steelhead produced by naturally spawning adults descended from the native population inhabiting the watershed. For this study, wild fish captured in commercial fisheries that were either allocated to harvest or sampled for age composition were identified by the presence of an intact adipose fin. Wild adult steelhead in the Skagit River generally enter freshwater in November through April and typically spawn in March through June. Based on 4,686 aged scale samples collected from returning wild adult steelhead captured in commercial net fisheries, an average of 70% of returning adults comprising a given brood year spent 2 years rearing in freshwater prior to migrating to sea as smolts (see Appendix S4 for more details on scale aging). Following freshwater rearing, individuals spend two to six years feeding and growing before returning to freshwater as sexually mature adults to initiate spawning (i.e., they reach sexual maturity at age three through eight; ~82% mature at age four or five). These fish then spend a year at sea before returning to freshwater to spawn.

Due to a combination of logistical constraints, only a fraction of the known spawning area was surveyed for wild spawners. Specifically, standardized index reach surveys were conducted annually in only two of five major sub-basins and 13 of 63 tributaries known to support wild steelhead production. A basin-wide estimate of wild spawners was generated annually by expanding each survey to account for estimated available habitat not surveyed. Redds or spawning nests constructed before approximately mid-March were not counted to avoid inclusion of any naturally spawning hatchery-origin steelhead, which were purposely bred for earlier spawn timing, or coho salmon in the abundance estimates (cf. Courter *et al.* 2019). Fisheries biologists in the Skagit River basin generally consider the escapement estimates to be conservative; it is more likely that escapement is underestimated than overestimated because unobserved spawning sites would serve to increase abundance. Our analyses begin with surveys in 1978 and continue through 2018.

In the model described below, we evaluate several environmental indicators of productivity. Specifically, flow conditions experienced by juveniles during freshwater rearing can have strong effects on their survival to adulthood via the following mechanisms: (1) spatial contraction of habitat as a result of low summer flows and high water temperatures that coincide with the period of highest metabolic demand (e.g., Crozier *et al.* 2010), and (2) habitat displacement or direct mortality resulting from peak winter flows (e.g., Irvine 1986). Therefore, we utilized long-term flow records from a gauge (#12178000) located in the mainstem Skagit River (48.66 N, 121.246 W), and maintained by the United States Geological Survey (see Appendix S1). Specifically, we obtained the observed maximum of daily peak flows occurring from October through May of the first freshwater rearing year, and the minimum of low summer flows occurring from June through September of the first summer of freshwater rearing.

Because conditions experienced by salmon and steelhead during their first year at sea are thought to be critical to overall survival and growth of a given year class (Beamish & Mahnken 2001), we chose the average North Pacific Gyre Oscillation index (NPGO) from January through December as an index of conditions experienced by juvenile steelhead during their first year in the ocean. Variability in the NPGO reflects annual changes in coastal upwelling and ocean circulation patterns that correlate strongly with primary and secondary production in coastal ecosystems (Di Lorenzo *et al.* 2008). Furthermore, the NPGO has been recently identified as an important indicator of early marine survival in other Pacific salmon species (Kilduff *et al.* 2015). Because most juvenile steelhead from the Skagit River migrate to sea during the spring of their second year, we lagged the NPGO indicator by two years beyond the birth year to reflect conditions experienced during the first year at sea.

From a management standpoint, we were interested in the possible effect of hatchery-reared juvenile steelhead on the productivity of wild steelhead. The Washington Department of Fish and Wildlife operates a “segregated” steelhead hatchery program that uses broodstock from a non-local source intentionally bred for early spawning, with the goal of minimizing temporal reproductive overlap with wild fish and hence minimizing gene flow into the wild population. Over the time series, hatchery fish were typically reared to age-1 and released in the spring (April or May) from multiple locations in the Skagit Basin. We hypothesized that hatchery fish would have the greatest potential for conspecific ecological interactions during the time juvenile steelhead are migrating to sea because observations at a juvenile fish trap (river km 27) indicate they overlap in time and space. Therefore, we assumed that a cohort born in year t would interact with hatchery fish released in year $t + 2$. We used the total number of juveniles released from the hatchery within a given year as our covariate.

Integrated population model

The number of offspring born in year t that survive to adulthood (R_t) equals the product of a nonlinear function of the number of spawning adults (S_t) and a time-varying stochastic error ε_t:

$$R_t = f(S_t|\boldsymbol{\theta})\ \mathrm{e}^{\varepsilon_t}. \tag{1}$$

Here we consider three general forms for f: a density independent model where $f(S_t) = \alpha S_t$, and two density dependent models (Ricker and Beverton-Holt model; Fig. 1).

The process errors (ε_t) are often assumed to be independent draws from a Gaussian distribution with a mean of zero and an unknown variance. However, the stochastic environmental drivers that the ε_t are meant to represent typically show relatively strong autocorrelation over time. Thus, we compared two different distributional forms for ε_t with non-zero, autocorrelated means. In the first, we assumed that

$$\varepsilon_t \sim \text{Normal}(\phi\varepsilon_{t-1}, \sigma_\varepsilon), \tag{2a}$$

$$\varepsilon_0 \sim \text{Normal}\left(0, \frac{\sigma_\varepsilon}{1-\phi^2}\right). \tag{2b}$$

Second, we considered models where the non-zero means were also a function of the various environmental drivers important to salmon productivity as discussed above. In those models,

$$\varepsilon_t \sim \text{Normal}(\mu_t + \phi\varepsilon_{t-1}, \sigma_\varepsilon) \tag{3a}$$

$$\mu_t = \textstyle\sum_{i=1}^{K} \gamma_i X_{i,t+h_i} \tag{3b}$$

Here, γ_i is the effect of covariate X_i measured at time t and shifted by an appropriate lag h_i based on the life stage that the covariate would affect most strongly. We standardized all covariates to have zero-mean and unit-variance to facilitate direct comparison of effect sizes.

The estimated numbers 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 $t - a$ from Equation (1) and the proportion of mature fish from that brood year that returned to spawn at age a ($\pi_{a,t-a}$), such that

$$N_{a,t} = R_{t-a}\ \pi_{a,t-a}. \tag{4}$$

Thus, in a table of the *true* numbers-at-age (columns) by calendar year (rows), $\pi_{a,t-a}$ has the effect of apportioning the total recruits (R_{t-a}) into their appropriate age classes of future returns (i.e., values along a diagonal of the table). Adult steelhead from the Skagit River return as 3-8 year-olds, and therefore the vector of age-specific return rates for brood year t is $\boldsymbol{\pi}_t = [\pi_3, \pi_4, \pi_5, \pi_6, \pi_7, \pi_8]_t$, which we modeled as a hierarchical random effect whereby $\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\eta}\,\tau)$. The mean vector $\boldsymbol{\eta}$ is also distributed as a Dirichlet; the precision parameter τ affects each of the elements in $\boldsymbol{\eta}$ such that large values of τ result in $\boldsymbol{\pi}_t$ very close to $\boldsymbol{\eta}$ and small values of τ lead to much more diffuse $\boldsymbol{\pi}_t$.

The spawner-recruit models above describe a process based on the true number of spawners, but our estimates of the numbers of spawning adults necessarily contain some sampling errors due to incomplete censuses, pre-spawn mortality, etc. Therefore, we assumed that our estimates of escapement, the number of adult fish that "escape the fishery" and ultimately spawn (E_t), are log-normally distributed about the true number of spawners (S_t):

$$\ln(E_t) \sim \text{Normal}(\ln(S_t), \sigma_s). \quad (5)$$

We cannot simultaneously estimate observation error for both escapement and harvest. Therefore, because catches of wild steelhead are closely recorded by state and tribal biologists, we assume the harvest is recorded without error. We then calculate S_t as the difference between the estimated total run size (N_t) and harvest (H_t), where

$$S_t = N_t - H_t, \quad (6)$$

and N_t is the sum of $N_{a,t}$ from Equation (3) over all age classes.

We obtained observations of the number of fish in each age class a in year t ($O_{a,t}$) from scale analyses of 10 – 408 adults per year; no scale samples were taken in 1978-1982, 1984, and 2000. These data were assumed to arise from a multinomial process with order Y_t and proportion vector $\mathbf{d}_t$, such that

$$\mathbf{O}_t \sim \text{Multinomial}(Y_t, \mathbf{d}_t). \quad (7)$$

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

$$Y_t = \textstyle\sum_{a=3}^{8} O_{t,a} \,. \quad (8)$$

Thus, if we have a table of the *observed* numbers-at-age (columns) by calendar year (rows), summing across each row gives Y_t. In contrast, the proportion vector $\mathbf{d}_t$ for the multinomial is based on the age-specific, model-derived estimates of adult returns in year t ($N_{a,t}$), such that

$$d_{a,t} = \frac{N_{a,t}}{\sum_{a=3}^{8} N_{a,t}}. \quad (9)$$

That is, if we consider the table of the *true* numbers-at-age (columns) by calendar year (rows) generated via Eqn (4) above, the numerator of Eqn (9) comes from each of the individual columns within a row, and the denominator is the sum across all columns.

We used Bayesian inference to estimate all model parameters and the unobserved true numbers of spawners and offspring over time. We used the freely available **R** software (v3.6, R Development Core Team 2019) combined with the JAGS software (v4.2.0, Plummer 2003) to perform Gibbs sampling with 4 parallel chains of 5×10^5 iterations. Following a burn-in period of 2.5×10^5 iterations, we thinned each chain by keeping every 400th sample to eliminate any possible autocorrelation, which resulted in 5000 samples from the posterior distributions. We assessed convergence and diagnostic statistics via the 'CODA' package in **R** (Plummer *et al.* 2006). Specifically, we used visual inspection of trace plots and density plots, and verified that Gelman and Rubin's (2017) potential scale reduction factor was less than 1.1, to ensure adequate chain mixing and parameter convergence. Data support for each model was evaluated using leave-one-out cross-validation (LOO) based upon Pareto-smoothed importance sampling as implemented in the 'loo' package (Vehtari *et al.* 2019). All of the code and data files necessary to replicate our analyses are available in the online supporting material and at https://github.com/mdscheuerell/steelhead_IPM.

RESULTS

We found the most data support for the Beverton-Holt form of process model, so all of the following results are based upon it (see Appendix S2 for full model selection results). Our estimates of the total population size reflect the uncertainty in the estimated numbers of adults over time, but the median values agreed quite well with the observed data (Fig. 2). As expected, the 95% credible intervals were widest in 1996 and 1997 when there were no direct estimates of spawning adults.

The population dynamics of steelhead in the Skagit River are currently under density-dependent regulation, despite their numbers being well below historical censuses, and there is considerable uncertainty in the relationship between spawning adults and their surviving offspring (Fig. 3). The median of α (i.e., the slope of the relationship at the origin) was 4.8 offspring per spawner, but a lack of data at low spawner abundance led to considerable uncertainty in the estimate (Fig. 3b). The lower 95% credible interval was about 1.4 offspring per spawner, which is still above replacement, while the upper 95% credible interval was 41 offspring per parent. On the other hand, our estimates of carrying capacity (K) were much more precise, with a median of about 7700 adults and 95% credible interval of approximately 5900 to 12 800 adults (Fig. 3c).

There were varying effects of the three environmental covariates on population productivity (Fig. 4). Peak winter flows were negatively related to productivity, suggesting high discharge events may transport juveniles downstream to lower quality habitats, or lead to direct mortality from channel avulsion or movement of sediment, wood, and other debris. The median of the posterior distribution was -0.13 (Fig. 4e), which means that a 1 SD increase in flow above the mean (i.e., from ~41 $m^3 s^{-1}$ to ~68 $m^3 s^{-1}$) would translate into a 12% decrease in offspring per parent. On the other hand, the effect of low summer flows was essentially zero (Fig. 4f); the median estimate was 0.08 with a 95% credible interval of -0.18 to 0.14. The NPGO had a largely positive effect (Fig. 4g), suggesting warmer waters in the North Pacific are better for steelhead productivity (median equals 0.12 with a 95% credible interval of -0.05 to 0.31.

We also found that the number of hatchery juveniles released into the river during the time that wild juveniles were migrating to sea was negatively related to productivity (Fig. 4h). The median effect size was -0.16, which means that a 1 SD increase in the number of hatchery juveniles released (i.e., from 328 000 to 452 000 fish) would, on average, result in an 15% decrease in productivity. Notably, hatchery production experienced three distinct phases over time (Fig. 4d): a low period between brood year 1978 and 1990 (range = 125 000 to 340 000 smolts), an increasing and high period between 1991 and 2005 (range = 314 000 to 584 000), and a decreasing period beginning in 2006 (range = 0 to 240 000 smolts).

The remaining, unexplained environmental variance was highly autocorrelated over time (Fig. 5). The process residuals were generally positive during the late 1970s and early 1980s when the population was growing (Fig. 2), they were near zero during the stable period of the 1990s, and then largely negative as the population primarily declined through the 2000s.

Based on our estimates of biological reference points, Skagit River steelhead appear to be managed rather conservatively from a harvest management perspective. The optimal yield profiles suggest it would take approximately 2000 to 3000 spawning adults to produce the maximum sustainable yield (Fig. 6a), but very few years have ever fallen below that throughout the time period presented here (i.e., the average number of spawning adults has been two to three times greater). In other words, the realized harvest rates have been kept low enough to insure very little risk of overfishing (Fig. 6b).

DISCUSSION

In territorial species such as steelhead trout, competition for limited resources commonly results in density dependent growth and survival amongst juveniles (Imre, Grant & Keeley 2004). Our analysis suggests that such effects have scaled up to the entire population level to govern patterns of steelhead productivity in the Skagit River basin. Importantly, we found strong evidence for density dependent interactions despite the fact that contemporary population censuses are well below historical estimates (Gayeski, McMillan & Trotter 2011). Similar results have been observed in populations of coho salmon *Oncorhynchus kisutch* Walbaum 1792 in Oregon (Buhle *et al.* 2009) and in populations of Chinook salmon *Oncorhynchus tshawytscha* Walbaum 1792 in Idaho (Thorson *et al.* 2013). Although we cannot be certain of the exact life-stage at which density dependent processes occurred, the freshwater juvenile stage seems likely given the extended duration of freshwater rearing typical for this species. When steelhead populations reach low numbers, the spatial contraction of spawners may exacerbate the effects of density dependence because their newly emerged offspring do not have the mobility to access other vacant habitats (Atlas *et al.* 2015). The evidence for density dependence presented here, combined with the substantial loss of juvenile rearing habitat in the Skagit River basin (Beechie, Beamer & Wasserman 1994), suggests that habitat restoration efforts, such as reconnecting floodplain habitats and improving riparian functioning (Beechie, Pess & Roni 2008), may benefit this population of steelhead.

Fluctuating environments can also affect population dynamics through density independent mechanisms, and anadromous salmon must contend with many different and unpredictable habitats over their lifespan. Our results are consistent with the notion that in the freshwater environment, large flow events during winter negatively affect steelhead productivity. Unfortunately, this may portend an uncertain future for these fish. In a recent study, Lee et al. (2015) estimated that future climate change in the Skagit River basin would create increased winter flows. These changes in hydrology will likely result in much greater exposure of steelhead to extreme high flow events due to their duration, intensity, and timing (Wade *et al.* 2013). Other evidence already exists that freshwater discharge from Puget Sound rivers has become much more variable, with notable negative effects on Chinook salmon *Oncorhynchus tshawytscha* Walbaum 1792 (Ward *et al.* 2015). Furthermore, although we found a weak relationship between low summer flow and productivity, extreme low-flow events are projected to occur at a higher frequency in the future (Lee *et al.* 2015). That said, we also acknowledge that modeling the effects of flow conditions from a single site within the Skagit River basin is not representative of the complexity of flow conditions experienced by juvenile steelhead during their first year of freshwater rearing.

We found evidence of positive effects of NPGO on productivity, which comports with previous studies that have made rather compelling cases for a strong positive relationship between the NPGO and salmon productivity (Kilduff *et al.* 2015). The NPGO is a synoptic measure of ocean conditions over a large region of the North Pacific Ocean (Kilduff *et al.* 2015), so we cannot say where and when, exactly, the effects of the ocean environment most manifest themselves. Recent evidence also indicates that steelhead smolts suffer high mortality during their relatively brief migration through Puget Sound (Moore *et al.* 2015), possibly due to predation by marine mammals (Berejikian, Moore & Jeffries 2016). Notably, too, the residual process errors not captured by our covariates (w_t in Equation 1) were correlated with the estimated marine survival of Skagit River hatchery steelhead (median Pearson's correlation coefficient = 0.29; 95% credible interval = [0.03, 0.50]), suggesting marine processes not captured by our covariates likely influenced productivity.

Among the various mitigation measures to address salmon declines, artificial propagation of salmon has been used widely for more than a century. Nevertheless, research in other river systems points to negative ecological effects of hatchery fish on wild Pacific salmon, including populations coho salmon (Buhle *et al.* 2009), and Chinook salmon (Levin, Zabel & Williams 2001). Our results provide further evidence that large releases of hatchery-reared juvenile steelhead have had a negative effect on productivity of wild steelhead, although we note some researchers have used an approach similar to ours and found no hatchery effect on productivity (Courter *et al.* 2019; Nelson *et al.* 2019). Although we provide evidence for a correlation between hatchery releases and wild steelhead productivity, we did not demonstrate causation nor identify a causal mechanism. In fact, very few empirical studies have been conducted at the appropriate spatial and temporal scales necessary to directly quantify the hypothesized mechanisms by which negative ecological interactions between hatchery and wild fish may occur (Weber & Fausch 2003). That said, competition for limiting freshwater food and habitat resources (Berejikian *et al.* 2000) is a plausible mechanism, either during the relatively brief period of overlap during downstream migration (ca. 2 – 4 weeks), or a more prolonged effect of any hatchery fish that do not migrate to sea, but instead “residualize” within freshwater. Additionally, predators are known to respond numerically to their prey, and it is possible that large numbers of hatchery fish attracted additional predators (Kostow 2009). Although breeding by hatchery individuals that stray onto natural spawning grounds may reduce the fitness of a wild population via gene flow from the hatchery stock into the wild population (Araki, Cooper & Blouin 2009), our study only considered within-cohort effects. Thus, it seems unlikely that a trans-generational genetic effect was the mechanism for the observed negative association between hatchery releases and wild productivity.

Throughout the Puget Sound region, steelhead have been exposed to varying degrees of influence by hatchery fish over the past 100 years, but they share the marine rearing environment, and thus have experienced relatively similar ocean conditions during the same time period. The marked decreases in abundance observed in many of these populations from the late 1980s to the late 2000’s, including the Skagit, mirrors observations of a general declining trend in marine survival of hatchery conspecifics across the same time period, suggesting some larger, unmeasured forces have been at work (Kendall, Marstrom & Klungle 2017). It is often difficult to separate hatchery management from ocean conditions because both are autocorrelated and slow to change over time. Indeed, the period of greatest Skagit River hatchery releases (brood years 1991 – 2005) generally coincided with declining steelhead abundance in the Skagit River and other nearby rivers. Furthermore, in response to the declining abundance of wild Skagit River steelhead coupled with declining marine survival of hatchery steelhead, fisheries managers increased hatchery production to replace lost fishing opportunities. Thus, it is plausible that declining wild productivity was simply coincident with higher hatchery production, rather than a consequence of it. It is also possible that multicollinearity among measured and unmeasured covariates increased the estimated effect sizes.

The life history complexity of steelhead may not lend well to the use of traditional spawner recruit models such as the forms used in this study. Steelhead exhibit significant phenotypic plasticity with respect to adopting partial migration strategies, with unknown proportions of a given cohort adopting a non-anadromous resident life history type (Kendall *et al.* 2015). Given that only anadromous individuals are included in the annual derivation of age structured abundance, there may be a large component of each cohort that is missed which likely resulted in substantial observation error not captured in our models. We also may have overestimated the biological reference points by not fully accounting for repeat spawners. Furthermore, the adult abundance estimates are subject to a variety of spawning survey assumptions; any tendency toward conservative, underestimates would be reflected in the management reference points accordingly. Future research to increase the accuracy and precision of abundance estimates, including quantifying the contribution of resident and repeat spawning life history types, would improve reference point estimation. Without these estimates, accurate assessments of the status of steelhead populations may not be possible, and we urge caution when interpreting the spawner recruit relationships and resulting management reference points presented here.

Our IPM also allowed us to assess the degree to which hatchery management actions are likely to affect the long-term viability of the population. Our results suggest that hatchery program goals for steelhead need to be considered carefully with respect to recovery goals and the quantity and quality of steelhead habitat. If releases of non-local origin hatchery steelhead have indeed limited the production potential of wild steelhead, there are likely significant tradeoffs between providing harvest opportunities via hatchery steelhead production and achieving wild steelhead recovery goals. IPMs have been used elsewhere to inform the adaptive harvest management decision framework for American waterfowl (Arnold *et al.* 2018), and our IPM provides a formal means for estimating the probability of fishing in a sustainable manner. We found compelling evidence that harvest rates for wild steelhead in the Skagit River basin over the time period considered here have been well below those that would drive the population toward extinction. This result, combined with the strong indication of density dependence, lends further support to the notion that habitat improvements may benefit this population most.

Two advantages of IPMs are 1) their ability to accommodate multiple data types of varying quality, which reduces otherwise inherent biases when using a single data set; and 2) more precise estimates of demographic rates than one would with a single data set (Zipkin, Inouye & Beissinger 2019). IPMs can also be used to evaluate the effect of various management actions, and provide decision-relevant information for conservation of at-risk populations, such as coastal turtles in the eastern U.S. (Crawford *et al.* 2018). Here we used incomplete information about the abundance and age structure of an at-risk fish population to estimate density dependent population dynamics in light of natural and human-induced variability in the environment. IPMs can also be used to identify data collection priorities that could reduce uncertainty in parameter estimates (Saunders, Cuthbert & Zipkin 2018), and future research could focus on the costs and benefits of different data types used in formal status evaluations of at-risk Pacific salmon.

ACKNOWLEDGEMENTS

We thank Eric Buhle and Jim Thorson for helpful discussions about model development. We also thank Rebecca Bernard, Pete Kairis, Brett Barkdull, Andrew Fowler, and numerous WDFW, Sauk-Suiattle, Swinomish, and Upper Skagit tribal biologists who compiled the escapement and age data. Annette Hoffman, Dan Rawding, Kris Ryding, and James Scott provided constructive criticism. Comments from two anonymous reviewers also improved the quality of the manuscript. This research was funded in part by a NOAA Fisheries And The Environment (FATE) grant (#15-01), and an Environmental Protection Agency Tribal Capacity grant (#PA-00J320-01).

AUTHORS' CONTRIBUTIONS

MS, CR and JA conceived the ideas and designed methodology; MS and CR analysed the data; MS and CR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Fish data available via the Zenodo open-access repository (Scheuerell *et al.* 2020); river flow data are available from the United States Geological Survey National Water Information System (http://waterdata.usgs.gov/nwis); The North Pacific Gyre Oscillation available via Emanuele Di Lorenzo at Georgia Technical University (http://www.o3d.org/npgo/).

ORCID

Mark D. Scheuerell https://orcid.org/0000-0002-8284-1254

REFERENCES

Ahrestani, F.S., Saracco, J.F., Sauer, J.R., Pardieck, K.L. & Royle, J.A. (2017) An integrated population model for bird monitoring in North America. *Ecological Applications,* **27,** 916-924.

Araki, H., Cooper, B. & Blouin, M.S. (2009) Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters,* **5,** 621-624.

Arnold, T.W., Clark, R.G., Koons, D.N. & Schaub, M. (2018) Integrated population models facilitate ecological understanding and improved management decisions. *Journal of Wildlife Management,* **82,** 266-274.

Atlas, W.I., Buehrens, T.W., McCubbing, D.J.F., Bison, R. & Moore, J.W. (2015) Implications of spatial contraction for density dependence and conservation in a depressed population of anadromous fish. *Canadian Journal of Fisheries and Aquatic Sciences,* **72,** 1682-1693.

Beamish, R.J. & Mahnken, C. (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography,* **49,** 423-437.

Beechie, T., Pess, G. & Roni, P. (2008) Setting river restoration priorities: a review of approaches and a general protocol for identifying and prioritizing actions. *North American Journal of Fisheries Management,* **28,** 891-905.

Beechie, T.J., Beamer, E.M. & Wasserman, L. (1994) Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *North American Journal of Fisheries Management,* **14,** 797-811.

Berejikian, B.A., Moore, M.E. & Jeffries, S.J. (2016) Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. *Marine Ecology Progress Series,* **543,** 21-35.

Berejikian, B.A., Tezak, E.P., Flagg, T.A., LaRae, A.L., Kummerow, E. & Mahnken, C.V.W. (2000) Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Sciences,* **57,** 628-636.

Buhle, E.R., Holsman, K.K., Scheuerell, M.D. & Albaugh, A. (2009) Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. *Biological Conservation,* **142,** 2449-2455.

Buhle, E.R., Scheuerell, M.D., Cooney, T.D., Ford, M.J., Zabel, R.W. & Thorson, J.T. (2018) *Using Integrated Population Models to Evaluate Fishery and Environmental Impacts on Pacific Salmon Viability*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-140.

Courter, II, Wyatt, G.J., Perry, R.W., Plumb, J.M., Carpenter, F.M., Ackerman, N.K., Lessard, R.B. & Galbreath, P.F. (2019) A natural-origin steelhead population's response to exclusion of hatchery fish. *Transactions of the American Fisheries Society,* **148,** 339-351.

Crawford, B.A., Moore, C.T., Norton, T.M. & Maerz, J.C. (2018) Integrated analysis for population estimation, management impact evaluation, and decision-making for a declining species. *Biological Conservation,* **222,** 33-43.

Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. (2010) Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *Journal of Animal Ecology,* **79,** 342-349.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M. & Riviere, P. (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters,* **35,** 6.

Gayeski, N., McMillan, B. & Trotter, P. (2011) Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. *Canadian Journal of Fisheries and Aquatic Sciences,* **68,** 498-510.

Hard, J.J., Myers, J.M., Connor, E.J., Hayman, R.A., Kope, R.G., Lucchetti, G., Marshall, A.R., Pess, G.R. & Thompson, B.E. (2015) *Viability Criteria for Steelhead within the Puget Sound Distinct Population Segment*. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-129., Springfield, VA.

Imre, I., Grant, J.W.A. & Keeley, E.R. (2004) The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). *Oecologia,* **138,** 371-378.

Irvine, J.R. (1986) Effects of varying discharge on the downstream movement of salmon fry, *Oncorhynchus tshawytscha* Walbaum. *Journal of Fish Biology,* **28,** 17-28.

Kendall, N.W., Marstrom, G.W. & Klungle, M.M. (2017) Declining patterns of Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. *Canadian Journal of Fisheries and Aquatic Sciences,* **74,** 1275-1290.

Kendall, N.W., McMillan, J.R., Sloat, M.R., Buehrens, T.W., Quinn, T.P., Pess, G.R., Kuzishchin, K.V., McClure, M.M. & Zabel, R.W. (2015) Anadromy and residency in steelhead and rainbow trout (Oncorhynchus mykiss): a review of the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences,* **72,** 319-342.

Kilduff, D.P., Di Lorenzo, E., Botsford, L.W. & Teo, S.L.H. (2015) Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences*.

Knape, J. & de Valpine, P. (2012) Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance? *Ecology Letters,* **15,** 17-23.

Kostow, K. (2009) Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries,* **19,** 9-31.

Lebreton, J.D. & Gimenez, O. (2013) Detecting and estimating density dependence in wildlife populations. *Journal of Wildlife Management,* **77,** 12-23.

Lee, A.M., Bjorkvoll, E.M., Hansen, B.B., Albon, S.D., Stien, A., Saether, B.E., Engen, S., Veiberg, V., Loe, L.E. & Grotan, V. (2015) An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos,* **124,** 806-816.

Levin, P.S., Zabel, R.W. & Williams, J.G. (2001) The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society of London B Biological Sciences,* **268,** 1153-1158.

Moore, M.E., Berejikian, B.A., Goetz, F.A., Berger, A.G., Hodgson, S.S., Connor, E.J. & Quinn, T.P. (2015) Multi-population analysis of Puget Sound steelhead survival and migration behavior. *Marine Ecology Progress Series,* **537,** 217-232.

Nelson, B.W., Walters, C.J., Trites, A.W. & McAllister, M.K. (2019) Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences,* **76,** 447-462.

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. Vienna, Austria.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News,* **6,** 7-11.

R Development Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Regehr, E.V., Hostetter, N.J., Wilson, R.R., Rode, K.D., St Martin, M. & Converse, S.J. (2018) Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. *Scientific Reports,* **8**.

Ruckelshaus, M.H., Levin, P., Johnson, J.B. & Kareiva, P.M. (2002) The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics,* **33,** 665-706.

Sanz-Aguilar, A., Manuel Igual, J., Oro, D., Genovart, M. & Tavecchia, G. (2016) Estimating recruitment and survival in partially monitored populations. *Journal of Applied Ecology,* **53,** 73-82.

Saunders, S.P., Cuthbert, F.J. & Zipkin, E.F. (2018) Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology,* **55,** 1380-1392.

Schaub, M. & Abadi, F. (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology,* **152,** 227-237.

Scheuerell, M.D. (2016) An explicit solution for calculating optimum spawning stock size from Ricker's stock recruitment model. *Peerj,* **4,** e1623.

Scheuerell, M.D., Hilborn, R., Ruckelshaus, M.H., Bartz, K.K., Lagueux, K., Haas, A. & Rawson, K. (2006) The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. *Canadian Journal of Fisheries and Aquatic Sciences,* **63,** 1596–1607.

Scheuerell, M.D., Ruff, C.P., Anderson, J.H. & Beamer, E.M. (2020) Data from: An integrated population model for estimating the relative effects of natural and anthropogenic factors on a threatened population of steelhead trout. *Zenodo,* http://doi.org/10.5281/zenodo.4126912.

Schindler, D.E. & Hilborn, R. (2015) Prediction, precaution, and policy under global change. *Science,* **347,** 953-954.

Thorson, J.T., Scheuerell, M.D., Buhle, E.R. & Copeland, T. (2013) Spatial diversity buffers temporal variability in early juvenile survival for an endangered Pacific salmon. *Journal of Animal Ecology,* **83,** 157-167.

Thorson, J.T., Skaug, H.J., Kristensen, K., Shelton, A.O., Ward, E.J., Harms, J.H. & Benante, J.A. (2015) The importance of spatial models for estimating the strength of density dependence. *Ecology,* **96,** 1202-1212.

Vehtari, A., Gabry, J., Yao, Y. & Gelman, A. (2019) loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.1.0.

Wade, A.A., Beechie, T.J., Fleishman, E., Mantua, N.J., Wu, H., Kimball, J.S., Stoms, D.M. & Stanford, J.A. (2013) Steelhead vulnerability to climate change in the Pacific Northwest. *Journal of Applied Ecology,* **50,** 1093-1104.

Waples, R.S. (1991) Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *US National Marine Fisheries Service Marine Fisheries Review,* **53,** 11-22.

Ward, E.J., Anderson, J.H., Beechie, T.J., Pess, G.R. & Ford, M.J. (2015) Increasing hydrologic variability threatens depleted anadromous fish populations. *Global Change Biology,* **21,** 2500-2509.

Ward, E.J., Holmes, E.E., Thorson, J.T. & Collen, B. (2014) Complexity is costly: a meta-analysis of parametric and non-parametric methods for short-term population forecasting. *Oikos,* **123,** 652-661.

Weber, E.D. & Fausch, K.D. (2003) Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences,* **60,** 1018-1036.

Yen, J.D.L., Tonkin, Z., Lyon, J., Koster, W., Kitchingman, A., Stamation, K. & Vesk, P.A. (2019) Integrating Multiple Data Types to Connect Ecological Theory and Data Among Levels. *Frontiers in Ecology and Evolution,* **7**.

Zabel, R.W. & Levin, P.S. (2002) Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. *Oecologia,* **133,** 349-355.

Zabel, R.W., Scheuerell, M.D., McClure, M.M. & Williams, J.G. (2006) The interplay between climate variability and density dependence in the population viability of Chinook salmon. *Conservation Biology,* **20,** 190-200.

Zipkin, E.F., Inouye, B.D. & Beissinger, S.R. (2019) Innovations in data integration for modeling populations. *Ecology,* **100**.

Zipkin, E.F. & Saunders, S.P. (2018) Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation,* **217,** 240-250.

FIGURE CAPTIONS

Figure 1. Deterministic forms of the (a) Ricker and (b) Beverton-Holt models used in the analyses (thick lines), including equations for carrying capacity (K) and the number of recruits corresponding to the maximum sustained yield (R_{MSY}). The parameter α defines the slope at the origin, the constant e is Euler's number, and $W(\cdot)$ is the Lambert function (see Scheuerell 2016 for details). The gray line is where $R_t = S_t$.

Figure 2. Time series of the estimated total population size (catch plus the adults that escaped to spawn). The observed data are the points; the solid line is the median estimate and the shaded region indicates the 95% credible interval.

Figure 3. Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming mean values for all covariates (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. Gray lines show the median relationship for each of the 41 years in the time series based on annual model estimates of productivity. 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.

Figure 4. Time series of the environmental covariates used in the model (a-d), and their standardized effects on population productivity (e-g). Small arrows under histograms denote the 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

Figure 5. Time series of the estimated process errors, which represent the population's productivity after accounting for the effects of density dependence and environmental covariates. The solid line is the median estimate and the shaded region indicates the 95% credible interval.

Figure 6. Plots of (a) the probability that a given number of spawners produces average yields achieving 95%, 85%, or 75% of the estimated maximum sustainable yield (MSY); and (b) the

cumulative probability of overfishing the population, based on harvest rates equal to those at 75% of MSY, at MSY, and at the maximum per recruit. The histograms above (a) and (b) are distributions of the posterior estimates for the number of spawners and harvest rates, respectively; the histogram in (a) has been truncated at 10^4.

SUPPORTING INFORMATION

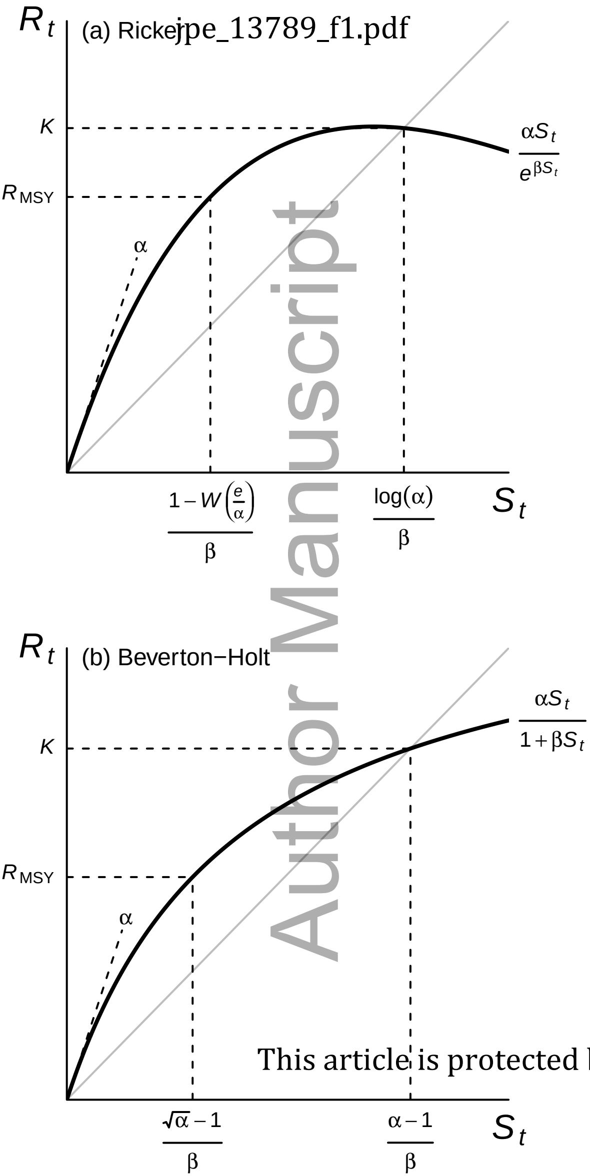
Additional Supporting Information may be found in the online version of this article:

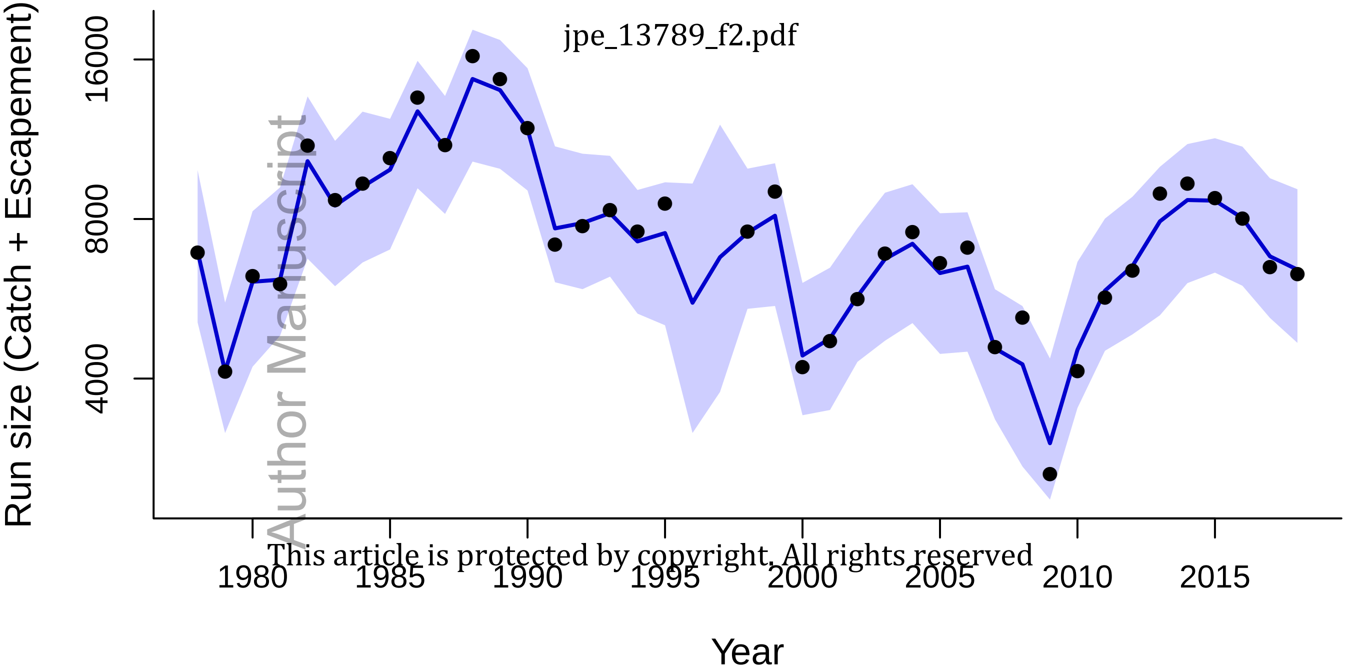
Appendix S1. Instructions for retrieving and archiving the environmental covariates.

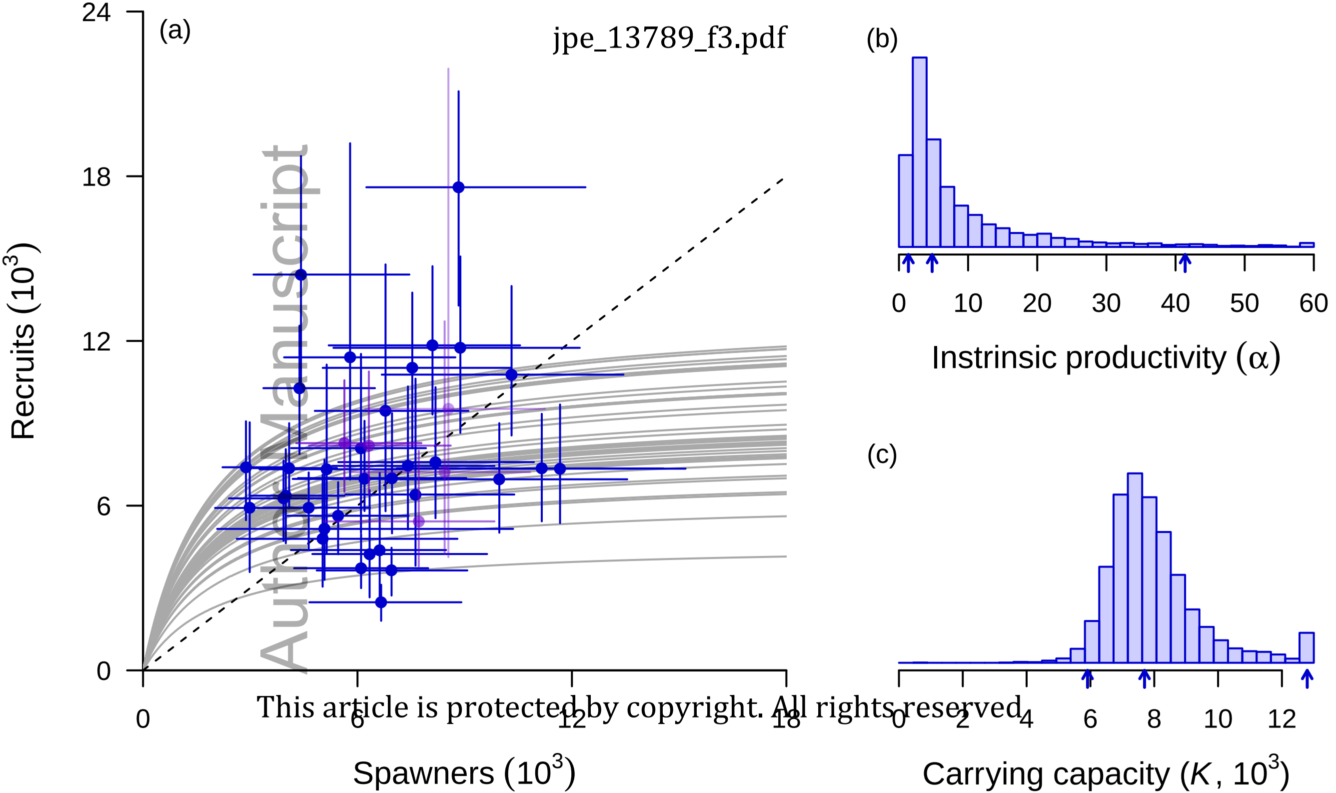
Appendix S2. Model definitions, model fitting, and model evaluation.

Appendix S3. Steps to recreate the manuscript figures.

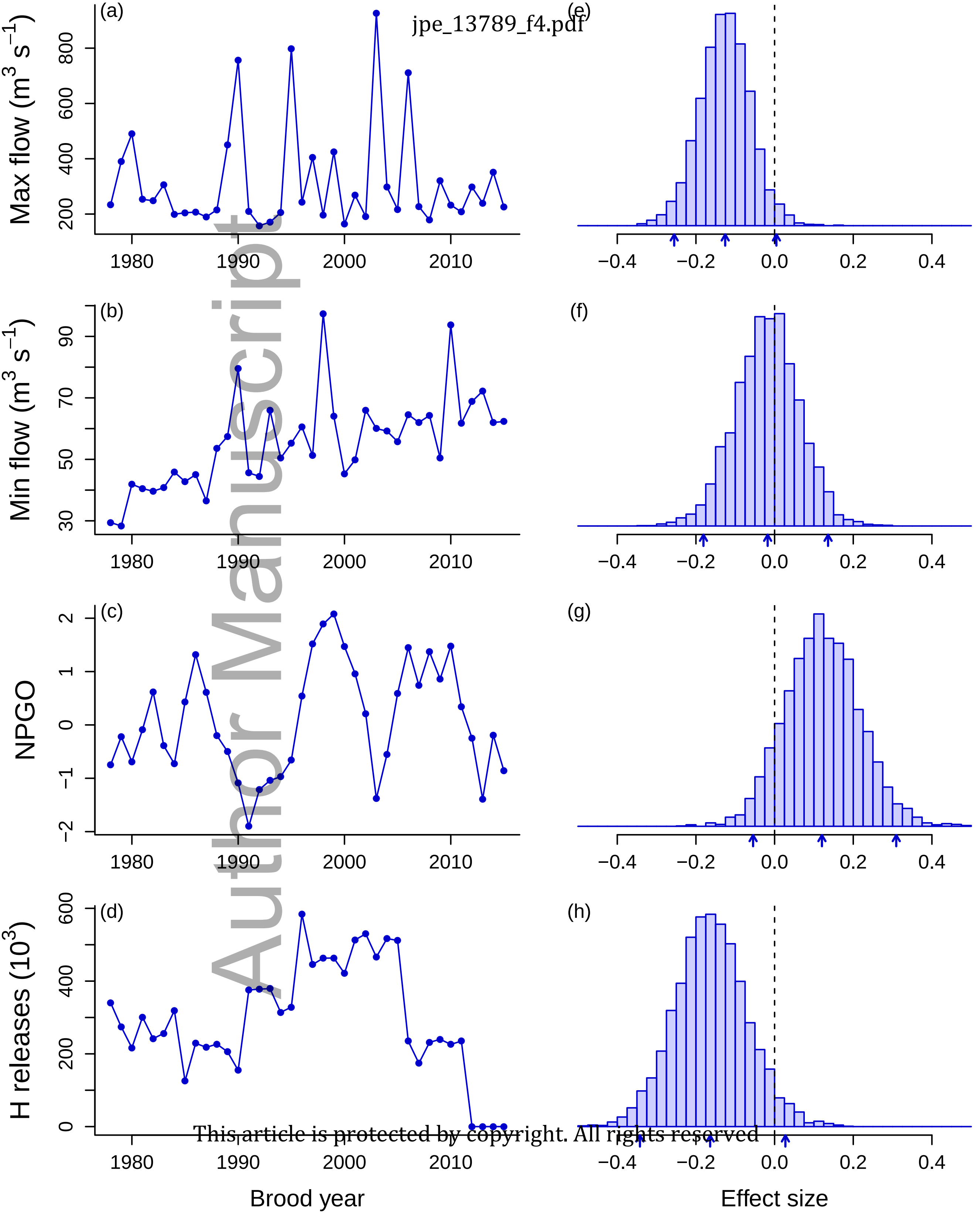
Appendix S4. Background information on the age composition.

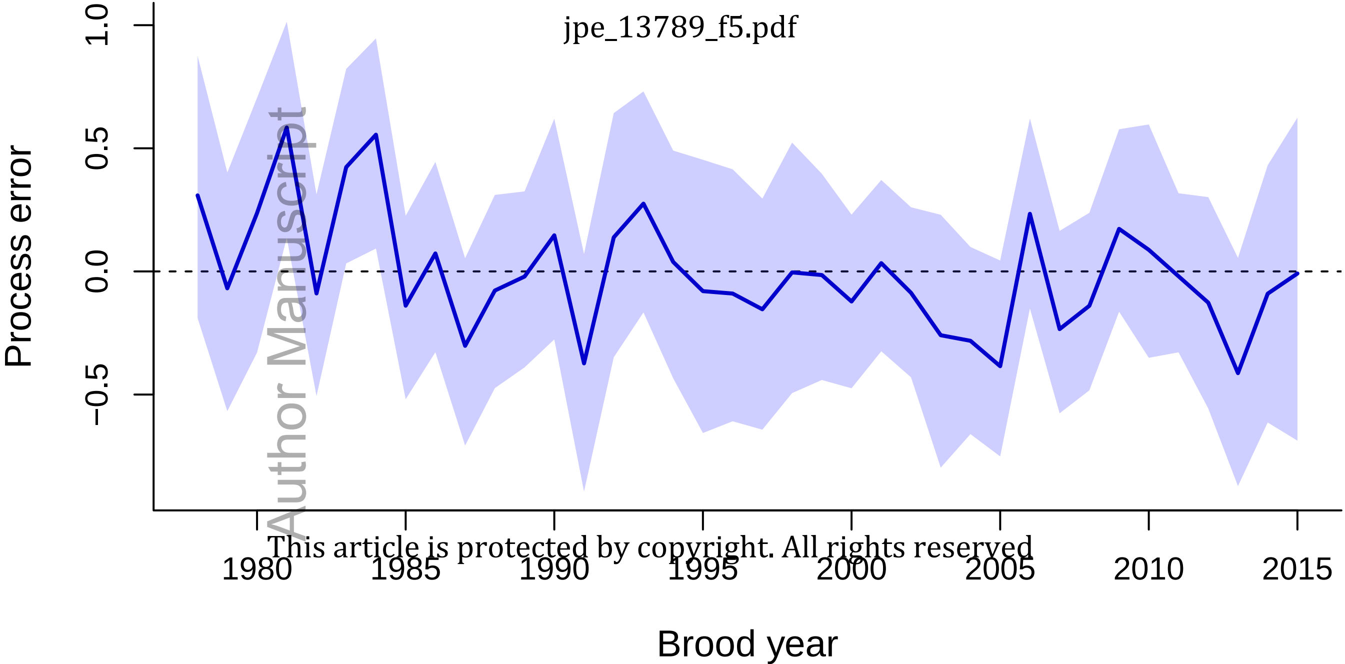

R_t
(a) Ricker
K
R_{MSY}
α
$\frac{\alpha S_t}{e^{\beta S_t}}$
$\frac{1 - W\left(\frac{e}{\alpha}\right)}{\beta}$
$\frac{\log(\alpha)}{\beta}$
S_t
R_t
(b) Beverton−Holt
K
R_{MSY}
α
$\frac{\alpha S_t}{1 + \beta S_t}$
$\frac{\sqrt{\alpha} - 1}{\beta}$
$\frac{\alpha - 1}{\beta}$
S_t

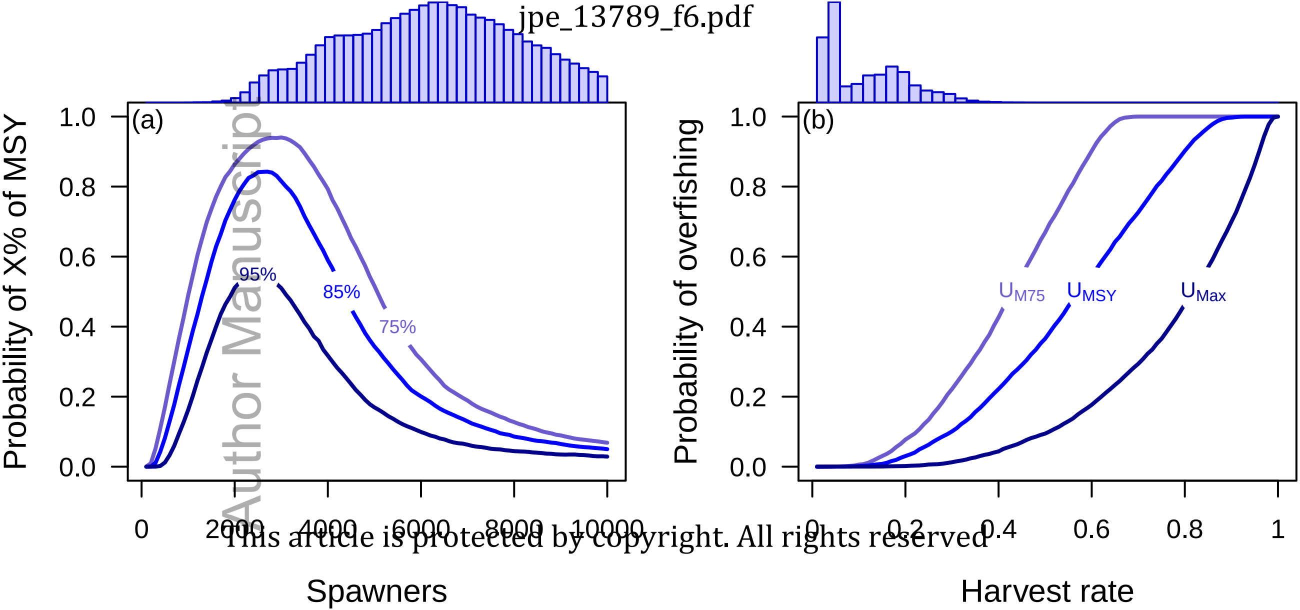

Run size (Catch + Escapement)
16000
8000
4000
1980
1985
1990
1995
2000
2005
2010
2015
Year


(a)
Recruits (10^3)
0
6
12
18
24
Spawners (10^3)
0
6
12
18
(b)
Instrinsic productivity (α)
0
10
20
30
40
50
60
(c)
Carrying capacity (K, 10^3)
0
2
4
6
8
10
12

jpe_13789_f4.pdf




Process error
1.0
0.5
0.0
−0.5
Brood year
1980
1985
1990
1995
2000
2005
2010
2015


(a)
(b)
Probability of X% of MSY
Probability of overfishing
1.0
0.8
0.6
0.4
0.2
0.0
95%
85%
75%
U$_{M75}$
U$_{MSY}$
U$_{Max}$
0
2000
4000
6000
8000
10000
0
0.2
0.4
0.6
0.8
1
Spawners
Harvest rate