

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

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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 programmes 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 trade-offs 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, harvest, hatchery, management, *Oncorhynchus*, river, salmon, steelhead

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1 | 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 (Knappe & 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 north-western 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 towards 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 submodels for (a) describing the stochastic and unobservable population dynamics; and (b) 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 et al., 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 ~6,900 km² in south-western Canada and north-western 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 (i.e. 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.

2 | MATERIALS AND METHODS

2.1 | 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 km² 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–April and typically spawn in March–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 ageing). Following freshwater rearing, individuals spend 2–6 years feeding and growing before returning to freshwater as sexually mature adults to initiate spawning (i.e. they reach sexual maturity at age 3–8; ~82% mature at age 4 or 5). 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 subbasins 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: (a) 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 (b) 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 to May of the first freshwater rearing year, and the minimum of low summer flows occurring from June to 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 to 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 2 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 programme 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.

2.2 | Integrated population model

The number of offspring born in year t that survives 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 :

$$R_t = f(S_t | \theta) \varepsilon_t. \quad (1)$$

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; Figure 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

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

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

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,

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

$$\mu_t = \sum_{i=1}^K \gamma_i X_{i,t+h_i}. \quad (3b)$$

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.

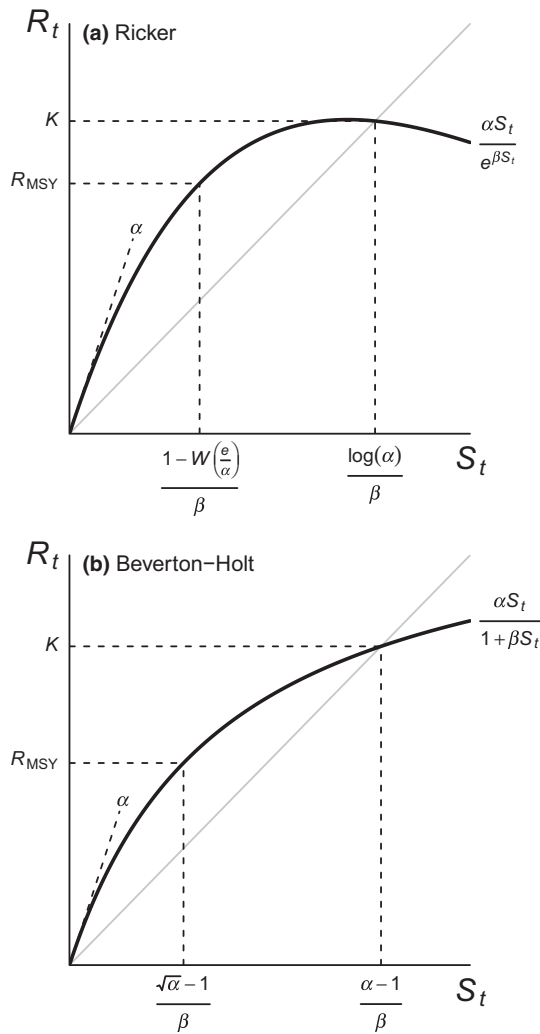


FIGURE 1 Deterministic forms of the (a) Ricker and (b) Beverton-Holt models used in the analyses (thick lines), including equations for carrying capacity (K) and the number of recruits corresponding to the maximum sustained yield (R_{MSY}). The parameter α defines the slope at the origin, the constant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

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

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

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- to 8 year-olds, and therefore, the vector of age-specific return rates for brood year t is $\pi_t = [\pi_3, \pi_4, \pi_5, \pi_6, \pi_7, \pi_8]_t$, which we modelled as a hierarchical random effect whereby $\pi_t \sim \text{Dirichlet}(\eta\tau)$. The mean vector η is also distributed as a Dirichlet; the precision parameter τ affects each of

the elements in η such that large values of τ result in π_t very close to η and small values of τ lead to much more diffuse π_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 :

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

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 Equation (4) above, the numerator of Equation (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 four 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 5,000 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 & Rubin's (1992) 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 on 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 Information and at https://github.com/mdscheuerell/steelhead_IPM.

3 | RESULTS

We found the most data support for the Beverton–Holt form of process model, so all of the following results are based on 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 (Figure 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 (Figure 3). The median of α (i.e. the slope of the

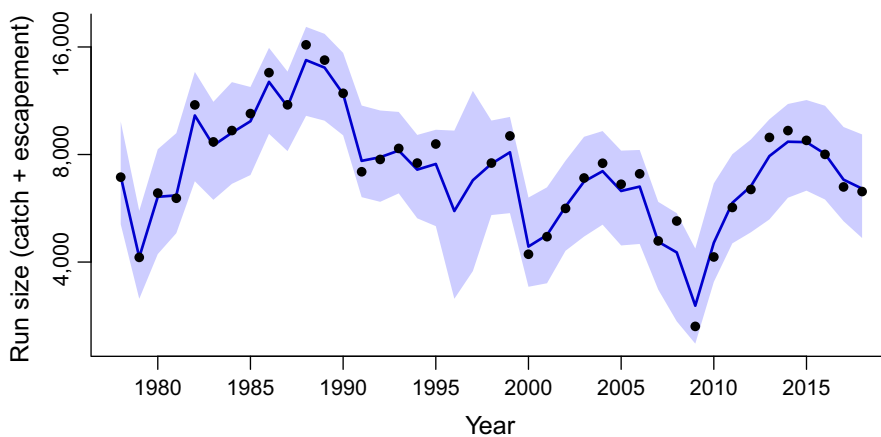


FIGURE 2 Time series of the estimated total population size (catch plus the adults that escaped to spawn). The observed data are the points; the solid line is the median estimate and the shaded region indicates the 95% credible interval

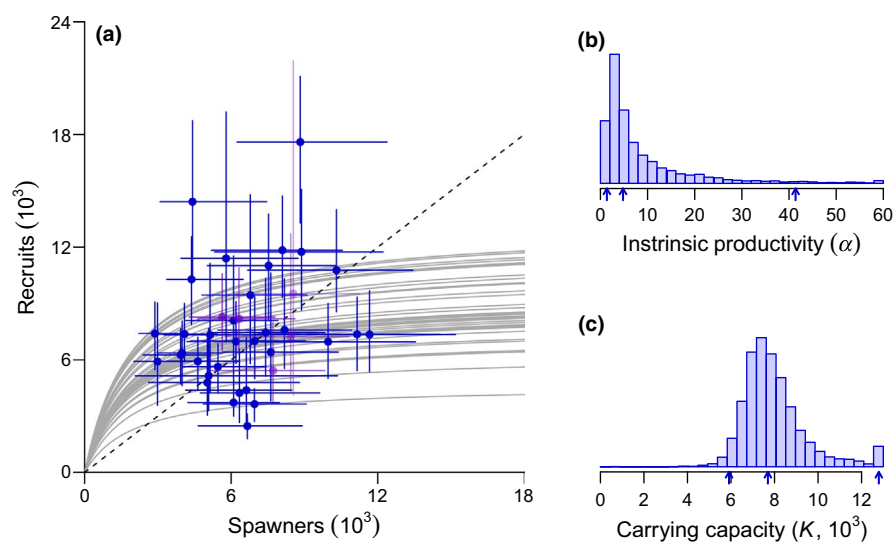


FIGURE 3 Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming mean values for all covariates (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the posterior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

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 (Figure 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. Our estimates of carrying capacity (K) were much more precise, with a median of about 7,700 adults and 95% credible interval of approximately 5900–12,800 adults (Figure 3c).

There were varying effects of the three environmental covariates on population productivity (Figure 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 (Figure 4e), which means that a 1 SD increase in flow above the mean (i.e. from ~ 41 to ~ 68 m^3/s) would translate into a 12% decrease in offspring per parent. The effect of low summer flows was essentially zero (Figure 4f); the median estimate was 0.08 with a 95% credible interval from -0.18 to 0.14. The NPGO had a

largely positive effect (Figure 4g), suggesting warmer waters in the North Pacific are better for steelhead productivity (median equals 0.12 with a 95% credible interval from -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 (Figure 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 a 15% decrease in productivity. Notably, hatchery production experienced three distinct phases over time (Figure 4d): a low period between brood year 1978 and 1990 (range = 125,000–340,000 smolts), an increasing and high period between 1991 and 2005 (range = 314,000–584,000) and a decreasing period beginning in 2006 (range = 0–240,000 smolts).

The remaining, unexplained environmental variance was highly autocorrelated over time (Figure 5). The process residuals were generally positive during the late 1970s and early 1980s when the population was growing (Figure 2), they were near zero during the stable

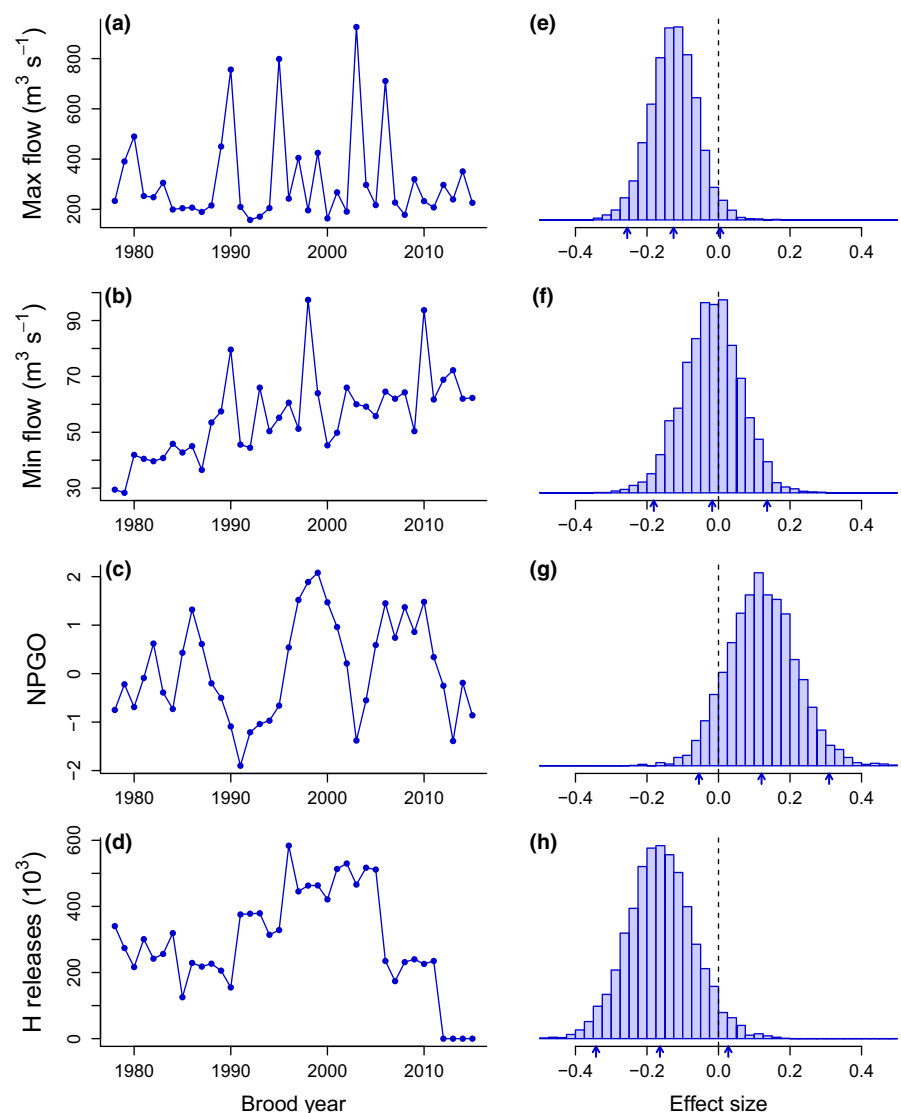


FIGURE 4 Time series of the environmental covariates used in the model (a–d), and their standardized effects on population productivity (e–h). Small arrows under histograms denote the 2.5th, 50th and 97.5th percentiles of the posterior distribution

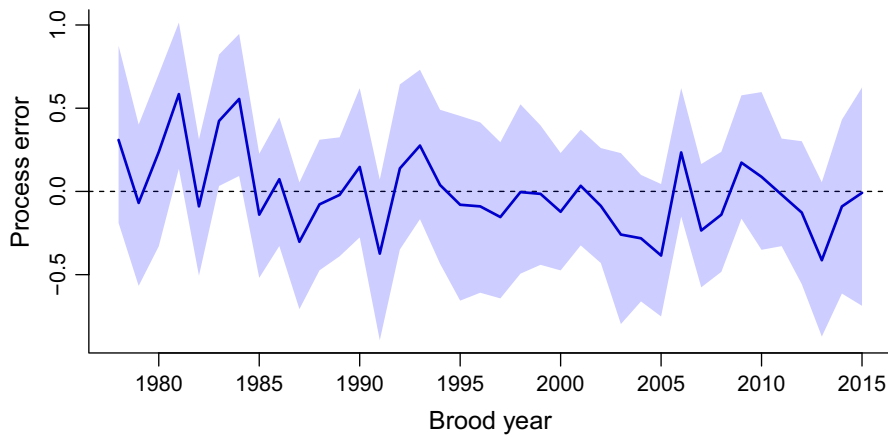


FIGURE 5 Time series of the estimated process errors, which represent the population's productivity after accounting for the effects of density dependence and environmental covariates. The solid line is the median estimate and the shaded region indicates the 95% credible interval

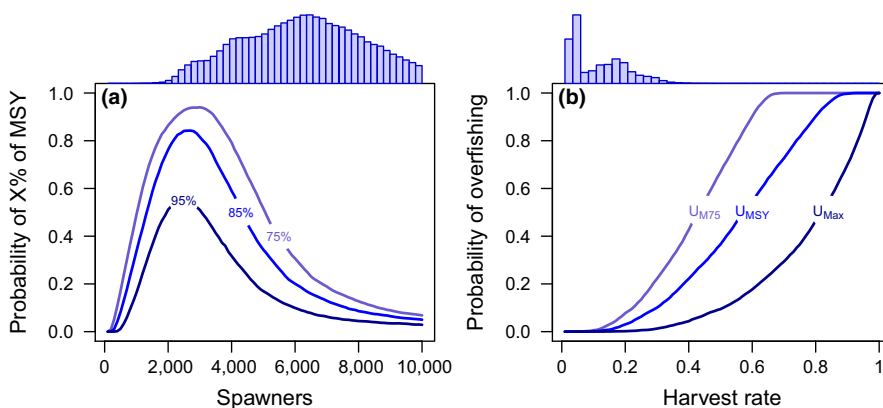


FIGURE 6 Plots of (a) the probability that a given number of spawners produces average yields achieving 95%, 85% or 75% of the estimated maximum sustainable yield (MSY); and (b) the cumulative probability of overfishing the population, based on harvest rates equal to those at 75% of MSY, at MSY and at 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

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 2,000–3,000 spawning adults to produce the maximum sustainable yield (Figure 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 (Figure 6b).

4 | DISCUSSION

In territorial species such as steelhead trout, competition for limited resources commonly results in density-dependent growth and survival amongst juveniles (Imre et al., 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 et al., 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 et al., 1994), suggests that habitat restoration efforts, such as reconnecting floodplain habitats and improving riparian functioning (Beechie et al., 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 *O. 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 modelling 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 et al., 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 of coho salmon (Buhle et al., 2009) and Chinook salmon (Levin et al., 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 (c. 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 et al., 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 2000s, including the Skagit, mirror 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 et al., 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 towards 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 programme 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 trade-offs 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 towards 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 (a) their ability to accommodate multiple data types of varying quality, which reduces otherwise inherent biases when using a single dataset; and (b) more precise estimates of demographic rates than one would with a single dataset (Zipkin et al., 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 United States (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 et al., 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.

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AUTHORS' CONTRIBUTIONS

M.D.S., C.P.R. and J.H.A. conceived the ideas and designed methodology; M.D.S. and C.P.R. analysed the data; M.D.S. and C.P.R. 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 <https://doi.org/10.5281/zenodo.4126912> (Scheuerell et al., 2020); river flow data available via 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/>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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