

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

Mark D. Scheuerell<sup>1,5</sup>, Casey P. Ruff<sup>2</sup>, Joseph H. Anderson<sup>3</sup>, Eric M. Beamer<sup>4</sup>

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

<sup>2</sup>*Skagit River System Cooperative, La Conner, WA USA, cruff@skagitcoop.org*

<sup>3</sup>*Washington Department of Fish and Wildlife, Olympia, WA USA, joseph.anderson@dfw.wa.gov*

<sup>4</sup>*Skagit River System Cooperative, La Conner, WA USA, ebeamer@skagitcoop.org*

<sup>5</sup>**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:**

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

1    **Summary**

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

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

12   3. We found compelling evidence that the population is under strong density dependence, despite  
13   being well below its historical population size. In the freshwater portion of the lifecycle, we  
14   found a negative relationship between productivity (offspring per parent) and peak winter flows,  
15   and a positive relationship with summer flows. We also found a negative relationship between  
16   productivity and releases of hatchery conspecifics. In the marine portion of the lifecycle, we  
17   found a positive correlation between productivity and the North Pacific Gyre Oscillation.  
18   Furthermore, harvest rates on wild fish have been sufficiently low to ensure very little risk of  
19   overfishing.

20   4. *Synthesis and applications.* The evidence for density dependent population regulation,  
21   combined with the substantial loss of juvenile rearing habitat in this river basin, suggests that  
22   habitat restoration could benefit this population of at-risk steelhead. Our results also imply that  
23   hatchery programs for steelhead need to be considered carefully with respect to habitat

24 availability and recovery goals for wild steelhead. If releases of hatchery steelhead have indeed  
25 limited the production potential of wild steelhead, there are likely significant tradeoffs between  
26 providing harvest opportunities via hatchery steelhead production, and achieving wild steelhead  
27 recovery goals.

28     **Introduction**

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

42         The productivity and carrying capacity of a population may also vary over time and space  
43         (Thorson *et al.* 2015), and explicit consideration of external drivers can improve estimates of  
44         population dynamics under density dependent conditions (Lebreton & Gimenez 2013). For at-  
45         risk species, these exogenous factors can be used to better understand drivers of historical  
46         population demographics and help identify possible recovery options. Incorporating covariates  
47         into population models can also improve forecasts of future dynamics, especially over shorter  
48         time horizons most relevant to natural resource management (Ward *et al.* 2014). Furthermore,  
49         accelerated global change will likely create synergistic effects that complicate efforts to make  
50         reliable long-term predictions (Schindler & Hilborn 2015). Thus, any reasonable assumptions

51 about future responses of populations should begin with an attempt to fully account for the  
52 uncertainty in population-environment relationships based on all of the current information.

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

65 More recently however, researchers have turned toward integrated population models  
66 (IPMs) as a means to convey the combined uncertainty in all of the data sources, which is  
67 particularly important in a conservation context (Buhle *et al.* 2018; Zipkin & Saunders 2018).  
68 IPMs are similar to state-space models in that they have specific sub-models for 1) describing the  
69 stochastic and unobservable population dynamics; and 2) addressing the noisy, incomplete data  
70 (Schaub & Abadi 2011; Yen *et al.* 2019). Although IPMs have been widely developed and  
71 applied to mammals (e.g., Regehr *et al.* 2018) and birds (e.g., Saunders, Cuthbert & Zipkin  
72 2018), there are very few examples for Pacific salmon (cf., Buhle *et al.* 2018).

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

88        **Materials and methods**

89        STUDY SPECIES AND DATA

90        The Skagit River system is predominantly a glacially fed system that consists of a  
91        combination of rain, snow-transitional, and snow-dominated tributaries providing approximately  
92        48 km<sup>2</sup> of potential habitat suitable for spawning and rearing by wild steelhead (Hard *et al.*  
93        2015). Adult steelhead in the Skagit River generally enter freshwater in November through April  
94        and typically spawn in March through June. The majority of juveniles rear in freshwater for 2  
95        years prior to migrating to sea as smolts where they spend 2 to 6 years feeding and growing

96 before returning to freshwater as sexually mature adults to initiate spawning (i.e., they reach  
97 sexual maturity at age three through eight; ~82% mature at age four or five). These fish then  
98 spend a year at sea before returning again to freshwater to spawn again.

99 Due to a combination of logistical constraints, only a fraction of the known spawning  
100 area was surveyed for wild spawners. Specifically, standardized index reach surveys were  
101 conducted annually in only 2 of 5 major sub-basins and 13 of 63 tributaries known to support  
102 wild steelhead production. A basin-wide estimate of wild spawners was generated annually by  
103 expanding each survey to account for estimated available habitat not surveyed. Fisheries  
104 biologists in the Skagit basin generally consider the escapement estimates to be conservative: it  
105 is more likely that escapement is underestimated than overestimated because unobserved  
106 spawning sites would serve to increase abundance. Our analyses begin with surveys in 1978 and  
107 continue through 2018.

108 In the model described below, we evaluate several environmental indicators of survival.  
109 Specifically, flow conditions experienced by juveniles during freshwater rearing can have strong  
110 effects on their survival to adulthood via the following mechanisms: (1) spatial contraction of  
111 habitat as a result of low summer flows and high water temperatures that coincide with the  
112 period of highest metabolic demand (e.g., Crozier *et al.* 2010), and (2) habitat displacement or  
113 direct mortality resulting from peak winter flows (e.g., Irvine 1986). Therefore, we utilized long-  
114 term flow records from a gage (#12178100) located in Newhalem Creek, a snowmelt dominated  
115 stream located in the Upper Skagit River (48.66 N, 121.246 W), and maintained by the United  
116 States Geological Survey (see Appendix S1). Specifically, we obtained the observed maximum  
117 of daily peak flows occurring from October through March of the first freshwater rearing year,

118 and the minimum of low summer flows occurring from June through September of the first  
119 summer of freshwater rearing.

120 Because conditions experienced by salmon and steelhead during their first year at sea are  
121 thought to be critical to overall survival and growth of a given year class (Beamish & Mahnken  
122 2001), we chose the average North Pacific Gyre Oscillation index (NPGO) from January through  
123 December as an index of conditions experienced by juvenile steelhead during their first year in  
124 the ocean. Variability in the NPGO reflects annual changes in coastal upwelling and ocean  
125 circulation patterns that correlate strongly with primary and secondary production in coastal  
126 ecosystems (Di Lorenzo *et al.* 2008). Furthermore, the NPGO has been recently identified as an  
127 important indicator of early marine survival in other Pacific salmon species (Kilduff *et al.* 2015).  
128 Because most juvenile steelhead from the Skagit River migrate to sea during the spring of their  
129 second year, we lagged the NPGO indicator by two years beyond the birth year to reflect  
130 conditions experienced during the first year at sea.

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

141 with hatchery fish released in year  $t + 2$ . We used the total number of juveniles released from the  
142 hatchery within a given year as our covariate.

143 INTEGRATED POPULATION MODEL

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

$$147 \quad R_t = f(S_t | \boldsymbol{\theta}) e^{\varepsilon_t}. \quad (1)$$

148 Here we consider two different forms for  $f$ : the Ricker model and the Beverton-Holt model (Fig.  
149 1).

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

$$155 \quad \varepsilon_t \sim \text{Normal}(\phi \varepsilon_{t-1}, \sigma_\varepsilon), \quad (2a)$$

$$156 \quad \varepsilon_0 \sim \text{Normal}\left(0, \frac{\sigma_\varepsilon}{1-\phi^2}\right). \quad (2b)$$

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

$$159 \quad \varepsilon_t \sim \text{Normal}(\mu_t + \phi \varepsilon_{t-1}, \sigma_\varepsilon) \quad (3a)$$

$$160 \quad \mu_t = \sum_{i=1}^K \gamma_i X_{i,t+h_i} \quad (3b)$$

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

164       The estimated numbers of fish of age  $a$  returning in year  $t$  ( $N_{a,t}$ ) is then product of the

165       total number of brood-year recruits in year  $t - a$  from Equation (1) and the proportion of mature

166       fish from that brood year that returned to spawn at age  $a$  ( $\pi_{a,t-a}$ ), such that

167       
$$N_{a,t} = R_{t-a} \pi_{a,t-a}. \quad (4)$$

168       Adult steelhead from the Skagit River return as 3-8 year-olds, and therefore the vector of age-

169       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 modeled as a

170       hierarchical random effect whereby  $\pi_t \sim \text{Dirichlet}(\eta\tau)$ . The mean vector  $\eta$  is also distributed as a

171       Dirichlet; the precision parameter  $\tau$  affects each of the elements in  $\eta$  such that large values of  $\tau$

172       result in  $\pi_t$  very close to  $\eta$  and small values of  $\tau$  lead to much more diffuse  $\pi_t$ .

173       The spawner-recruit models above describe a process based on the true number of

174       spawners, but our estimates of the numbers of spawning adults necessarily contain some

175       sampling errors due to incomplete censuses, pre-spawn mortality, etc. Therefore, we assumed

176       that our estimates of escapement, the number of adult fish that “escape the fishery” and

177       ultimately spawn ( $E_t$ ), are log-normally distributed about the true number of spawners ( $S_t$ ):

178       
$$\ln(E_t) \sim \text{Normal}(\ln(S_t), \sigma_s). \quad (5)$$

179       Catches of wild steelhead are closely recorded by state and tribal biologists, and so we

180       assume the harvest is recorded without error. We then calculate  $S_t$  as the difference between the

181       estimated total run size ( $N_t$ ) and harvest ( $H_t$ ), where

182       
$$S_t = N_t - H_t, \quad (6)$$

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

184       We obtained observations of the number of fish in each age class  $a$  in year  $t$  ( $O_{a,t}$ ) from

185       scale analyses of 10 – 408 adults per year; no scale samples were taken in 1978-1982, 1984, and

186 2000. These data were assumed to arise from a multinomial process with order  $Y_t$  and proportion  
187 vector  $\mathbf{d}_t$ , such that

$$188 \quad \mathbf{O}_t \sim \text{Multinomial}(Y_t, \mathbf{d}_t). \quad (7)$$

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

$$191 \quad Y_t = \sum_{a=3}^8 O_{t,a}. \quad (8)$$

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

$$194 \quad d_{a,t} = \frac{N_{a,t}}{\sum_{a=3}^8 N_{a,t}}. \quad (9)$$

195 We used Bayesian inference to estimate all model parameters and the unobserved true  
196 numbers of spawners and offspring over time. We used the freely available **R** software (v3.6, R  
197 Development Core Team 2019) combined with the JAGS software (v4.2.0, Plummer 2003) to  
198 perform Gibbs sampling with 4 parallel chains of  $5 \times 10^5$  iterations. Following a burn-in period of  
199  $2.5 \times 10^5$  iterations, we thinned each chain by keeping every 400<sup>th</sup> sample to eliminate any  
200 possible autocorrelation, which resulted in 5000 samples from the posterior distributions. We  
201 assessed convergence and diagnostic statistics via the ‘CODA’ package in **R** (Plummer *et al.*  
202 2006). Specifically, we used visual inspection of trace plots and density plots, and verified that  
203 Gelman and Rubin’s (2017) potential scale reduction factor was less than 1.1, to ensure adequate  
204 chain mixing and parameter convergence. Data support for each model was evaluated using  
205 leave-one-out cross-validation (LOO) based upon Pareto-smoothed importance sampling as  
206 implemented in the ‘loo’ package (Vehtari *et al.* 2019). All of the code and data files necessary  
207 to replicate our analyses are available in the online supporting material and at  
208 [https://github.com/mdscheuerell/steelhead\\_IPM](https://github.com/mdscheuerell/steelhead_IPM).

209 **Results**

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

216 The population dynamics of steelhead in the Skagit River are currently under density-  
217 dependent regulation, despite their numbers being well below historical censuses, and there is  
218 considerable uncertainty in the relationship between spawning adults and their surviving  
219 offspring (Fig. 3). The median of  $\alpha$  (i.e., the slope of the relationship at the origin) was 6.8  
220 offspring per spawner, but a lack of data at low spawner abundance led to considerable  
221 uncertainty in the estimate (Fig. 3b). The lower 95% credible interval was about 1.5 offspring per  
222 spawner, which is still above replacement, while the upper 95% credible interval was 44  
223 offspring per parent. On the other hand, our estimates of carrying capacity ( $K$ ) were much more  
224 precise, with a median of about 7400 adults and 95% credible interval of approximately 6100 to  
225 10 900 adults (Fig. 3c).

226 There were varying effects of the three environmental covariates on population  
227 productivity (Fig. 4). Peak winter flows were negatively related to survival, suggesting high  
228 discharge events may transport juveniles downstream to lower quality habitats, or lead to direct  
229 mortality from channel avulsion or movement of sediment, wood, and other debris. The median  
230 of the posterior distribution was -0.11 (Fig. 4e), which means that a 1 SD increase in flow above  
231 the mean (i.e., from  $\sim 41 \text{ m}^3 \text{ s}^{-1}$  to  $\sim 68 \text{ m}^3 \text{ s}^{-1}$ ) would translate into a 11% decrease in offspring

232 per parent. Conversely, the effect of low summer flows was positive (Fig. 4f), possibly indicative  
233 of greater rearing habitat (the median estimate was 0.08 with a 95% credible interval of -0.09 to  
234 0.25). The NPGO had a similar effect to summer flow (Fig. 4g), suggesting warmer waters in the  
235 North Pacific are better for steelhead survival (median equals 0.09 with a 95% credible interval  
236 of -0.08 to 0.27).

237 We also found that the number of hatchery juveniles released into the river during the  
238 time that wild juveniles were migrating to sea was negatively related to productivity (Fig. 4h).  
239 The median effect size was -0.20, which means that a 1 SD increase in the number of hatchery  
240 juveniles released (i.e., from 328 000 to 452 000 fish) would, on average, result in a 18%  
241 decrease in survival to adulthood. Notably, hatchery production experienced three distinct phases  
242 over time (Fig. 4d): a low period between brood year 1978 and 1990 (range = 125 000 to 340  
243 000 smolts), an increasing and high period between 1991 and 2005 (range = 314 000 to 584  
244 000), and a decreasing period beginning in 2006 (range = 0 to 240 000 smolts).

245 The remaining, unexplained environmental variance was indeed highly autocorrelated  
246 over time (Fig. 5). The process residuals were generally positive during the late 1970s and early  
247 1980s when the population was growing (Fig. 2), they were near zero during the stable period of  
248 the 1990s, and then largely negative as the population primarily declined through the 2000s.

249 Based on our estimates of biological reference points, Skagit River steelhead appear to be  
250 managed along a rather conservative harvest management perspective. The optimal yield profiles  
251 suggest it would take approximately 2000 to 3000 spawning adults to produce the maximum  
252 sustainable yield (Fig. 6a), but very few years have ever fallen below that throughout the time  
253 period presented here (i.e., the average number of spawning adults has been two to three times

254 greater). In other words, the realized harvest rates have been kept low enough to insure very little  
255 risk of overfishing (Fig. 6b).

256 **Discussion**

257 In territorial species such as steelhead trout, competition for limited resources commonly  
258 results in density dependent growth and survival amongst juveniles (Imre, Grant & Keeley  
259 2004). Our analysis suggests that such effects have scaled up to the entire population level to  
260 govern patterns of steelhead productivity in the Skagit River basin. Importantly, we found strong  
261 evidence for density dependent interactions despite the fact that contemporary population  
262 censuses are well below historical estimates (Gayeski, McMillan & Trotter 2011). Similar results  
263 have been observed in populations of coho salmon *Oncorhynchus kisutch* Walbaum 1792 in  
264 Oregon (Buhle *et al.* 2009) and in populations of Chinook salmon *Oncorhynchus tshawytscha*  
265 Walbaum 1792 in Idaho (Thorson *et al.* 2013). Although we cannot be certain of the exact life-  
266 stage at which density dependent processes occurred, the freshwater juvenile stage seems likely  
267 given the extended duration of freshwater rearing typical for this species. When steelhead  
268 populations reach low numbers, the spatial contraction of spawners may exacerbate the effects of  
269 density dependence because their newly emerged offspring do not have the mobility to access  
270 other vacant habitats (Atlas *et al.* 2015). The evidence for density dependence presented here,  
271 combined with the substantial loss of juvenile rearing habitat in the Skagit River basin (Beechie,  
272 Beamer & Wasserman 1994), suggests that habitat restoration efforts, such as reconnecting  
273 floodplain habitats and improving riparian functioning (Beechie, Pess & Roni 2008), may benefit  
274 this population of steelhead.

275 Fluctuating environments can also affect population dynamics through density  
276 independent mechanisms, and anadromous salmon must contend with many different and

unpredictable habitats over their lifespan. Our results indicate 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 somewhat weaker 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).

We found evidence of positive effects of NPGO on survival, which comports with previous studies that have made rather compelling cases for a strong positive relationship between the NPGO and salmon survival (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.

300 Among the various mitigation measures to address salmon declines, artificial propagation  
301 of salmon has been used widely for more than a century. Nevertheless, research in other river  
302 systems points to negative ecological effects of hatchery fish on wild Pacific salmon, including  
303 populations coho salmon (Buhle *et al.* 2009), and Chinook salmon (Levin, Zabel & Williams  
304 2001). Our results provide further evidence that large releases of hatchery-reared juvenile  
305 steelhead have had a negative effect on productivity of wild steelhead, although we note some  
306 researchers have used an approach similar to ours and found no hatchery effect on productivity  
307 (Courter *et al.* 2019; Nelson *et al.* 2019). Our study was unable determine the mechanism  
308 responsible for the correlation between hatchery releases and wild steelhead productivity. In fact,  
309 very few empirical studies have been conducted at the appropriate spatial and temporal scales  
310 necessary to directly quantify the hypothesized mechanisms by which negative ecological  
311 interactions between hatchery and wild fish may occur (Weber & Fausch 2003). That said,  
312 however, competition for limiting freshwater food and habitat resources (Berejikian *et al.* 2000)  
313 is a plausible mechanism, either during the relatively brief period of overlap during downstream  
314 migration (ca. 2 – 4 weeks), or a more prolonged effect of any hatchery fish that do not migrate  
315 to sea, but instead “residualize” within freshwater. Additionally, predators are known to respond  
316 numerically to their prey, and it is possible that large numbers of hatchery fish attracted  
317 additional predators (Kostow 2009). Although breeding by hatchery individuals that stray onto  
318 natural spawning grounds may reduce the fitness of a wild population via gene flow from the  
319 hatchery stock into the wild population (Araki, Cooper & Blouin 2009), our study only  
320 considered within-cohort effects. Thus, it seems unlikely that a trans-generational genetic effect  
321 was the mechanism for the observed negative association between hatchery releases and wild  
322 productivity.

323       Throughout the Puget Sound region, steelhead have been exposed to varying degrees of  
324 influence by hatchery fish over the past 100 years, but they share the marine rearing  
325 environment, and thus have experienced relatively similar ocean conditions during the same time  
326 period. The marked decreases in abundance observed in many of these populations from the late  
327 1980s to the late 2000's, including the Skagit, mirrors observations of a general declining trend  
328 in marine survival of hatchery conspecifics across the same time period, suggesting some larger,  
329 unmeasured forces have been at work (Kendall, Marstrom & Klungle 2017). Furthermore, in  
330 response to the declining abundance of wild Skagit River steelhead coupled with declining  
331 marine survival of hatchery steelhead, fisheries managers increased hatchery production to  
332 replace lost fishing opportunities. Thus, it is plausible that declining wild productivity was  
333 simply coincident with higher hatchery production, rather than a consequence of it. It is also  
334 possible that multicollinearity among measured and unmeasured covariates increased the  
335 estimated effect sizes.

336       The life history complexity of steelhead may not lend well to the use of traditional  
337 spawner recruit models such as the forms used in this study. Notably, steelhead exhibit  
338 significant phenotypic plasticity with respect to adopting partial migration strategies, with  
339 unknown proportions of a given cohort adopting a non-anadromous resident life history type  
340 (Kendall *et al.* 2015). Given that only anadromous individuals are included in the annual  
341 derivation of age structured abundance, there may be a large component of each cohort that is  
342 missed which likely resulted in substantial observation error not captured in our models.  
343 Therefore, caution should be used when interpreting the spawner recruit relationships and  
344 resulting management reference points presented here. Furthermore, future research should aim  
345 at quantifying the contribution of individuals adopting the resident life history type to overall

346 productivity. Without these estimates, accurate assessments of the status of steelhead populations  
347 may not be possible. The “precautionary approach” to fisheries management aims to balance the  
348 trade-off between catch and the risk of over-fishing such that minimizing the risk of overfishing  
349 takes precedence (Hilborn *et al.* 2001). Our Bayesian state-space model provides a formal means  
350 for estimating the probability of fishing in a sustainable manner. We found compelling evidence  
351 that harvest rates for wild steelhead in the Skagit River basin over the time period considered  
352 here have been well below those that would drive the population toward extinction. This result,  
353 combined with the strong indication of density dependence, lends further support to the notion  
354 that habitat improvements may benefit this population most. However, some caution is warranted  
355 because we may have overestimated the biological reference points by not fully accounting for  
356 repeat spawners.

357 Here we have demonstrated how to use incomplete information about the abundance and  
358 age structure of a population to estimate density dependent population dynamics in light of  
359 natural and human-induced variability in the environment. Our study adds to the growing body  
360 of evidence that habitat, hatchery practices, and environmental variability are intricately linked in  
361 affecting productivity of wild Pacific salmon stocks. Future research should focus on quantifying  
362 habitat limitation on productivity at specific life stages to better focus restoration actions needed  
363 to recover wild steelhead. Our modeling framework also allowed us to assess the degree to which  
364 hatchery and harvest management actions are likely to affect the long-term viability of the  
365 population. Our results suggest that hatchery program goals for steelhead need to be considered  
366 carefully with respect to recovery goals and the quantity and quality of steelhead habitat. If  
367 releases of non-local origin hatchery steelhead have indeed limited the production potential of

368 wild steelhead, there are likely significant tradeoffs between providing harvest opportunities via  
369 hatchery steelhead production and achieving wild steelhead recovery goals.

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377 01).

378 **Authors' Contributions**

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

382 **Data Accessibility**

383 All of the fish data have been archived at Figshare and are available via the following links:  
384 abundance (<https://dx.doi.org/10.6084/m9.figshare.3458183.v1>);  
385 age composition (<https://dx.doi.org/10.6084/m9.figshare.3458204.v1>);  
386 harvest (<https://dx.doi.org/10.6084/m9.figshare.3458189.v1>); and  
387 hatchery releases (<https://dx.doi.org/10.6084/m9.figshare.3457163.v1>).

388 The river flow data are available from the United States Geological Survey National Water  
389 Information System (<http://waterdata.usgs.gov/nwis>). The North Pacific Gyre Oscillation data

390 are available from Emanuele Di Lorenzo at Georgia Technical University

391 (<http://www.o3d.org/nngo/>).

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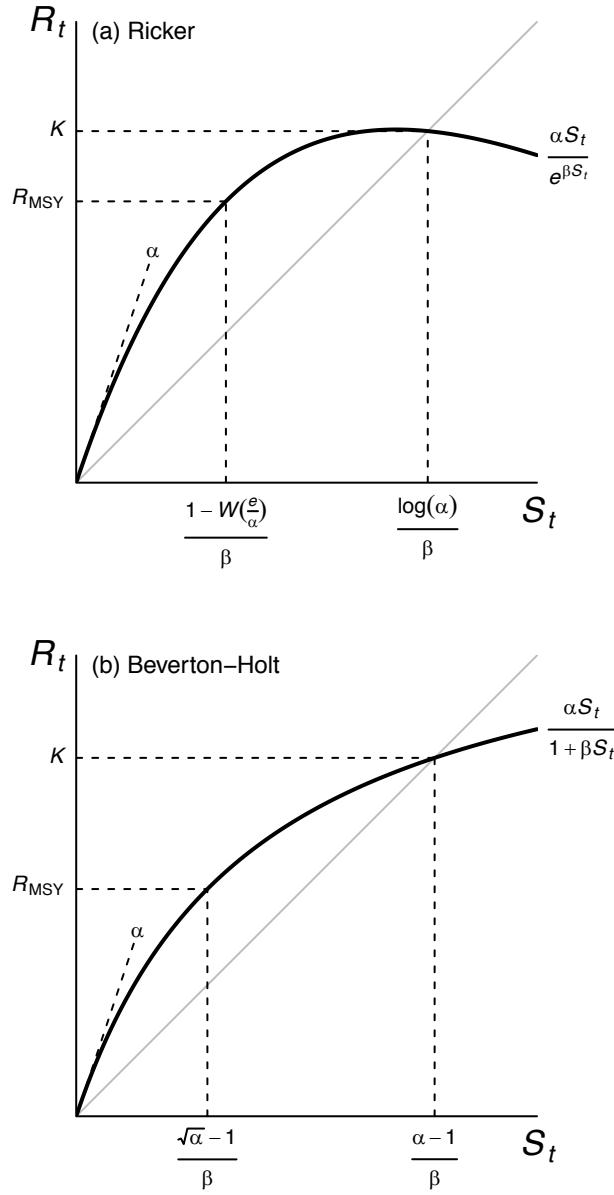
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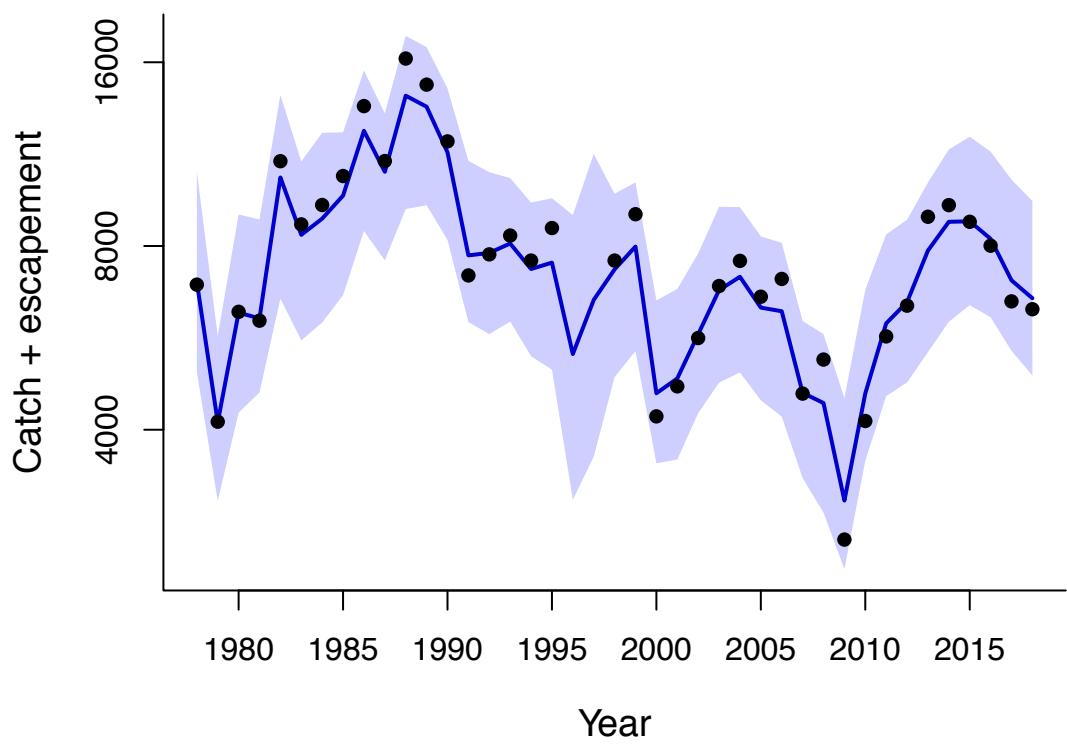
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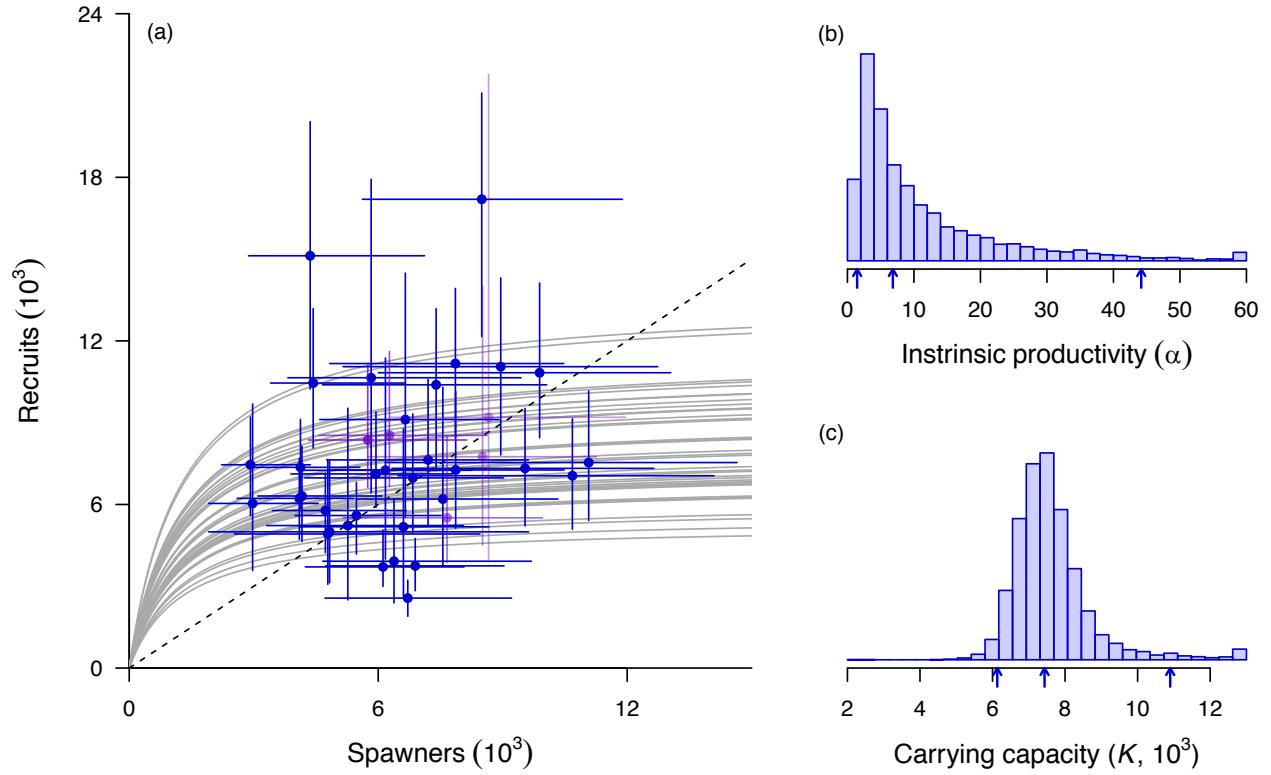
## FIGURES



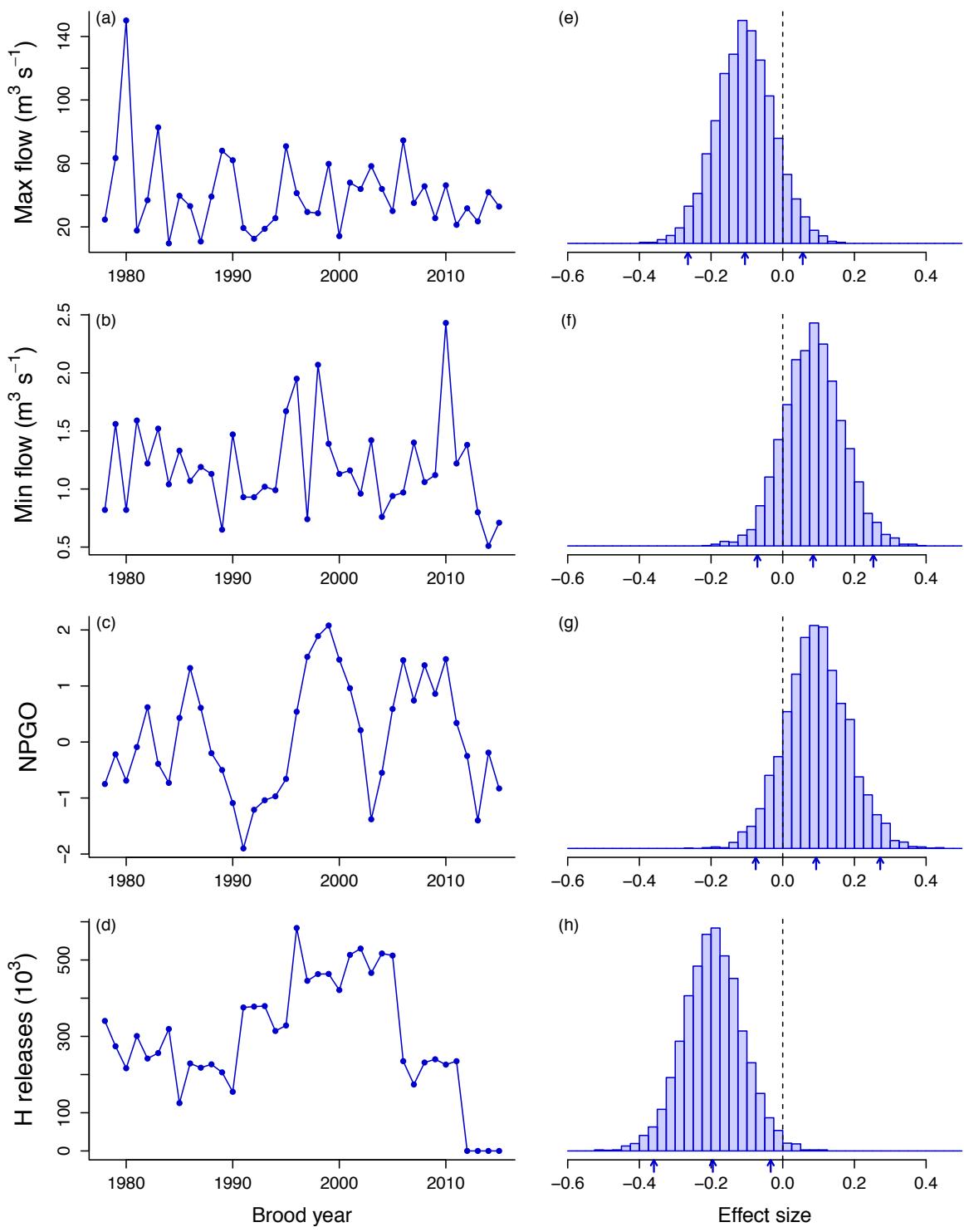
**Figure 1.** Deterministic forms of the (a) Ricker and (b) Beverton-Holt models used in the analyses (thick lines), including equations for carrying capacity ( $K$ ) and the number of recruits corresponding to the maximum sustained yield ( $R_{MSY}$ ). The parameter  $\alpha$  defines the slope at the 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  $R_t = S_t$ .



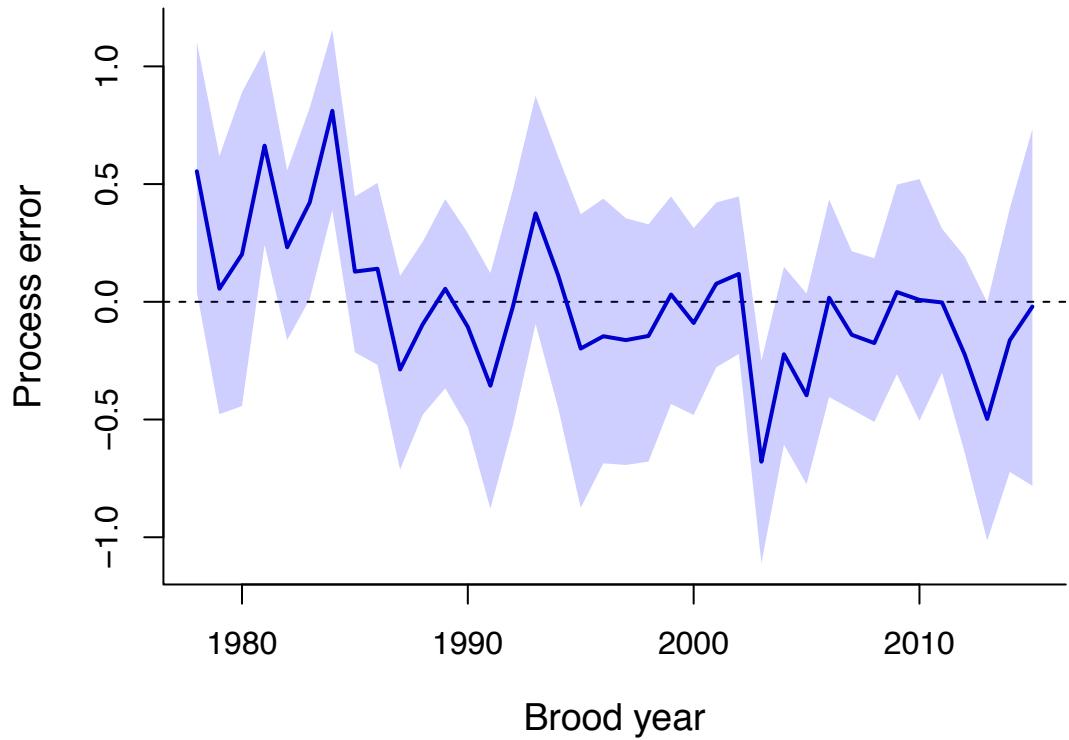
**Figure 2.** Time series of the estimated total population size (catch plus the adults that escaped to spawn). The observed data are the points; the solid line is the median estimate and the shaded region indicates the 95% credible interval.



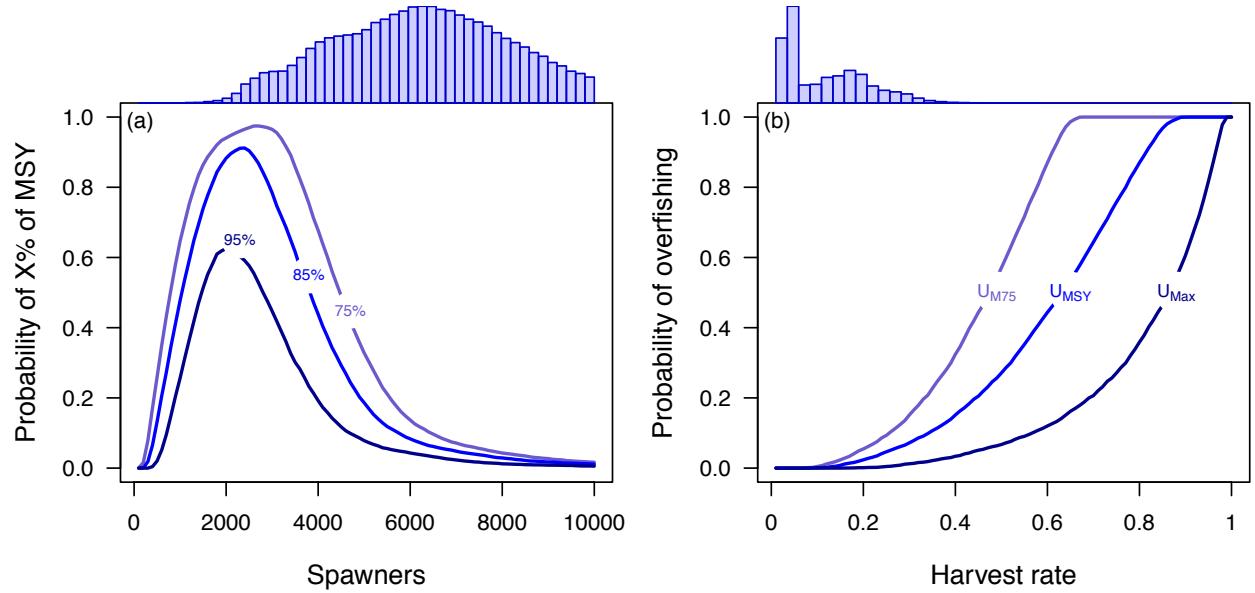
**Figure 3.** Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming mean values for all covariates (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the posterior 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 2.5<sup>th</sup>, 50<sup>th</sup>, and 97.5<sup>th</sup> 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 2.5<sup>th</sup>, 50<sup>th</sup>, and 97.5<sup>th</sup> 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 figures from main text.