

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

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Running title: Density dependent populations dynamics

Key words: density dependence, population dynamics, missing data, state-space, Bayesian, hierarchical, hatchery, *Oncorhynchus*

Number of words: 6971 (total); 310 (summary); 4670 (main text); 79 (acknowledgements); 1617 (references), 0 (tables); 295 (figure legends)

Number of tables: 0

Number of figures: 6

Number of references: 58

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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 available 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; Maunder & Punt 2013; Yen *et al.* 2019). Although IPMs have been
71 widely developed and applied to mammals (e.g., Eacker *et al.* 2017; Regehr *et al.* 2018) and
72 birds (e.g., Crawford *et al.* 2018; Saunders, Cuthbert & Zipkin 2018), there are very few
73 examples for Pacific salmon (cf., Buhle *et al.* 2018).

74 Here we combine incomplete data on adult abundance, age composition, and harvest into
75 a Bayesian IPM to answer important questions relevant to management of a threatened
76 population of anadromous steelhead trout *Oncorhynchus mykiss* Walbaum 1792 from the Skagit
77 River basin, which drains ~6900 km² in southwestern Canada and northwestern United States.
78 Specifically, we used 39 years of age structured abundance data (1978-2018) to quantify the
79 degree of density dependence and the effects of a specific suite of environmental drivers on
80 intrinsic productivity within the Skagit River steelhead population. We found that although
81 recent population censuses are well below historical estimates, the population still operates under
82 relatively strong density dependence. We also found that streamflow during winter and releases
83 of hatchery-reared juvenile steelhead were negatively related to wild steelhead survival, but that
84 survival was positively related to streamflow during summers as juveniles and sea-surface
85 temperatures experienced as adults in the North Pacific. In light of remaining uncertainty in the
86 factors governing the population dynamics of Skagit River steelhead, this modelling framework
87 is an effective tool for setting near term recovery goals and evaluating population level response
88 recovery actions.

89 **Materials and methods**

90 STUDY SPECIES AND DATA

91 The Skagit River system is predominantly a glacially fed system that consists of a
92 combination of rain, snow-transitional, and snow-dominated tributaries providing approximately
93 48 km² of potential habitat suitable for spawning and rearing by wild winter run steelhead (Hard
94 *et al.* 2015). Adult steelhead trout in the Skagit River generally enter freshwater in November
95 through April and typically spawn in March through June. The majority of juveniles rear in
96 freshwater for 2 years prior to migrating to sea as smolts where they spend 2 to 6 years feeding

97 and growing before returning to freshwater as sexually mature adults to initiate spawning (i.e.,
98 they reach sexual maturity at age three through eight; ~82% mature at age four or five). Scale
99 samples taken from wild steelhead indicate that, on average, 9% of returning adults are repeat
100 spawners. These fish then spend a year at sea before returning again to freshwater to spawn
101 again.

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

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

120 we obtained the observed maximum of daily peak flows occurring from October through March
121 of the first freshwater rearing year, and the minimum of low summer flows occurring from June
122 through September of the first summer of freshwater rearing.

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

134 From a management standpoint, we were interested in the possible effect of hatchery-
135 reared juvenile steelhead on the productivity of wild steelhead. The Washington Department of
136 Fish and Wildlife operates a “segregated” steelhead hatchery program (*sensu* Mobrand *et al.*
137 2005) that uses broodstock from a non-local source intentionally bred for early spawning, with
138 the goal of minimizing temporal reproductive overlap with wild fish and hence minimizing gene
139 flow into the wild population. Over the time series, hatchery fish were typically reared to age-1
140 and released in the spring (April or May) from multiple locations in the Skagit Basin. We
141 hypothesized that hatchery fish would have the greatest potential for conspecific ecological
142 interactions during the time juvenile steelhead are migrating to sea because observations at a

143 juvenile fish trap (river km 27) indicate they overlap in time and space. Therefore, we assumed
144 that a cohort born in year t would interact with hatchery fish released in year $t + 2$. We used the
145 total number of juveniles released from the hatchery within a given year as our covariate.

146 INTEGRATED POPULATION MODEL

147 The IPM we describe here expands upon models developed by others (e.g., Su &
148 Peterman 2012; Fleischman *et al.* 2013; Winship, O'Farrell & Mohr 2014) in that we include the
149 effects of extrinsic drivers on population dynamics. As with other IPMs, our model comprises
150 two major components: a process model describing the production of age-specific offspring, and
151 observation models to account for errors in the estimates of spawning escapement and age
152 composition. Following other, more traditional analyses of Pacific salmon population dynamics,
153 our modeling framework also assumes no consistent bias in estimates of adult spawners or age
154 composition of returning adults.

155 We begin with our process model where the number of offspring born in year t that
156 survive to adulthood (R_t) equals the product of a nonlinear function of the number of spawning
157 adults (S_t) and a time-varying stochastic error ε_t :

$$158 \quad R_t = f(S_t | \boldsymbol{\Theta}) e^{\varepsilon_t}. \quad (1)$$

159 Here we consider two different forms for f : the Ricker model (Ricker 1954) and the Beverton-
160 Holt model (Beverton & Holt 1957); see Fig. 1 for model forms and descriptions of their
161 parameters and associated reference points.

162 The process errors (ε_t) are often assumed to be independent draws from a Gaussian
163 distribution with a mean of zero and an unknown variance. However, the stochastic
164 environmental drivers that the ε_t are meant to represent typically show relatively strong

165 autocorrelation over time. Thus, we compared two different distributional forms for ε_t with non-
166 zero, autocorrelated means. In the first, we assumed that

167 $\varepsilon_t \sim \text{Normal}(\phi\varepsilon_{t-1}, \sigma_\varepsilon),$ (2a)

168 $\varepsilon_0 \sim \text{Normal}\left(0, \frac{\sigma_\varepsilon}{1-\phi^2}\right).$ (2b)

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

171 $\varepsilon_t \sim \text{Normal}(\mu_t + \phi\varepsilon_{t-1}, \sigma_\varepsilon)$ (3a)

172 $\mu_t = \sum_{i=1}^K \gamma_i X_{i,t+h_i}$ (3b)

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

176 The estimated numbers of fish of age a returning in year t ($N_{a,t}$) is then product of the
177 total number of brood-year recruits in year $t-a$ from Equation (1) and the proportion of mature
178 fish from that brood year that returned to spawn at age a ($\pi_{a,t-a}$), such that

179 $N_{a,t} = R_{t-a} \pi_{a,t-a}.$ (4)

180 Adult steelhead from the Skagit River return as 3-8 year-olds, and therefore the vector of age-
181 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
182 hierarchical random effect whereby $\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\eta} \tau)$. The mean vector $\boldsymbol{\eta}$ is also distributed as a
183 Dirichlet; the precision parameter τ affects each of the elements in $\boldsymbol{\eta}$ such that large values of τ
184 result in $\boldsymbol{\pi}_t$ very close to $\boldsymbol{\eta}$ and small values of τ lead to much more diffuse $\boldsymbol{\pi}_t$.

185 The spawner-recruit models above describe a process based on the true number of
186 spawners, but our estimates of the numbers of spawning adults necessarily contain some
187 sampling errors due to incomplete censuses, pre-spawn mortality, etc. Therefore, we assumed

188 that our estimates of escapement, the number of adult fish that “escape the fishery” and
189 ultimately spawn (E_t), are log-normally distributed about the true number of spawners (S_t):

190 $\ln(E_t) \sim \text{Normal}(\ln(S_t), \sigma_s)$. (5)

191 Catches of wild steelhead are closely recorded by state and tribal biologists, and so we
192 assume the harvest is recorded without error. We then calculate S_t as the difference between the
193 estimated total run size (N_t) and harvest (H_t), where

194 $S_t = N_t - H_t$, (6)

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

196 We obtained observations of the number of fish in each age class a in year t ($O_{a,t}$) from
197 scale analyses of 10 – 408 adults per year; no scale samples were taken in 1978-1982, 1984, and
198 2000. These data were assumed to arise from a multinomial process with order Y_t and proportion
199 vector \mathbf{d}_t , such that

200 $\mathbf{O}_t \sim \text{Multinomial}(Y_t, \mathbf{d}_t)$. (7)

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

203 $Y_t = \sum_{a=3}^8 O_{t,a}$. (8)

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

206 $d_{a,t} = \frac{N_{a,t}}{\sum_{a=3}^8 N_{a,t}}$. (9)

207 We used Bayesian inference to estimate all model parameters and the unobserved true
208 numbers of spawners and offspring over time. We used the freely available **R** software (v3.6, R
209 Development Core Team 2019) combined with the JAGS software (v4.2.0, Plummer 2003) to
210 perform Gibbs sampling with 4 parallel chains of 5×10^5 iterations. Following a burn-in period of

211 2.5×10⁵ iterations, we thinned each chain by keeping every 400th sample to eliminate any
212 possible autocorrelation, which resulted in 5000 samples from the posterior distributions. We
213 assessed convergence and diagnostic statistics via the ‘CODA’ package in R (Plummer *et al.*
214 2006). Specifically, we used visual inspection of trace plots and density plots, and verified that
215 Gelman and Rubin’s (2017) potential scale reduction factor was less than 1.1, to ensure adequate
216 chain mixing and parameter convergence. Data support for each model was evaluated using
217 leave-one-out cross-validation (LOO) based upon Pareto-smoothed importance sampling
218 (Vehtari, Gelman & Gabry 2017) as implemented in the ‘loo’ package (Vehtari *et al.* 2019). All
219 of the code and data files necessary to replicate our analyses are available in the online
220 supporting material and at https://github.com/mdscheuerell/skagit_sthd.

221 **Results**

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

228 The population dynamics of steelhead in the Skagit River are currently under density-
229 dependent regulation, despite their numbers being well below historical censuses, and there is
230 considerable uncertainty in the relationship between spawning adults and their surviving
231 offspring (Fig. 3). The median of α (i.e., the slope of the relationship at the origin) was 6.8
232 offspring per spawner, but a lack of data at low spawner abundance led to considerable
233 uncertainty in the estimate (Fig. 3b). The lower 95% credible interval was about 1.5 offspring per

234 spawner, which is still above replacement, while the upper 95% credible interval was 44
235 offspring per parent. On the other hand, our estimates of carrying capacity (K) were much more
236 precise, with a median of about 7400 adults and 95% credible interval of approximately 6100 to
237 10 900 adults (Fig. 3c).

238 There were varying effects of the three environmental covariates on population
239 productivity (Fig. 4). Peak winter flows were negatively related to survival, suggesting high
240 discharge events may transport juveniles downstream to lower quality habitats, or lead to direct
241 mortality from channel avulsion or movement of sediment, wood, and other debris. The median
242 of the posterior distribution was -0.11 (Fig. 4e), which means that a 1 SD increase in flow above
243 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
244 per parent. Conversely, the effect of low summer flows was positive (Fig. 4f), possibly indicative
245 of greater rearing habitat (the median estimate was 0.08 with a 95% credible interval of -0.09 to
246 0.25). The NPGO had a similar effect to summer flow (Fig. 4g), suggesting warmer waters in the
247 North Pacific are better for steelhead survival (median equals 0.09 with a 95% credible interval
248 of -0.08 to 0.27).

249 We also found that the number of hatchery juveniles released into the river during the
250 time that wild juveniles were migrating to sea was negatively related to productivity (Fig. 4h).
251 The median effect size was -0.20, which means that a 1 SD increase in the number of hatchery
252 juveniles released (i.e., from 328 000 to 452 000 fish) would, on average, result in a 18%
253 decrease in survival to adulthood. Notably, hatchery production experienced three distinct phases
254 over time (Fig. 4d): a low period between brood year 1978 and 1990 (range = 125 000 to 340
255 000 smolts), an increasing and high period between 1991 and 2005 (range = 314 000 to 584
256 000), and a decreasing period beginning in 2006 (range = 0 to 240 000 smolts).

257 The remaining, unexplained environmental variance was indeed highly autocorrelated
258 over time (Fig. 5). The process residuals were generally positive during the late 1970s and early
259 1980s when the population was growing (Fig. 2), they were near zero during the stable period of
260 the 1990s, and then largely negative as the population primarily declined through the 2000s.

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

268 **Discussion**

269 In territorial species such as steelhead trout, competition for limited resources commonly
270 results in density dependent growth and survival amongst juveniles (Imre, Grant & Keeley
271 2004). Our analysis suggests that such effects have scaled up to the entire population level to
272 govern patterns of steelhead productivity in the Skagit River basin. Importantly, we found strong
273 evidence for density dependent interactions despite the fact that contemporary population
274 censuses are well below historical estimates (Gayeski, McMillan & Trotter 2011). Similar results
275 have been observed in populations of coho salmon *Oncorhynchus kisutch* Walbaum 1792 in
276 Oregon (Buhle *et al.* 2009) and in populations of Chinook salmon *Oncorhynchus tshawytscha*
277 Walbaum 1792 in Idaho (Thorson *et al.* 2013). Although we cannot be certain of the exact life-
278 stage at which density dependent processes occurred, the freshwater juvenile stage seems likely
279 given the extended duration of freshwater rearing typical for this species. When steelhead

280 populations reach low numbers, the spatial contraction of spawners may exacerbate the effects of
281 density dependence because their newly emerged offspring do not have the mobility to access
282 other vacant habitats (Atlas *et al.* 2015). The evidence for density dependence presented here,
283 combined with the substantial loss of juvenile rearing habitat in the Skagit River basin (Beechie,
284 Beamer & Wasserman 1994), suggests that habitat restoration efforts, such as reconnecting
285 floodplain habitats and improving riparian functioning (Beechie, Pess & Roni 2008), may benefit
286 this population of steelhead.

287 Fluctuating environments can also affect population dynamics through density
288 independent mechanisms, and anadromous salmon must contend with many different and
289 unpredictable habitats over their lifespan. Our results indicate that in the freshwater environment,
290 large flow events during winter negatively affect steelhead productivity. Unfortunately, this may
291 portend an uncertain future for these fish. In a recent study, Lee *et al.* (2015) estimated that
292 future climate change in the Skagit River basin would create increased winter flows. These
293 changes in hydrology will likely result in much greater exposure of steelhead to extreme high
294 flow events due to their duration, intensity, and timing (Wade *et al.* 2013). Other evidence
295 already exists that freshwater discharge from Puget Sound rivers has become much more
296 variable, with notable negative effects on Chinook salmon *Oncorhynchus tshawytscha* Walbaum
297 1792 (Ward *et al.* 2015). Furthermore, although we found a somewhat weaker relationship
298 between low summer flow and productivity, extreme low-flow events are projected to occur at a
299 higher frequency in the future (Lee *et al.* 2015).

300 We found evidence of positive effects of NPGO on survival, which comports with
301 previous studies that have made rather compelling cases for a strong positive relationship
302 between the NPGO and salmon survival (Kilduff *et al.* 2015). The NPGO is a synoptic measure

303 of ocean conditions over a large region of the North Pacific Ocean (Kilduff *et al.* 2015), so we
304 cannot say where and when, exactly, the effects of the ocean environment most manifest
305 themselves. Recent evidence also indicates that steelhead smolts suffer high mortality during
306 their relatively brief migration through Puget Sound (Moore *et al.* 2015), possibly due to
307 predation by marine mammals (Berejikian, Moore & Jeffries 2016). Notably, too, the residual
308 process errors not captured by our covariates (w_t in Equation 1) were correlated with the
309 estimated marine survival of Skagit River hatchery steelhead (median Pearson's correlation
310 coefficient = 0.29; 95% credible interval = [0.03, 0.50]), suggesting marine processes not
311 captured by our covariates likely influenced productivity.

312 Among the various mitigation measures to address salmon declines, artificial propagation
313 of salmon has been used widely for more than a century. Nevertheless, research in other river
314 systems points to negative ecological effects of hatchery fish on wild Pacific salmon, including
315 populations coho salmon (Buhle *et al.* 2009), and Chinook salmon (Levin, Zabel & Williams
316 2001). Our results provide further evidence that large releases of hatchery-reared juvenile
317 steelhead have had a negative effect on productivity of wild steelhead, although we note some
318 researchers have used an approach similar to ours and found no hatchery effect on productivity
319 (Courter *et al.* 2019; Nelson *et al.* 2019). Our study was unable determine the mechanism
320 responsible for the correlation between hatchery releases and wild steelhead productivity. In fact,
321 very few empirical studies have been conducted at the appropriate spatial and temporal scales
322 necessary to directly quantify the hypothesized mechanisms by which negative ecological
323 interactions between hatchery and wild fish may occur (Weber & Fausch 2003). That said,
324 however, competition for limiting freshwater food and habitat resources (Berejikian *et al.* 2000)
325 is a plausible mechanism, either during the relatively brief period of overlap during downstream

326 migration (ca. 2 – 4 weeks), or a more prolonged effect of any hatchery fish that do not migrate
327 to sea, but instead “residualize” within freshwater. Additionally, predators are known to respond
328 numerically to their prey, and it is possible that large numbers of hatchery fish attracted
329 additional predators (Kostow 2009). Although breeding by hatchery individuals that stray onto
330 natural spawning grounds may reduce the fitness of a wild population via gene flow from the
331 hatchery stock into the wild population (Araki, Cooper & Blouin 2009), our study only
332 considered within-cohort effects. Thus, it seems unlikely that a trans-generational genetic effect
333 was the mechanism for the observed negative association between hatchery releases and wild
334 productivity.

335 Throughout the Puget Sound region, steelhead have been exposed to varying degrees of
336 influence by hatchery fish over the past 100 years, but they share the marine rearing
337 environment, and thus have experienced relatively similar ocean conditions during the same time
338 period. The marked decreases in abundance observed in many of these populations from the late
339 1980s to the late 2000’s, including the Skagit, mirrors observations of a general declining trend
340 in marine survival of hatchery conspecifics across the same time period, suggesting some larger,
341 unmeasured forces have been at work (Kendall, Marstrom & Klungle 2017). Furthermore, in
342 response to the declining abundance of wild Skagit River steelhead coupled with declining
343 marine survival of hatchery steelhead, fisheries managers increased hatchery production to
344 replace lost fishing opportunities. Thus, it is plausible that declining wild productivity was
345 simply coincident with higher hatchery production, rather than a consequence of it. It is also
346 possible that multicollinearity among measured and unmeasured covariates increased the
347 estimated effect sizes.

348 The life history complexity of steelhead may not lend well to the use of traditional
349 spawner recruit models such as the forms used in this study. Notably, steelhead exhibit
350 significant phenotypic plasticity with respect to adopting partial migration strategies, with
351 unknown proportions of a given cohort adopting a non-anadromous resident life history type
352 (Kendall *et al.* 2015). Given that only anadromous individuals are included in the annual
353 derivation of age structured abundance, there may be a large component of each cohort that is
354 missed which likely resulted in substantial observation error not captured in our models.
355 Therefore, caution should be used when interpreting the spawner recruit relationships and
356 resulting management reference points presented here. Furthermore, future research should aim
357 at quantifying the contribution of individuals adopting the resident life history type to overall
358 productivity. Without these estimates, accurate assessments of the status of steelhead populations
359 may not be possible. The “precautionary approach” to fisheries management aims to balance the
360 trade-off between catch and the risk of over-fishing such that minimizing the risk of overfishing
361 takes precedence (Hilborn *et al.* 2001). Our Bayesian state-space model provides a formal means
362 for estimating the probability of fishing in a sustainable manner. We found compelling evidence
363 that harvest rates for wild steelhead in the Skagit River basin over the time period considered
364 here have been well below those that would drive the population toward extinction. This result,
365 combined with the strong indication of density dependence, lends further support to the notion
366 that habitat improvements may benefit this population most. However, some caution is warranted
367 because we may have overestimated the biological reference points by not fully accounting for
368 repeat spawners.

369 Here we have demonstrated how to use incomplete information about the abundance and
370 age structure of a population to estimate density dependent population dynamics in light of

371 natural and human-induced variability in the environment. Our study adds to the growing body
372 of evidence that habitat, hatchery practices, and environmental variability are intricately linked in
373 affecting productivity of wild Pacific salmon stocks. Future research should focus on quantifying
374 habitat limitation on productivity at specific life stages to better focus restoration actions needed
375 to recover wild steelhead. Our modeling framework also allowed us to assess the degree to which
376 hatchery and harvest management actions are likely to affect the long-term viability of the
377 population. Our results suggest that hatchery program goals for steelhead need to be considered
378 carefully with respect to recovery goals and the quantity and quality of steelhead habitat. If
379 releases of non-local origin hatchery steelhead have indeed limited the production potential of
380 wild steelhead, there are likely significant tradeoffs between providing harvest opportunities via
381 hatchery steelhead production and achieving wild steelhead recovery goals.

382 **Acknowledgements**

383 We thank Eric Buhle and Jim Thorson for helpful discussions about model development. We
384 also thank Rebecca Bernard, Pete Kairis, Brett Barkdull, Andrew Fowler, and numerous WDFW,
385 Sauk-Suiattle, Swinomish, and Upper Skagit tribal biologists who compiled the escapement and
386 age data. Annette Hoffman, Dan Rawding, Kris Ryding, and James Scott provided constructive
387 criticism. This research was funded in part by a NOAA Fisheries And The Environment (FATE)
388 grant (#15-01), and an Environmental Protection Agency Tribal Capacity grant (#PA-00J320-
389 01).

390 **Authors' Contributions**

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

394 **Data Accessibility**

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

400 The river flow data are available from the United States Geological Survey National Water
401 Information System (<http://waterdata.usgs.gov/nwis>). The North Pacific Gyre Oscillation data
402 are available from Emanuele Di Lorenzo at Georgia Technical University
403 (<http://www.o3d.org/npgc/>).

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FIGURES

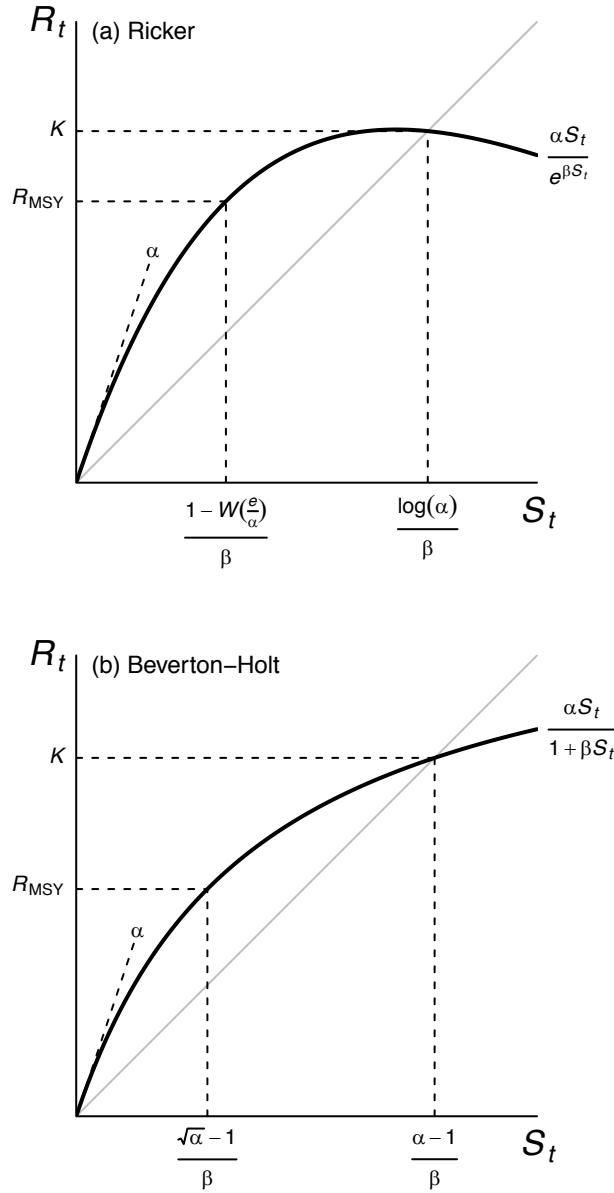


Figure 1. Deterministic forms of the (a) Ricker and (b) Beverton-Holt models used in the analyses (thick lines), including equations for carrying capacity (K) and the number of recruits corresponding to the maximum sustained yield (R_{MSY}). The parameter α defines the slope at the origin, the constant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

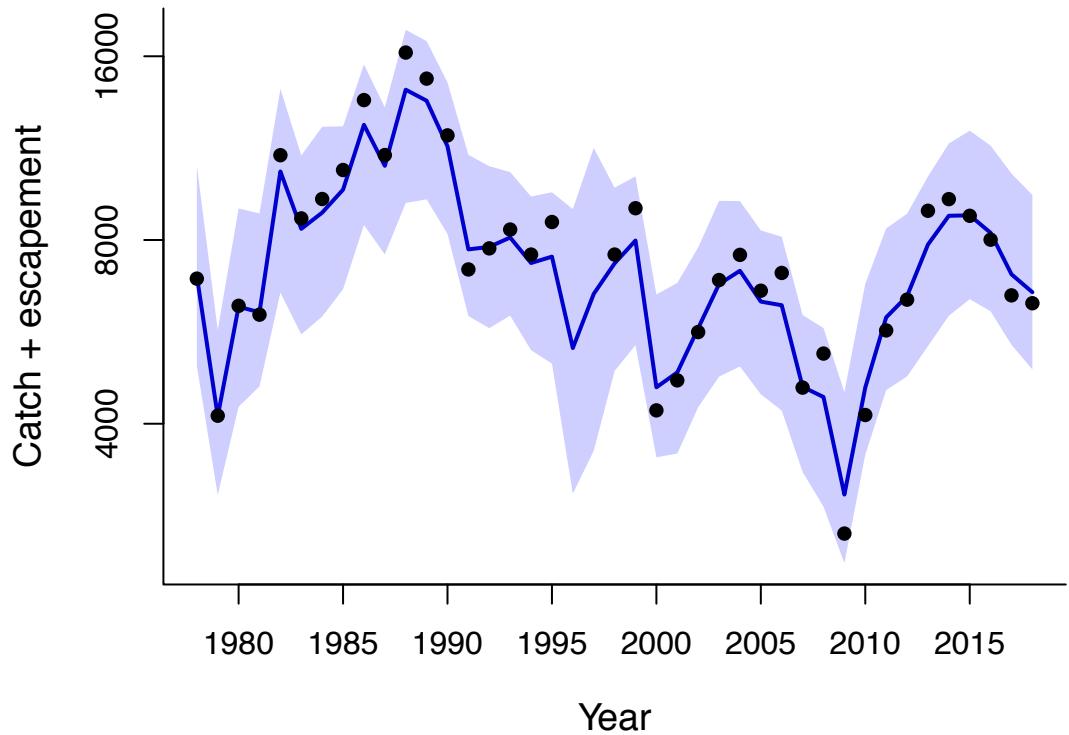


Figure 2. Time series of the estimated total population size (catch plus the adults that escaped to spawn). The observed data are the points; the solid line is the median estimate and the shaded region indicates the 95% credible interval.

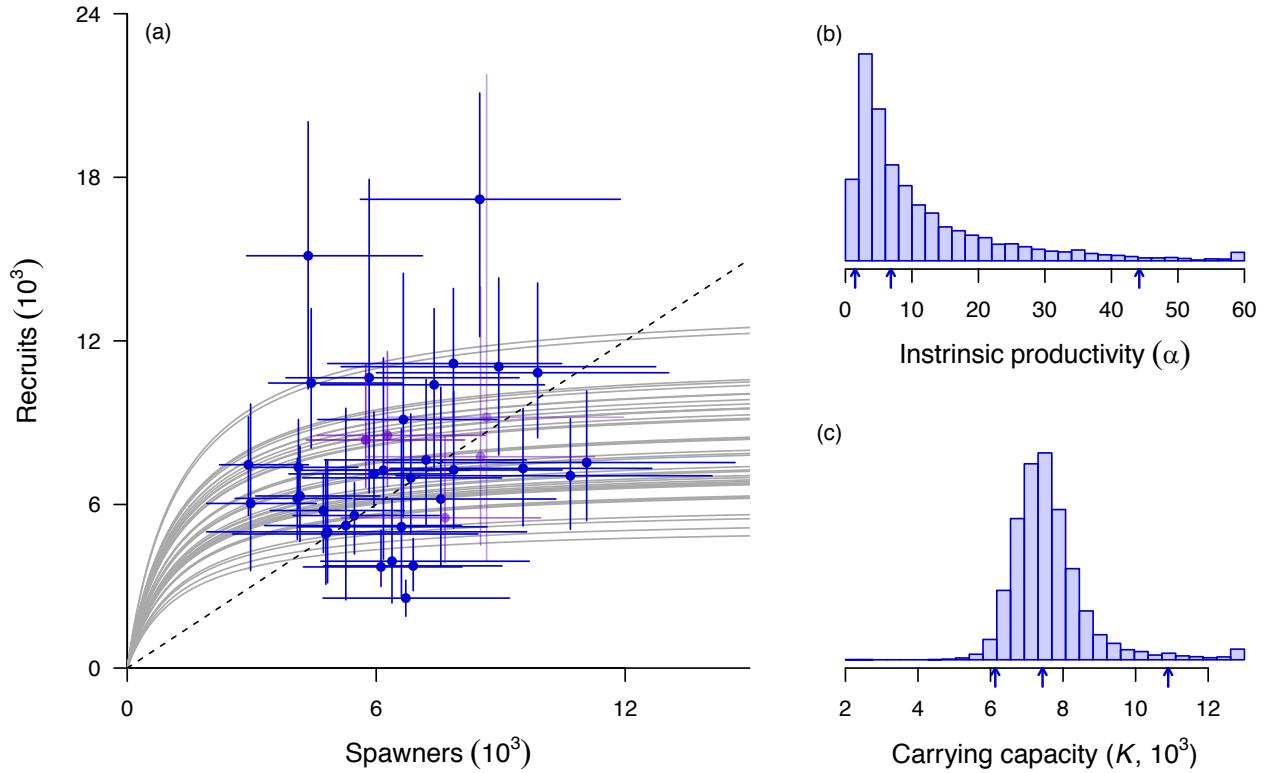


Figure 3. Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming mean values for all covariates (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the posterior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

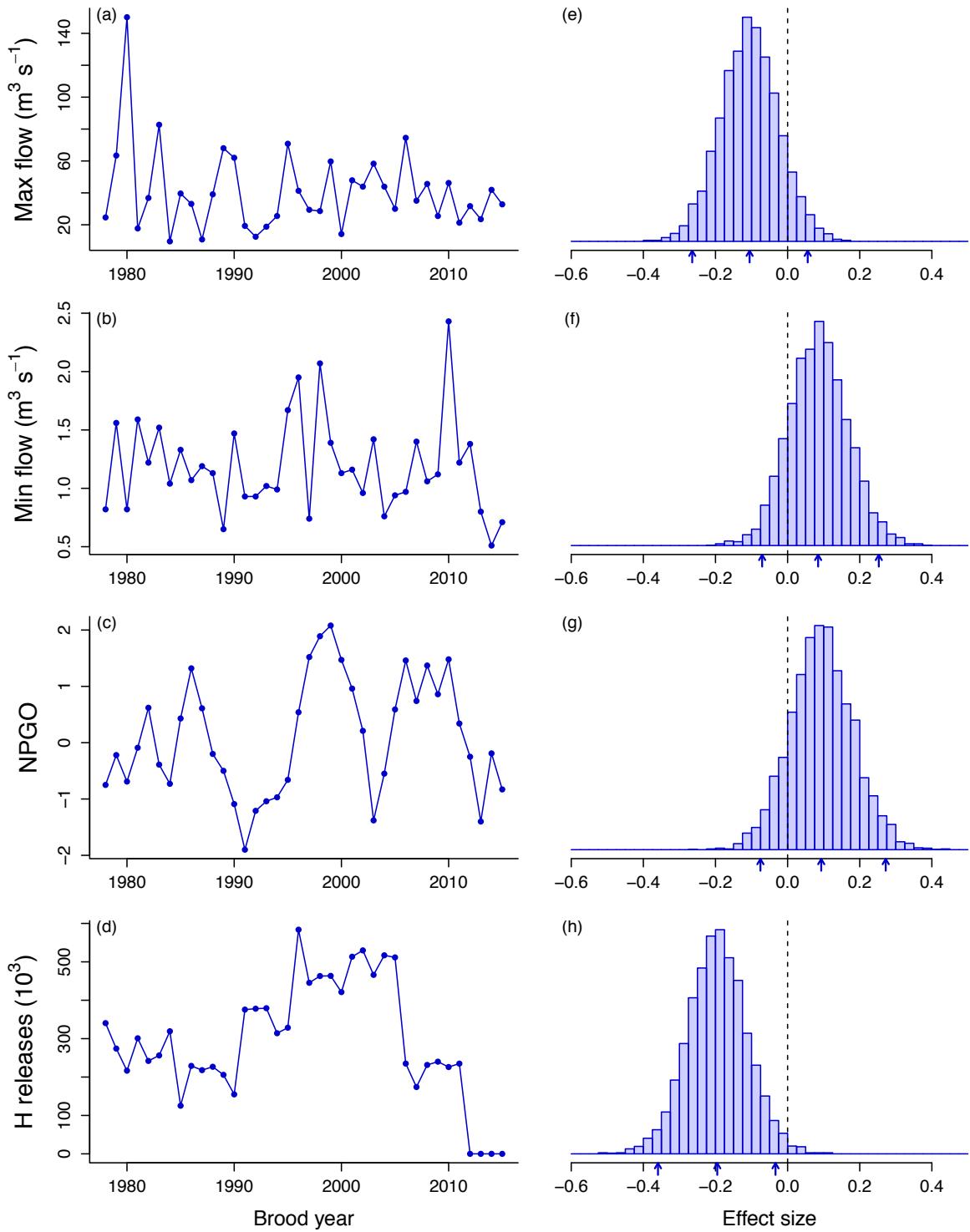


Figure 4. Time series of the environmental covariates used in the model (a-d), and their standardized effects on population productivity (e-g). Small arrows under histograms denote the 2.5th, 50th, and 97.5th percentiles of the posterior distribution.

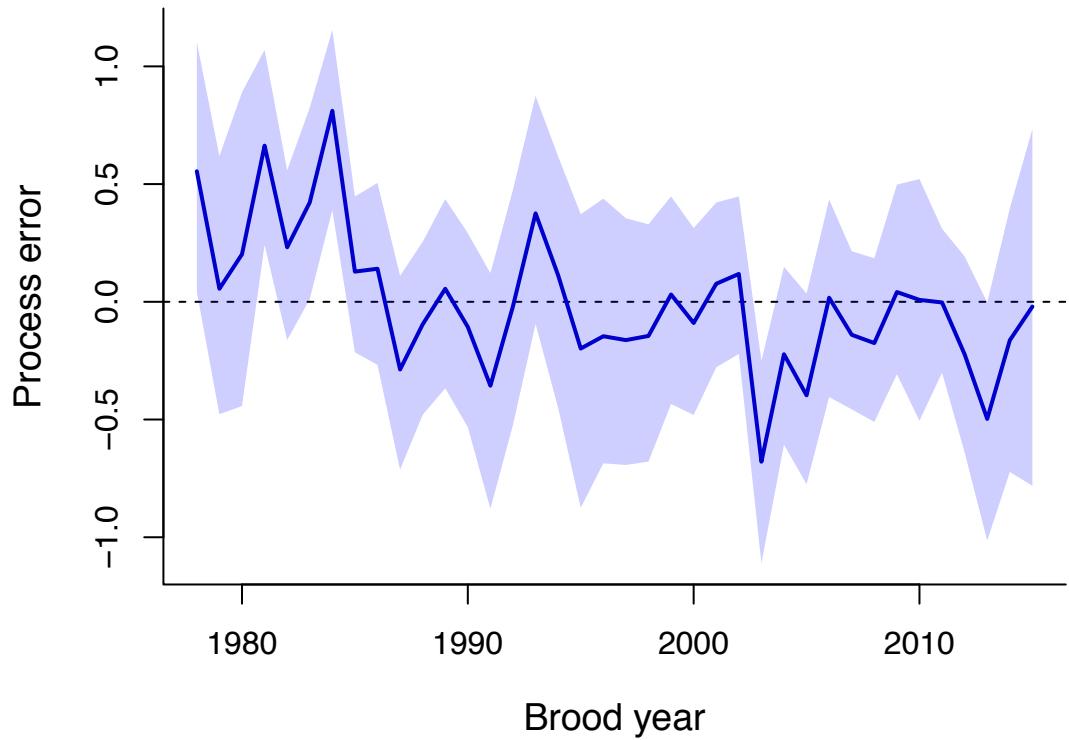


Figure 5. Time series of the estimated process errors, which represent the population's productivity after accounting for the effects of density dependence and environmental covariates. The solid line is the median estimate and the shaded region indicates the 95% credible interval.

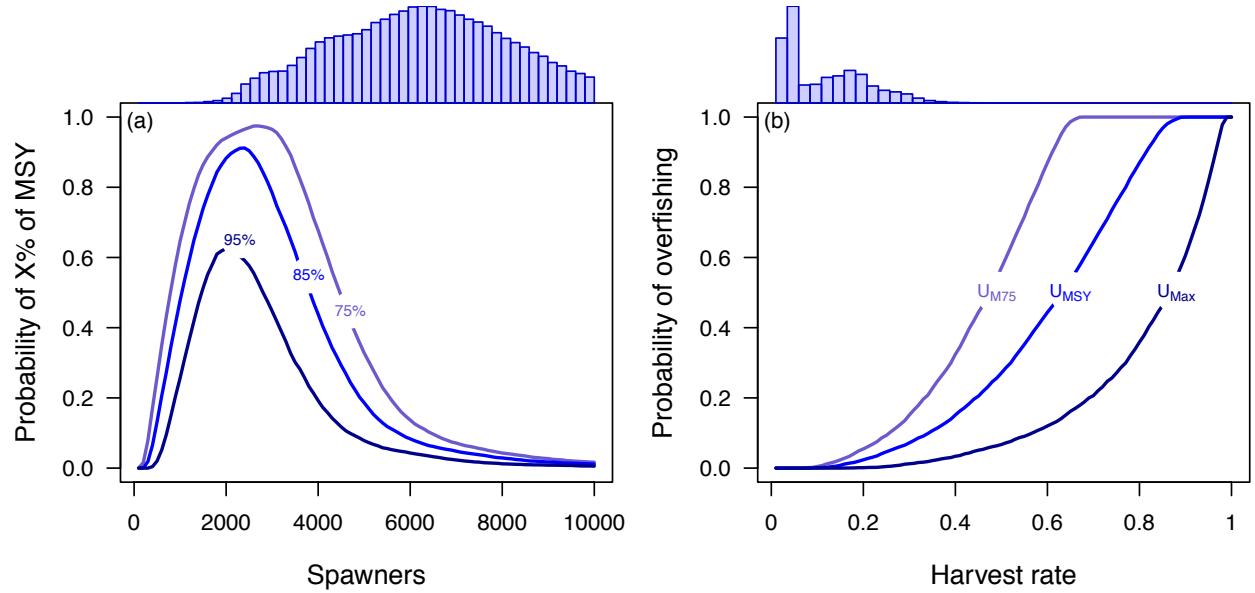


Figure 6. Plots of (a) the probability that a given number of spawners produces average yields achieving 95%, 85%, or 75% of the estimated maximum sustainable yield (MSY); and (b) the cumulative probability of overfishing the population, based on harvest rates equal to those at 75% of MSY, at MSY, and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