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 programs for steelhead need to be considered carefully with respect to habitat availability and recovery goals for wild steelhead. If releases of hatchery steelhead have indeed

24   limited the production potential of wild steelhead, there are likely significant tradeoffs between

25   providing harvest opportunities via hatchery steelhead production, and achieving wild steelhead

26   recovery goals. Furthermore, harvest rates on wild fish have been sufficiently low to ensure very

27   little risk of overfishing.

28   **KEYWORDS**

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

INTRODUCTION

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

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

53   about future responses of populations should begin with an attempt to fully account for the

54   uncertainty in population-environment relationships based on all of the current information.

55   Many populations of Pacific salmon (*Oncorhynchus* spp.) throughout the northwestern

56   United States have declined markedly since the early 1900s due to a variety of causes such as

57   habitat alteration, hydropower development, and overharvest (Ruckelshaus *et al.* 2002). For

58   conservation purposes, Pacific salmon species are grouped into evolutionarily significant units

59   (ESU, Waples 1991); 28 of the 49 extant ESUs of Pacific salmon are currently listed as

60   "threatened" or "endangered" under the U.S. Endangered Species Act. As a result, a number of

61   life-cycle models have been developed to evaluate the possible future benefits of conservation

62   actions such as habitat restoration (e.g., Scheuerell *et al.* 2006) and the potentially negative

63   consequences of climate change (e.g., Zabel *et al.* 2006). However, these models were assembled

64   by first obtaining parameter values from the literature, or estimating them from disparate data

65   sources, and then putting all of the pieces together post hoc. Consequently, they do not reflect a

66   comprehensive assessment of the total uncertainty in population demographics.

67   More recently however, researchers have turned toward integrated population models

68   (IPMs) as a means to convey the combined uncertainty in all of the data sources, which is

69   particularly important in a conservation context (Buhle *et al.* 2018; Zipkin & Saunders 2018).

70   IPMs are similar to state-space models in that they have specific sub-models for 1) describing the

71   stochastic and unobservable population dynamics; and 2) addressing the noisy, incomplete data

72   (Schaub & Abadi 2011; Yen *et al.* 2019). Although IPMs have been widely developed and

73   applied to mammals (e.g., Regehr *et al.* 2018) and birds (e.g., Saunders, Cuthbert & Zipkin

74   2018), there are very few examples for Pacific salmon (cf., Buhle *et al.* 2018).

75   Here we combine incomplete data on adult abundance, age composition, and harvest into

76   a Bayesian IPM to answer important questions relevant to management of a threatened

77   population of anadromous steelhead trout *Oncorhynchus mykiss* Walbaum 1792 from the Skagit

78   River basin, which drains ~6900 km^2 in southwestern Canada and northwestern United States.

79   Specifically, we used 39 years of age structured abundance data (1978-2018) to quantify the

80   degree of density dependence and the effects of a specific suite of environmental drivers on

81   intrinsic productivity (ie., recruits per spawner in the absence of density-dependence). We found

82   that although recent population censuses are well below historical estimates, the population still

83   operates under relatively strong density dependence. We also found that streamflow during

84   winter and releases of hatchery-reared juvenile steelhead were negatively related to wild

85   steelhead productivity, but that productivity was positively related to streamflow during summers

86   as juveniles and sea-surface temperatures experienced as adults in the North Pacific. In light of

87   remaining uncertainty in the factors governing the population dynamics of Skagit River

88   steelhead, this modelling framework is an effective tool for setting near term recovery goals and

89   evaluating population level response recovery actions.

90   **MATERIALS AND METHODS**

91   **Study species and data**

92   The Skagit River system is predominantly a glacially fed system that consists of a

93   combination of rain, snow-transitional, and snow-dominated tributaries providing approximately

94   48 km^2 of potential habitat suitable for spawning and rearing by wild steelhead (Hard *et al.*

95   2015). We use the term "wild" to describe steelhead produced by naturally spawning adults

96   descended from the native population inhabiting the watershed. For this study, wild fish captured

97   in commercial fisheries that were either allocated to harvest or sampled for age composition were

98   identified by the presence of an intact adipose fin. Wild adult steelhead in the Skagit River

99   generally enter freshwater in November through April and typically spawn in March through

100   June. Based on 4,686 aged scale samples collected from returning wild adult steelhead captured

101   in commercial net fisheries, an average of 70% of returning adults comprising a given brood year

102   spent 2 years rearing in freshwater prior to migrating to sea as smolts (see Appendix S4 for more

103   details on scale aging). Following freshwater rearing, individuals spend two to six years feeding

104   and growing before returning to freshwater as sexually mature adults to initiate spawning (i.e.,

105   they reach sexual maturity at age three through eight; ~82% mature at age four or five). These

106   fish then spend a year at sea before returning to freshwater to spawn.

107   Due to a combination of logistical constraints, only a fraction of the known spawning

108   area was surveyed for wild spawners. Specifically, standardized index reach surveys were

109   conducted annually in only two of five major sub-basins and 13 of 63 tributaries known to

110   support wild steelhead production. A basin-wide estimate of wild spawners was generated

111   annually by expanding each survey to account for estimated available habitat not surveyed.

112   Redds or spawning nests constructed before approximately mid-March were not counted to avoid

113   inclusion of any naturally spawning hatchery-origin steelhead, which were purposely bred for

114   earlier spawn timing, or coho salmon in the abundance estimates (cf. Courter *et al.* 2019).

115   Fisheries biologists in the Skagit River basin generally consider the escapement estimates to be

116   conservative; it is more likely that escapement is underestimated than overestimated because

117   unobserved spawning sites would serve to increase abundance. Our analyses begin with surveys

118   in 1978 and continue through 2018.

119   In the model described below, we evaluate several environmental indicators of

120   productivity. Specifically, flow conditions experienced by juveniles during freshwater rearing

121   can have strong effects on their survival to adulthood via the following mechanisms: (1) spatial

122   contraction of habitat as a result of low summer flows and high water temperatures that coincide

123   with the period of highest metabolic demand (e.g., Crozier *et al.* 2010), and (2) habitat

124   displacement or direct mortality resulting from peak winter flows (e.g., Irvine 1986). Therefore,

125   we utilized long-term flow records from a gauge (#12178000) located in the mainstem Skagit

126   River (48.66 N, 121.246 W), and maintained by the United States Geological Survey (see

127   Appendix S1). Specifically, we obtained the observed maximum of daily peak flows occurring

128   from October through May of the first freshwater rearing year, and the minimum of low summer

129   flows occurring from June through September of the first summer of freshwater rearing.

130   Because conditions experienced by salmon and steelhead during their first year at sea are

131   thought to be critical to overall survival and growth of a given year class (Beamish & Mahnken

132   2001), we chose the average North Pacific Gyre Oscillation index (NPGO) from January through

133   December as an index of conditions experienced by juvenile steelhead during their first year in

134   the ocean. Variability in the NPGO reflects annual changes in coastal upwelling and ocean

135   circulation patterns that correlate strongly with primary and secondary production in coastal

136   ecosystems (Di Lorenzo *et al.* 2008). Furthermore, the NPGO has been recently identified as an

137   important indicator of early marine survival in other Pacific salmon species (Kilduff *et al.* 2015).

138   Because most juvenile steelhead from the Skagit River migrate to sea during the spring of their

139   second year, we lagged the NPGO indicator by two years beyond the birth year to reflect

140   conditions experienced during the first year at sea.

141   From a management standpoint, we were interested in the possible effect of hatchery-

142   reared juvenile steelhead on the productivity of wild steelhead. The Washington Department of

143   Fish and Wildlife operates a "segregated" steelhead hatchery program that uses broodstock from

144   a non-local source intentionally bred for early spawning, with the goal of minimizing temporal

145   reproductive overlap with wild fish and hence minimizing gene flow into the wild population.

146   Over the time series, hatchery fish were typically reared to age-1 and released in the spring

147   (April or May) from multiple locations in the Skagit Basin. We hypothesized that hatchery fish

148   would have the greatest potential for conspecific ecological interactions during the time juvenile

149   steelhead are migrating to sea because observations at a juvenile fish trap (river km 27) indicate

150   they overlap in time and space. Therefore, we assumed that a cohort born in year t would interact

151   with hatchery fish released in year $t + 2$. We used the total number of juveniles released from the

152   hatchery within a given year as our covariate.

153   **Integrated population model**

154   The number of offspring born in year t that survive to adulthood (R_t) equals the product

155   of a nonlinear function of the number of spawning adults (S_t) and a time-varying stochastic error

156   ε_t:

157
$$R_t = f(S_t|\boldsymbol{\theta})\, e^{\varepsilon_t}. \tag{1}$$

158   Here we consider three general forms for f: a density independent model where $f(S_t) = \alpha S_t$, and

159   two density dependent models (Ricker and Beverton-Holt model; Fig. 1).

160   The process errors (ε_t) are often assumed to be independent draws from a Gaussian

161   distribution with a mean of zero and an unknown variance. However, the stochastic

162   environmental drivers that the ε_t are meant to represent typically show relatively strong

163   autocorrelation over time. Thus, we compared two different distributional forms for ε_t with non-

164   zero, autocorrelated means. In the first, we assumed that

165
$$\varepsilon_t \sim \text{Normal}(\phi\varepsilon_{t-1}, \sigma_\varepsilon), \tag{2a}$$

166
$$\varepsilon_0 \sim \text{Normal}\left(0, \frac{\sigma_\varepsilon}{1-\phi^2}\right). \tag{2b}$$

167   Second, we considered models where the non-zero means were also a function of the

168 various environmental drivers important to salmon productivity as discussed above. In those

169 models,

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

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

172 Here, γ_i is the effect of covariate X_i measured at time t and shifted by an appropriate lag h_i based

173 on the life stage that the covariate would affect most strongly. We standardized all covariates to

174 have zero-mean and unit-variance to facilitate direct comparison of effect sizes.

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

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

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

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

179 Thus, in a table of the *true* numbers-at-age (columns) by calendar year (rows), $\pi_{a,t-a}$ has the effect

180 of apportioning the total recruits (R_{t-a}) into their appropriate age classes of future returns (i.e.,

181 values along a diagonal of the table). Adult steelhead from the Skagit River return as 3-8 year-

182 olds, and therefore the vector of age-specific return rates for brood year t is $\boldsymbol{\pi}_t = [\pi_3, \pi_4, \pi_5, \pi_6,$

183 $\pi_7, \pi_8]_t$, which we modeled as a hierarchical random effect whereby $\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\eta}\tau)$. The

184 mean vector $\boldsymbol{\eta}$ is also distributed as a Dirichlet; the precision parameter τ affects each of the

185 elements in $\boldsymbol{\eta}$ such that large values of τ result in $\boldsymbol{\pi}_t$ very close to $\boldsymbol{\eta}$ and small values of τ lead to

186 much more diffuse $\boldsymbol{\pi}_t$.

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

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

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

190   that our estimates of escapement, the number of adult fish that "escape the fishery" and

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

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

193   We cannot simultaneously estimate observation error for both escapement and harvest.

194   Therefore, because catches of wild steelhead are closely recorded by state and tribal biologists,

195   we assume the harvest is recorded without error. We then calculate S_t as the difference between

196   the estimated total run size (N_t) and harvest (H_t), where

197    $$S_t = N_t - H_t, \tag{6}$$

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

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

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

201   2000. These data were assumed to arise from a multinomial process with order Y_t and proportion

202   vector $\mathbf{d}_t$, such that

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

204   The order of the multinomial is simply the sum of the observed numbers of fish across all ages

205   returning in year t:

206    $$Y_t = \sum_{a=3}^{8} O_{t,a}\ . \tag{8}$$

207   Thus, if we have a table of the *observed* numbers-at-age (columns) by calendar year (rows),

208   summing across each row gives Y_t. In contrast, the proportion vector $\mathbf{d}_t$ for the multinomial is

209   based on the age-specific, model-derived estimates of adult returns in year t ($N_{a,t}$), such that

210    $$d_{a,t} = \frac{N_{a,t}}{\sum_{a=3}^{8} N_{a,t}}. \tag{9}$$

211   That is, if we consider the table of the *true* numbers-at-age (columns) by calendar year (rows)

212   generated via Eqn (4) above, the numerator of Eqn (9) comes from each of the individual

213   columns within a row, and the denominator is the sum across all columns.

214   We used Bayesian inference to estimate all model parameters and the unobserved true

215   numbers of spawners and offspring over time. We used the freely available **R** software (v3.6, R

216   Development Core Team 2019) combined with the JAGS software (v4.2.0, Plummer 2003) to

217   perform Gibbs sampling with 4 parallel chains of 5×10^5 iterations. Following a burn-in period of

218   2.5×10^5 iterations, we thinned each chain by keeping every 400th sample to eliminate any

219   possible autocorrelation, which resulted in 5000 samples from the posterior distributions. We

220   assessed convergence and diagnostic statistics via the 'CODA' package in **R** (Plummer *et al.*

221   2006). Specifically, we used visual inspection of trace plots and density plots, and verified that

222   Gelman and Rubin's (2017) potential scale reduction factor was less than 1.1, to ensure adequate

223   chain mixing and parameter convergence. Data support for each model was evaluated using

224   leave-one-out cross-validation (LOO) based upon Pareto-smoothed importance sampling as

225   implemented in the 'loo' package (Vehtari *et al.* 2019). All of the code and data files necessary

226   to replicate our analyses are available in the online supporting material and at

227   https://github.com/mdscheuerell/steelhead_IPM.

228   **RESULTS**

229   We found the most data support for the Beverton-Holt form of process model, so all of

230   the following results are based upon it (see Appendix S2 for full model selection results). Our

231   estimates of the total population size reflect the uncertainty in the estimated numbers of adults

232   over time, but the median values agreed quite well with the observed data (Fig. 2). As expected,

233　the 95% credible intervals were widest in 1996 and 1997 when there were no direct estimates of

234　spawning adults.

235　　The population dynamics of steelhead in the Skagit River are currently under density-

236　dependent regulation, despite their numbers being well below historical censuses, and there is

237　considerable uncertainty in the relationship between spawning adults and their surviving

238　offspring (Fig. 3). The median of α (i.e., the slope of the relationship at the origin) was 4.8

239　offspring per spawner, but a lack of data at low spawner abundance led to considerable

240　uncertainty in the estimate (Fig. 3b). The lower 95% credible interval was about 1.4 offspring per

241　spawner, which is still above replacement, while the upper 95% credible interval was 41

242　offspring per parent. On the other hand, our estimates of carrying capacity (K) were much more

243　precise, with a median of about 7700 adults and 95% credible interval of approximately 5900 to

244　12 800 adults (Fig. 3c).

245　　There were varying effects of the three environmental covariates on population

246　productivity (Fig. 4). Peak winter flows were negatively related to productivity, suggesting high

247　discharge events may transport juveniles downstream to lower quality habitats, or lead to direct

248　mortality from channel avulsion or movement of sediment, wood, and other debris. The median

249　of the posterior distribution was -0.13 (Fig. 4e), which means that a 1 SD increase in flow above

250　the mean (i.e., from ~41 m^3 s^{-1} to ~68 m^3 s^{-1}) would translate into a 12% decrease in offspring

251　per parent. On the other hand, the effect of low summer flows was essentially zero (Fig. 4f); the

252　median estimate was 0.08 with a 95% credible interval of -0.18 to 0.14. The NPGO had a largely

253　positive effect (Fig. 4g), suggesting warmer waters in the North Pacific are better for steelhead

254　productivity (median equals 0.12 with a 95% credible interval of -0.05 to 0.31.

255   We also found that the number of hatchery juveniles released into the river during the

256   time that wild juveniles were migrating to sea was negatively related to productivity (Fig. 4h).

257   The median effect size was -0.16, which means that a 1 SD increase in the number of hatchery

258   juveniles released (i.e., from 328 000 to 452 000 fish) would, on average, result in an 15%

259   decrease in productivity. Notably, hatchery production experienced three distinct phases over

260   time (Fig. 4d): a low period between brood year 1978 and 1990 (range = 125 000 to 340 000

261   smolts), an increasing and high period between 1991 and 2005 (range = 314 000 to 584 000), and

262   a decreasing period beginning in 2006 (range = 0 to 240 000 smolts).

263   The remaining, unexplained environmental variance was highly autocorrelated over time

264   (Fig. 5). The process residuals were generally positive during the late 1970s and early 1980s

265   when the population was growing (Fig. 2), they were near zero during the stable period of the

266   1990s, and then largely negative as the population primarily declined through the 2000s.

267   Based on our estimates of biological reference points, Skagit River steelhead appear to be

268   managed rather conservatively from a harvest management perspective. The optimal yield

269   profiles suggest it would take approximately 2000 to 3000 spawning adults to produce the

270   maximum sustainable yield (Fig. 6a), but very few years have ever fallen below that throughout

271   the time period presented here (i.e., the average number of spawning adults has been two to three

272   times greater). In other words, the realized harvest rates have been kept low enough to insure

273   very little risk of overfishing (Fig. 6b).

274   **DISCUSSION**

275   In territorial species such as steelhead trout, competition for limited resources commonly

276   results in density dependent growth and survival amongst juveniles (Imre, Grant & Keeley

277   2004). Our analysis suggests that such effects have scaled up to the entire population level to

14

278   govern patterns of steelhead productivity in the Skagit River basin. Importantly, we found strong

279   evidence for density dependent interactions despite the fact that contemporary population

280   censuses are well below historical estimates (Gayeski, McMillan & Trotter 2011). Similar results

281   have been observed in populations of coho salmon *Oncorhynchus kisutch* Walbaum 1792 in

282   Oregon (Buhle *et al.* 2009) and in populations of Chinook salmon *Oncorhynchus tshawytscha*

283   Walbaum 1792 in Idaho (Thorson *et al.* 2013). Although we cannot be certain of the exact life-

284   stage at which density dependent processes occurred, the freshwater juvenile stage seems likely

285   given the extended duration of freshwater rearing typical for this species. When steelhead

286   populations reach low numbers, the spatial contraction of spawners may exacerbate the effects of

287   density dependence because their newly emerged offspring do not have the mobility to access

288   other vacant habitats (Atlas *et al.* 2015). The evidence for density dependence presented here,

289   combined with the substantial loss of juvenile rearing habitat in the Skagit River basin (Beechie,

290   Beamer & Wasserman 1994), suggests that habitat restoration efforts, such as reconnecting

291   floodplain habitats and improving riparian functioning (Beechie, Pess & Roni 2008), may benefit

292   this population of steelhead.

293   Fluctuating environments can also affect population dynamics through density

294   independent mechanisms, and anadromous salmon must contend with many different and

295   unpredictable habitats over their lifespan. Our results are consistent with the notion that in the

296   freshwater environment, large flow events during winter negatively affect steelhead productivity.

297   Unfortunately, this may portend an uncertain future for these fish. In a recent study, Lee et al.

298   (2015) estimated that future climate change in the Skagit River basin would create increased

299   winter flows. These changes in hydrology will likely result in much greater exposure of

300   steelhead to extreme high flow events due to their duration, intensity, and timing (Wade *et al.*

301   2013). Other evidence already exists that freshwater discharge from Puget Sound rivers has

302   become much more variable, with notable negative effects on Chinook salmon *Oncorhynchus*

303   *tshawytscha* Walbaum 1792 (Ward *et al.* 2015). Furthermore, although we found a weak

304   relationship between low summer flow and productivity, extreme low-flow events are projected

305   to occur at a higher frequency in the future (Lee *et al.* 2015). That said, we also acknowledge

306   that modeling the effects of flow conditions from a single site within the Skagit River basin is

307   not representative of the complexity of flow conditions experienced by juvenile steelhead during

308   their first year of freshwater rearing.

309   We found evidence of positive effects of NPGO on productivity, which comports with

310   previous studies that have made rather compelling cases for a strong positive relationship

311   between the NPGO and salmon productivity (Kilduff *et al.* 2015). The NPGO is a synoptic

312   measure of ocean conditions over a large region of the North Pacific Ocean (Kilduff *et al.* 2015),

313   so we cannot say where and when, exactly, the effects of the ocean environment most manifest

314   themselves. Recent evidence also indicates that steelhead smolts suffer high mortality during

315   their relatively brief migration through Puget Sound (Moore *et al.* 2015), possibly due to

316   predation by marine mammals (Berejikian, Moore & Jeffries 2016). Notably, too, the residual

317   process errors not captured by our covariates (w_t in Equation 1) were correlated with the

318   estimated marine survival of Skagit River hatchery steelhead (median Pearson's correlation

319   coefficient = 0.29; 95% credible interval = [0.03, 0.50]), suggesting marine processes not

320   captured by our covariates likely influenced productivity.

321   Among the various mitigation measures to address salmon declines, artificial propagation

322   of salmon has been used widely for more than a century. Nevertheless, research in other river

323   systems points to negative ecological effects of hatchery fish on wild Pacific salmon, including

324 populations coho salmon (Buhle *et al.* 2009), and Chinook salmon (Levin, Zabel & Williams

325 2001). Our results provide further evidence that large releases of hatchery-reared juvenile

326 steelhead have had a negative effect on productivity of wild steelhead, although we note some

327 researchers have used an approach similar to ours and found no hatchery effect on productivity

328 (Courter *et al.* 2019; Nelson *et al.* 2019). Although we provide evidence for a correlation

329 between hatchery releases and wild steelhead productivity, we did not demonstrate causation nor

330 identify a causal mechanism. In fact, very few empirical studies have been conducted at the

331 appropriate spatial and temporal scales necessary to directly quantify the hypothesized

332 mechanisms by which negative ecological interactions between hatchery and wild fish may occur

333 (Weber & Fausch 2003). That said, competition for limiting freshwater food and habitat

334 resources (Berejikian *et al.* 2000) is a plausible mechanism, either during the relatively brief

335 period of overlap during downstream migration (ca. 2 – 4 weeks), or a more prolonged effect of

336 any hatchery fish that do not migrate to sea, but instead "residualize" within freshwater.

337 Additionally, predators are known to respond numerically to their prey, and it is possible that

338 large numbers of hatchery fish attracted additional predators (Kostow 2009). Although breeding

339 by hatchery individuals that stray onto natural spawning grounds may reduce the fitness of a wild

340 population via gene flow from the hatchery stock into the wild population (Araki, Cooper &

341 Blouin 2009), our study only considered within-cohort effects. Thus, it seems unlikely that a

342 trans-generational genetic effect was the mechanism for the observed negative association

343 between hatchery releases and wild productivity.

344 Throughout the Puget Sound region, steelhead have been exposed to varying degrees of

345 influence by hatchery fish over the past 100 years, but they share the marine rearing

346 environment, and thus have experienced relatively similar ocean conditions during the same time

347 period. The marked decreases in abundance observed in many of these populations from the late

348 1980s to the late 2000's, including the Skagit, mirrors observations of a general declining trend

349 in marine survival of hatchery conspecifics across the same time period, suggesting some larger,

350 unmeasured forces have been at work (Kendall, Marstrom & Klungle 2017). It is often difficult

351 to separate hatchery management from ocean conditions because both are autocorrelated and

352 slow to change over time. Indeed, the period of greatest Skagit River hatchery releases (brood

353 years 1991 – 2005) generally coincided with declining steelhead abundance in the Skagit River

354 and other nearby rivers. Furthermore, in response to the declining abundance of wild Skagit

355 River steelhead coupled with declining marine survival of hatchery steelhead, fisheries managers

356 increased hatchery production to replace lost fishing opportunities. Thus, it is plausible that

357 declining wild productivity was simply coincident with higher hatchery production, rather than a

358 consequence of it. It is also possible that multicollinearity among measured and unmeasured

359 covariates increased the estimated effect sizes.

360   The life history complexity of steelhead may not lend well to the use of traditional

361 spawner recruit models such as the forms used in this study. Steelhead exhibit significant

362 phenotypic plasticity with respect to adopting partial migration strategies, with unknown

363 proportions of a given cohort adopting a non-anadromous resident life history type (Kendall *et*

364 *al.* 2015). Given that only anadromous individuals are included in the annual derivation of age

365 structured abundance, there may be a large component of each cohort that is missed which likely

366 resulted in substantial observation error not captured in our models. We also may have

367 overestimated the biological reference points by not fully accounting for repeat spawners.

368 Furthermore, the adult abundance estimates are subject to a variety of spawning survey

369 assumptions; any tendency toward conservative, underestimates would be reflected in the

370　management reference points accordingly. Future research to increase the accuracy and precision

371　of abundance estimates, including quantifying the contribution of resident and repeat spawning

372　life history types, would improve reference point estimation. Without these estimates, accurate

373　assessments of the status of steelhead populations may not be possible, and we urge caution

374　when interpreting the spawner recruit relationships and resulting management reference points

375　presented here.

376　　　Our IPM also allowed us to assess the degree to which hatchery management actions are

377　likely to affect the long-term viability of the population. Our results suggest that hatchery

378　program goals for steelhead need to be considered carefully with respect to recovery goals and

379　the quantity and quality of steelhead habitat. If releases of non-local origin hatchery steelhead

380　have indeed limited the production potential of wild steelhead, there are likely significant

381　tradeoffs between providing harvest opportunities via hatchery steelhead production and

382　achieving wild steelhead recovery goals. IPMs have been used elsewhere to inform the adaptive

383　harvest management decision framework for American waterfowl (Arnold *et al.* 2018), and our

384　IPM provides a formal means for estimating the probability of fishing in a sustainable manner.

385　We found compelling evidence that harvest rates for wild steelhead in the Skagit River basin

386　over the time period considered here have been well below those that would drive the population

387　toward extinction. This result, combined with the strong indication of density dependence, lends

388　further support to the notion that habitat improvements may benefit this population most.

389　　　Two advantages of IPMs are 1) their ability to accommodate multiple data types of

390　varying quality, which reduces otherwise inherent biases when using a single data set; and 2)

391　more precise estimates of demographic rates than one would with a single data set (Zipkin,

392　Inouye & Beissinger 2019). IPMs can also be used to evaluate the effect of various management

393 actions, and provide decision-relevant information for conservation of at-risk populations, such

394 as coastal turtles in the eastern U.S. (Crawford *et al.* 2018). Here we used incomplete

395 information about the abundance and age structure of an at-risk fish population to estimate

396 density dependent population dynamics in light of natural and human-induced variability in the

397 environment. IPMs can also be used to identify data collection priorities that could reduce

398 uncertainty in parameter estimates (Saunders, Cuthbert & Zipkin 2018), and future research

399 could focus on the costs and benefits of different data types used in formal status evaluations of

400 at-risk Pacific salmon.

AUTHORS' CONTRIBUTIONS

411 MS, CR and JA conceived the ideas and designed methodology; MS and CR analysed the data;

412 MS and CR led the writing of the manuscript. All authors contributed critically to the drafts and

413 gave final approval for publication.

DATA AVAILABILITY STATEMENT

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

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580

FIGURE CAPTIONS

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

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

Figure 3. Relationship between the number of spawning adults and their subsequent surviving offspring (recruits), assuming mean values for all covariates (a); and the estimated posterior distributions for the intrinsic productivity (b) and carrying capacity (c). Points in (a) are medians of the posterior estimates; error bars indicate the 95% credible intervals. Blue points are for estimates with complete broods; purple points are for the most recent years with incomplete broods. Gray lines show the median relationship for each of the 41 years in the time series based on annual model estimates of productivity. Note that for plotting purposes only in (b) and (c), the density in the largest bin for each parameter contains counts for all values greater than or equal to it. Vertical arrows under the x-axes in (b) and (c) indicate the 2.5^{th}, 50th, and 97.5^{th} percentiles.
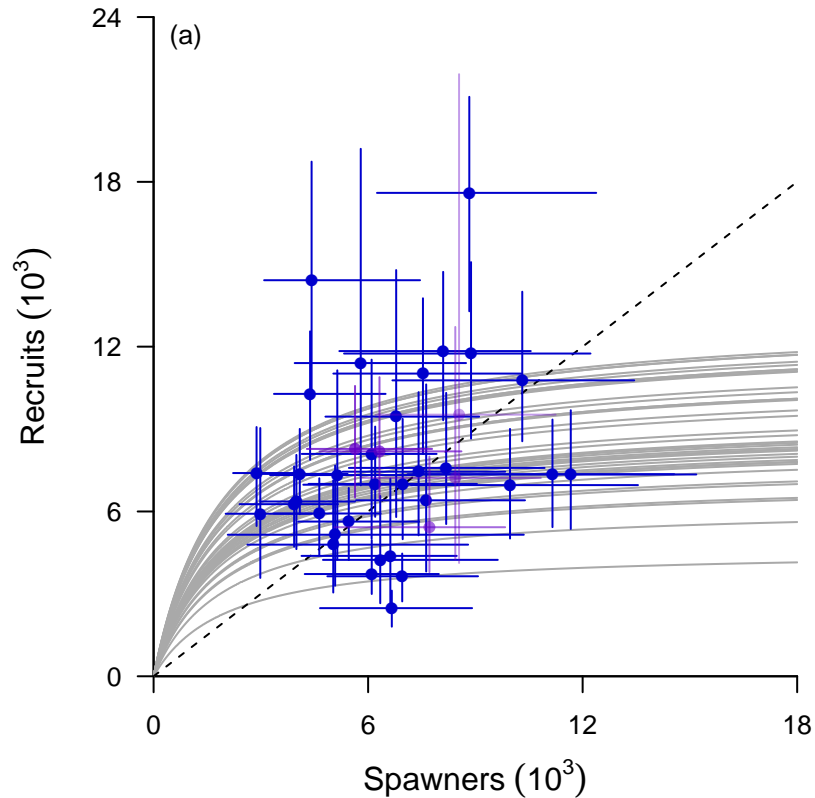
Figure 4. Time series of the environmental covariates used in the model (a-d), and their standardized effects on population productivity (e-g). Small arrows under histograms denote the 2.5^{th}, 50th, and 97.5^{th} percentiles of the posterior distribution.
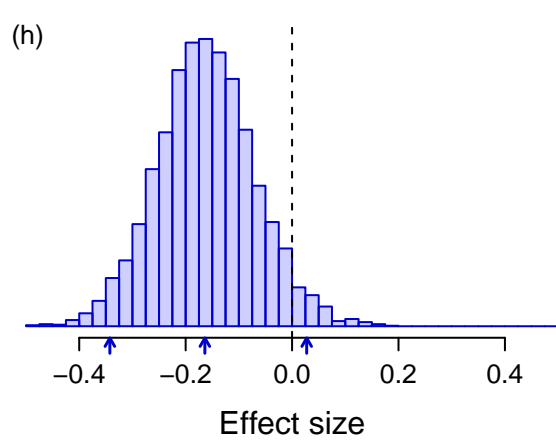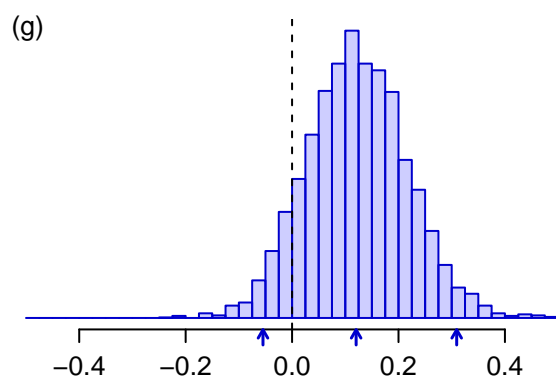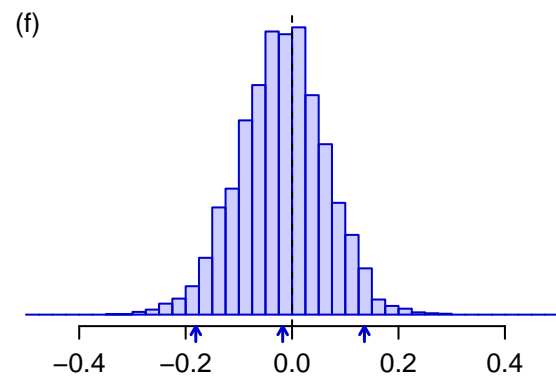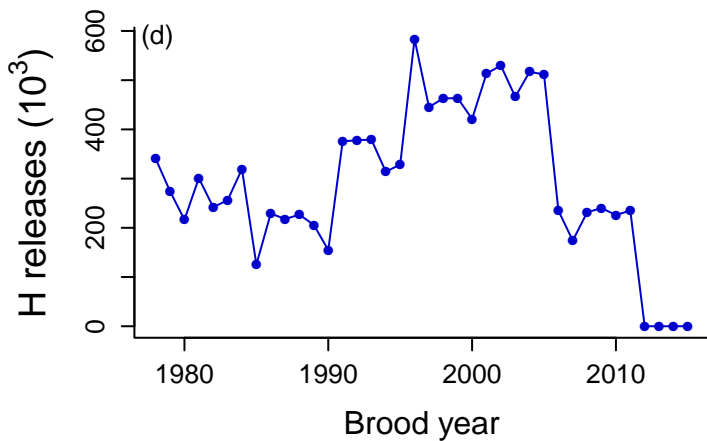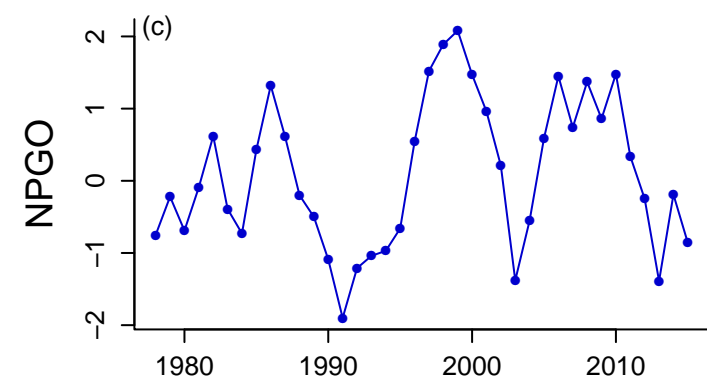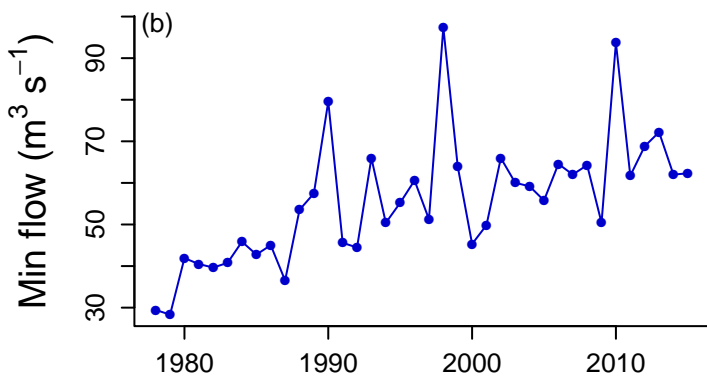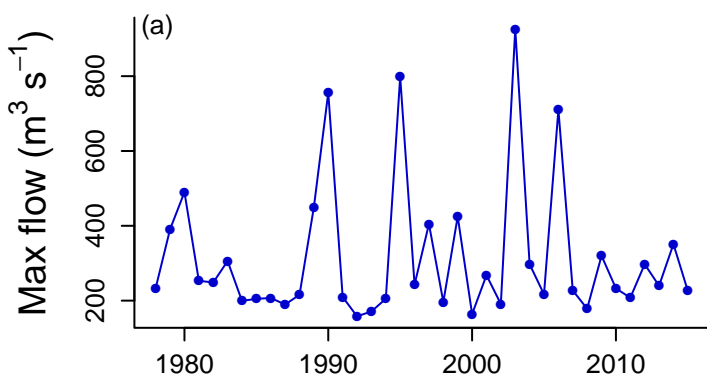
Figure 5. Time series of the estimated process errors, which represent the population's productivity after accounting for the effects of density dependence and environmental covariates. The solid line is the median estimate and the shaded region indicates the 95% credible interval.

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.
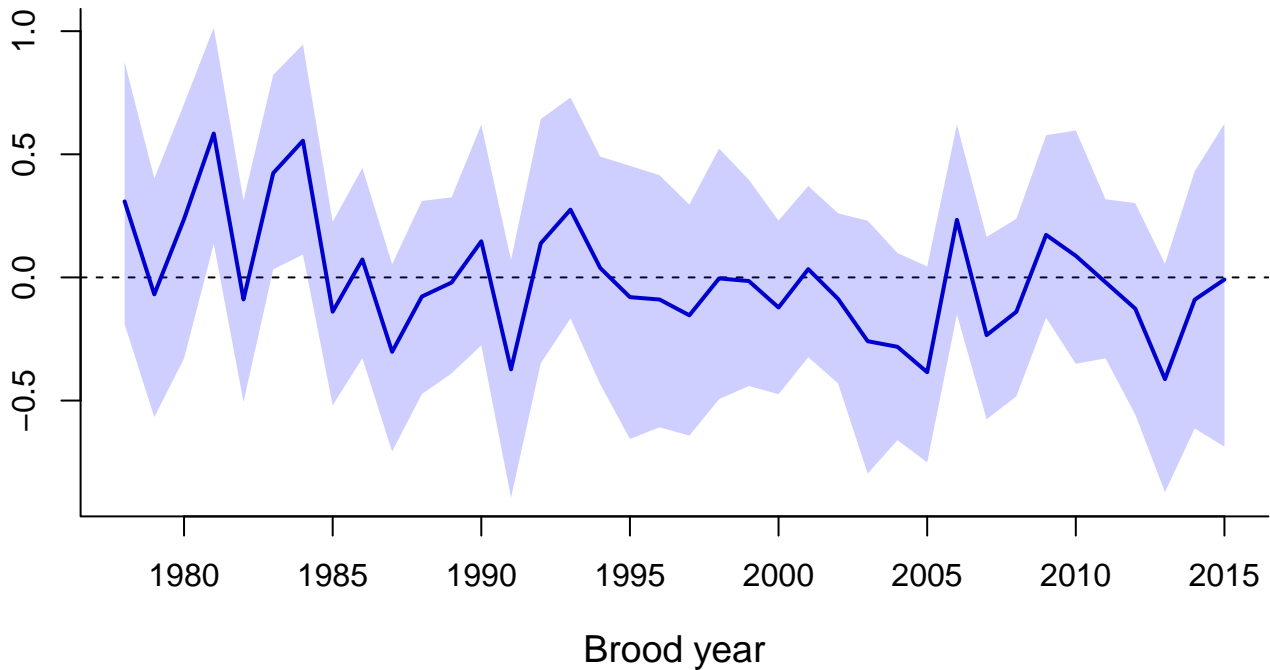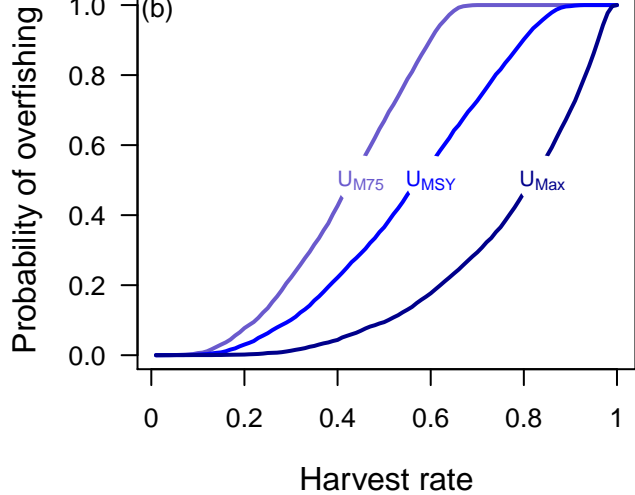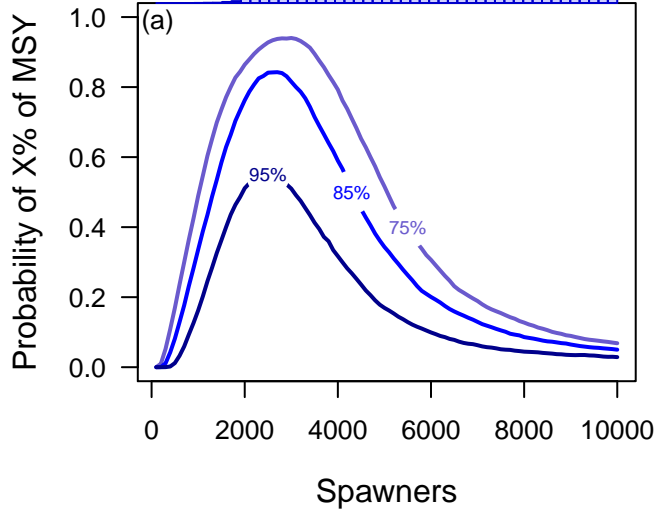
(a) Ricker

R_t

K

R_{MSY}

α

$\dfrac{\alpha S_t}{e^{\beta S_t}}$

$\dfrac{1 - W\left(\frac{e}{\alpha}\right)}{\beta}$ $\dfrac{\log(\alpha)}{\beta}$

S_t

(b) Beverton−Holt

R_t

K

R_{MSY}

α

$\dfrac{\alpha S_t}{1 + \beta S_t}$

$\dfrac{\sqrt{\alpha} - 1}{\beta}$ $\dfrac{\alpha - 1}{\beta}$

S_t

(a)

Recruits (10^3)

Spawners (10^3)

(b)

Instrinsic productivity (α)

(c)

Carrying capacity (K, 10^3)
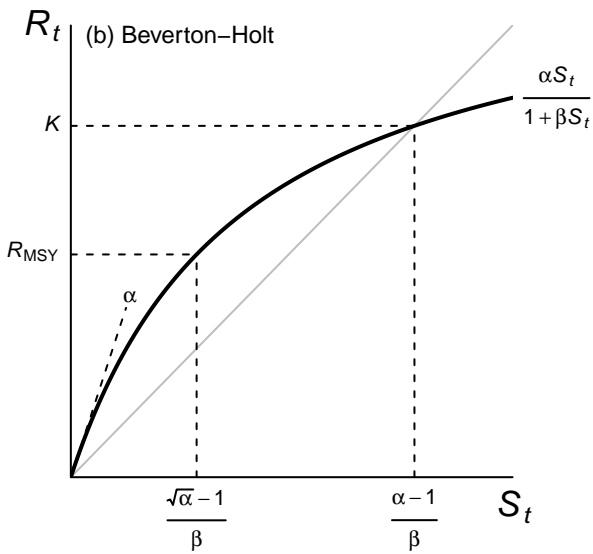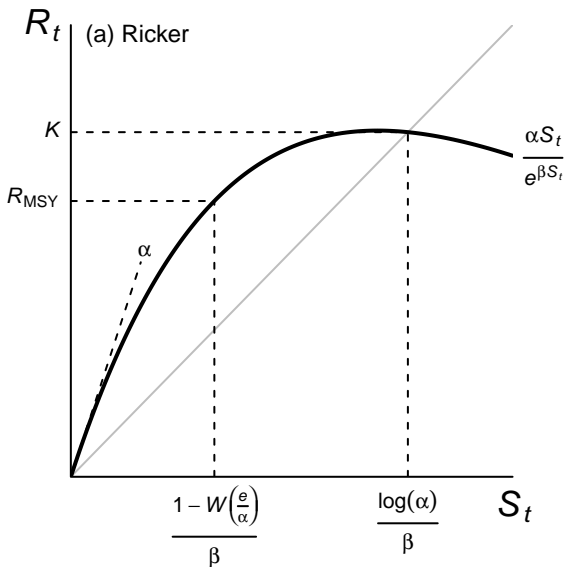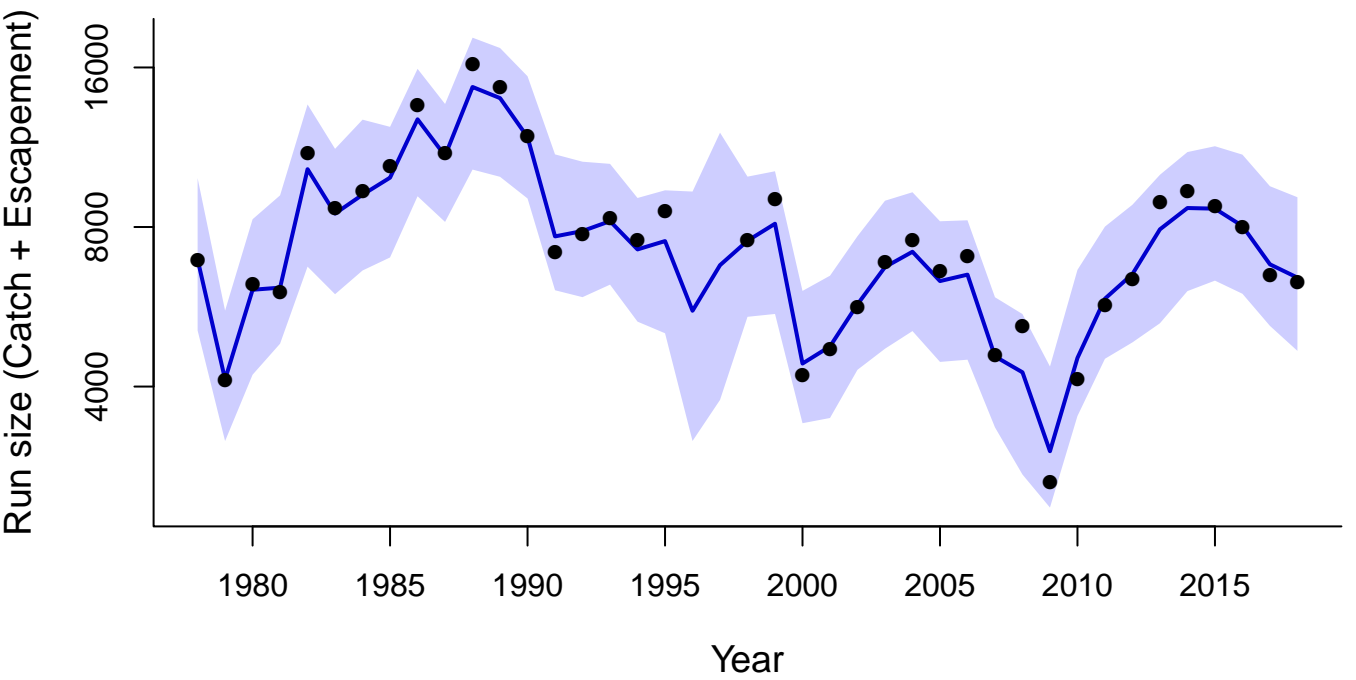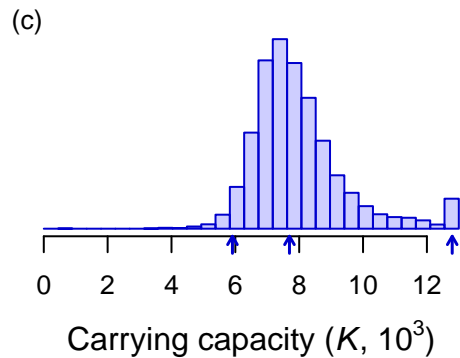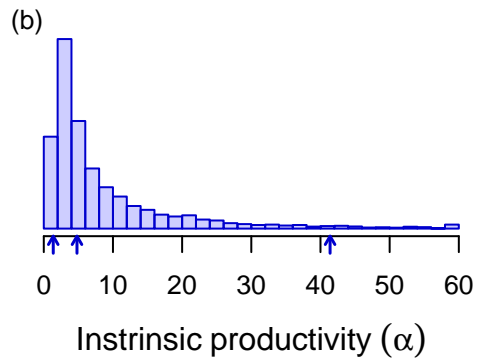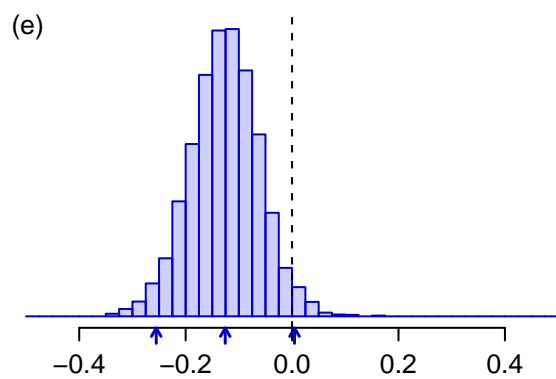
SUPPORTING INFORMATION

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

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

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

Appendix S3. Steps to recreate the manuscript figures.

Appendix S4. Background information on the age composition.