

1 **Hatchery propagation did not reduce natural steelhead productivity relative to habitat**
2 **conditions and predation in a mid-Columbia River subbasin**

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24 *Running title:* Factors affecting natural steelhead population productivity

25

26 ABSTRACT

27 For over 150-years, hatchery-origin anadromous salmon and trout have been reared and released
28 throughout the Pacific Northwest to mitigate for lost habitat and sustain harvest opportunity.
29 Some studies demonstrate that introgression of hatchery and naturally produced fish may
30 constrain conservation efforts through maladaptive genetic processes. However, empirical
31 demonstrations of the influence of these genetic interactions on population productivity are
32 lacking, making it difficult to assess their importance relative to other drivers of productivity. We
33 estimated the effect of the proportion of hatchery-origin spawners (pHOS), proportionate natural
34 influence (PNI), and hatchery fish releases on natural adult winter steelhead recruitment in the
35 Hood River, Oregon over a 27-year period of record. Adult winter steelhead productivity was not
36 associated with pHOS and PNI. However, natural winter steelhead productivity was positively
37 associated with ocean conditions, stream flow, and hatchery fish release numbers, while
38 negatively associated with pinniped abundance. Our analysis highlights the importance of
39 quantifying the influence of hatchery programs on fish production relative to environmental
40 factors known to affect natural-origin anadromous fish recruitment.

41

42 Keywords: *Oncorhynchus mykiss*, stock-recruitment, Bayesian, state-space, hatchery

43 supplementation, predation, habitat, productivity

44 INTRODUCTION

45 Numerous factors have contributed to declines of Pacific salmon (*Oncorhynchus spp.*) and
46 steelhead (*O. mykiss*) abundance, including overfishing, urbanization, hydropower development,
47 irrigation, and flood control. Since construction of the first salmon hatchery in the Pacific
48 Northwest on the Clackamas River in 1877, hatcheries have been used extensively throughout
49 the region to mitigate for lost habitat, sustain fisheries, and reintroduce extirpated fish runs.
50 Though widely accepted as a critical tool for conservation and management, hatcheries have also
51 been implicated in the declining abundance of natural-origin fish. Some researchers have found
52 that hatchery-origin fish may impair the productivity of naturally-produced salmon and steelhead
53 through ecological interactions, such as attraction of predators (Nickelson 2003) or competition
54 for habitat (Buhle et al. 2009). Additionally, introgression between domesticated hatchery fish
55 and natural-origin fish has been proposed as a potential cause of reduced population productivity
56 (Christie et al. 2014).

57

58 Perhaps the most widely cited case study of hatchery-origin anadromous fish impacts on natural-
59 origin fish occurred in the Hood River, Oregon. Araki et al. (2007a) estimated that Hood River
60 steelhead experienced a 40.5% loss in reproductive success per generation of captive rearing,
61 suggesting that the offspring of natural-origin spawners may experience rapid genetic changes in
62 captivity. Based on results of their pedigree analysis, the authors posited that naturally-spawning
63 hatchery-origin fish may pose a threat to steelhead populations and stocking programs should be
64 reconsidered. Araki et al. (2007a) and companion papers (Araki et al. 2007b, 2009; Christie et al.
65 2012a, 2012b) were subsequently cited as the basis for suspension of the Hood River winter
66 steelhead hatchery program in 2021, as well as modifications to numerous anadromous fish

67 augmentation programs in the Pacific Northwest (HSRG 2014), Canada (Withler et al. 2018),
68 and Europe (Harrison et al. 2019).

69
70 Similar genetic parentage analyses of anadromous fish populations have been conducted
71 elsewhere, including Wenatchee River Chinook salmon (Williamson et al. 2010), Johnson Creek
72 Chinook salmon (Hess et al. 2012), Imnaha River steelhead (Berntson et al. 2011), Umpqua
73 River coho salmon (Thériault et al. 2011), and Malbaie River Atlantic salmon (Milot et al. 2013).
74 In each case, researchers documented the reproductive success of naturally spawning hatchery
75 and natural-origin fish. A review of these six studies by Christie et al. (2014) concluded that fish
76 with hatchery ancestry tend to produce fewer offspring in the wild, which may reduce the
77 productivity of an entire population, regardless of whether local or non-local broodstock is used
78 in the hatchery. However, recent findings from a long-term study of Chinook salmon in Johnson
79 Creek, Idaho demonstrated that hatchery fish spawning with natural-origin fish had similar
80 reproductive success relative to natural-origin pairs and that hatchery supplementation provided
81 a demographic boost to the population (Janowitz-Koch et al. 2019). Moreover, reproductive
82 success is influenced by spawning location for both Chinook salmon and steelhead (Williamson
83 et al. 2010, Ford et al. 2016). While studies of relative reproductive success provide insight about
84 the influence of captive rearing on individual fitness, the effect of fitness loss on population
85 productivity in the naturally spawning population is not directly quantified.

86
87 Given the number of factors that can influence anadromous salmonid fitness (Koch and Narum
88 2021), and complexity of genetic and behavioral interactions between hatchery and natural-
89 origin fish, population-level assessments are needed to determine the magnitude of impact

90 hatcheries have relative to other drivers of abundance and productivity. Therefore, we developed
91 a Bayesian state-space stock-recruitment model for Hood River winter-run steelhead. To account
92 for annual variation in recruitment, we first fit the model with a suite of habitat and predation
93 covariates shown by previous studies to be useful for predicting trends in steelhead productivity.
94 The model was then used to quantify the influence of juvenile hatchery fish releases, the
95 proportion of spawning hatchery-origin adults, and the proportion of natural-origin fish used as
96 broodstock on productivity of the naturally spawning population.

97 METHODS

98 *Study Area.* — The Hood River basin drains 545 km² of the north and east flanks of Mount Hood
99 in northern Oregon, entering the Columbia River at river kilometer (rkm) 270 (Figure 1). The
100 basin has an extreme elevation profile from its peak on Mount Hood at 3,427 meters to 23 meters
101 at its confluence with the Columbia River. The river is transitional between the mild, moist, and
102 rain-dominated watersheds west of the Cascade Mountains, and the drier, snow-dominated
103 systems to the east. As such, flows in the Hood River are influenced by snow and glacial melt, as
104 well as frequent rain events.

105
106 The transitional climatic attributes of the basin are also reflected in the river's biological
107 communities. This is illustrated by life history diversity evident in anadromous rainbow trout,
108 commonly referred to as “steelhead”. Much like salmon, steelhead migrate to the ocean as
109 juveniles and return to freshwater to spawn as adults. Adult steelhead along the Pacific Coast of
110 North America typically enter freshwater in the winter, early spring, or summer dependent upon
111 habitat conditions and migration distance to natal spawning and rearing areas (Withler 1966). In
112 general, coastal rivers support winter adult migration timing, while interior rivers support
113 summer migration timing. However, the Hood River is one of the few streams in the region that
114 has distinct populations of both native summer-run and winter-run steelhead (Matala et al. 2009).
115

116 Natural-origin winter steelhead adults typically return to the Hood River from December to May
117 after two to three years in the ocean, with peak migration occurring between late February and
118 early April, and spawning occurring from March until early June. Juveniles rear for one to three
119 years in freshwater and the majority emigrate to the ocean after two years. Hood River winter

120 steelhead are iteroparous and it has been estimated that up to 15% of a spawning cohort may be
121 comprised of repeat spawners (ODFW and CTWS 2017). Mean annual spawner escapement
122 from 1992, when regular monitoring began, to 2018 was 460 natural-origin winter steelhead,
123 ranging from 161 to 1,233 (Figure 2). Annual spawner escapement of hatchery steelhead during
124 the same period averaged 341 and ranged from 5 to 853.

125

126 Hatchery steelhead releases have occurred in the Hood River dating back to at least the 1960s.
127 Historical hatchery releases used both native broodstock sources as well as out of basin stocks.
128 Prior to 1991, the Oregon Department of Fish and Wildlife (ODFW) released juveniles from Big
129 Creek Hatchery, a stock developed in the Lower Columbia Basin and characterized by early
130 adult migration and spawn timing. However, from 1992 to 2021, all hatchery winter steelhead
131 juveniles originated from native Hood River broodstock.

132

133 *Data handling.* — We obtained adult steelhead abundance and age data collected at Powerdale
134 Dam from 1992 to 2010 and at a resistance board weir on the East Fork Hood River (East Fork
135 Weir) located downstream of the primary winter steelhead spawning areas from 2011 to 2018
136 (Table 1; Figure 1)¹. Fish counts from Powerdale Dam were considered census data with a low
137 degree of potential error. Estimates of spawning escapement from the East Fork Weir were
138 calculated using Lincoln-Peterson mark-recapture and Cormack-Jolly Seber open population
139 models using PIT tag detections at Bonneville Dam and the mouth of Hood River and capture at
140 the East Fork Weir (ODFW and CTWS 2017). These estimates are regarded as a good surrogate
141 for census counts because the majority of spawning occurs in the East Fork, but they included a

¹ Supplementary Data

142 higher degree of error due to reduced PIT tag detection rates and trap efficiency during high flow
143 events, with a mean coefficient of variation of 41.2% (CTWS and ODFW 2019). All in-basin
144 hatchery releases were marked with fin and maxillary clips and the origin of unmarked adults
145 was confirmed with scale analysis (Olsen et al. 1997; CTWS and ODFW 2019).

146
147 To estimate total escapement to the Hood River, natural-origin adult abundance data were
148 adjusted to account for recreational fishing impacts. We assumed that the encounter rate of
149 natural-origin fish in the recreational fishery was equal to the rate observed for hatchery-origin
150 fish, calculated using reported catch divided by the sum of catch and hatchery-origin spawner
151 escapement (ODFW 2011, 2020). The encounter rate was then multiplied by an assumed 5%
152 catch-and-release mortality (Fausch et al. 2019) to estimate the number of natural-origin
153 steelhead lost to recreational fishing.

154
155 *Analytical Approach.* — Imperfect fish counts and age data can result in biased recruitment
156 estimates (Zabel and Levin 2002; Sanz-Aguilar et al. 2016). Therefore, to estimate observation
157 error and process error, as well as provide measures of uncertainty for our recruitment estimates,
158 we used a Ricker stock-recruitment model within a Bayesian state-space framework adapted
159 from Fleischman et al. (2013) and Courter et al. (2019) (Equation 1)¹. With this approach,
160 interannual variation in recruitment was driven by productivity covariates (e.g., ocean
161 conditions), density dependence, and observation error in age composition and spawning
162 escapement. To account for differences in precision for adult abundance data from Powerdale
163 Dam and the East Fork Weir, spawning escapement observation error was calculated separately
164 for the two periods. The model was developed using R statistical software (R Core Team 2019),

165 and the “Runjags” package for Markov Chain Monte Carlo sampling (Plummer 2003; Denwood
166 2016).

167

$$168 \quad (1) \quad \ln(R_t) = \ln(S_t) + \ln(\alpha_t) - \beta S_t + \varphi \omega_{t-1} + \varepsilon_t$$

169

170 where R_t is the abundance of natural-origin winter steelhead produced from brood year t ; S_t is the
171 total spawner escapement in year t ; α_t is productivity parameter for year t ; β is the density
172 dependence parameter; φ is the lag-1 autoregressive coefficient; ω_{t-1} is the model residual; and ε_t
173 is the normally-distributed process error with variance σ_t^2 .

174

175 R_t was estimated using age-at-return data measured from scale samples collected at Powerdale
176 Dam and the East Fork Weir (1992–2014). Scale samples indicated that adults returned from
177 age-2 to age-7 and most returned at age-4 (Table 2). Approximately 5.5% of returns were repeat
178 spawners (ODFW and CTWS 2017), so we expect recruitment estimates may have a slight
179 positive bias. We assumed that age count data $x_{A=2:7,y}$ sampled in return year y followed a
180 multinomial distribution with sample size $\Sigma x_{.,y}$ and proportion parameters:

181

$$182 \quad (2) \quad X_{A,y} = \frac{N_{A,y}}{N_{.,y}}$$

183

184 where $N_{A,y}$ is the total number of age- A natural-origin fish returning in year y , and $N_{.,y}$ is the total
185 number of fish returning in year y . $N_{.,y}$ was considered the true return abundance, estimated by
186 reported fish counts ($\hat{N}_{.,y}$). Reported returns likely included sampling error potentially due to
187 factors such as imperfect dam counts, variable weir efficiency, or variation in pre-spawn

188 mortality. Therefore, we assumed that spawning escapement was log-normally distributed with
 189 mean $N_{.,y}$:

190

$$191 \quad (3) \quad \ln(\hat{N}_{.,y}) \sim \text{Normal}(\ln(N_{.,y}), \sigma^2)$$

192

193 where σ was estimated separately for abundance data from Powerdale Dam and the East Fork
 194 Weir. Return probabilities by age and brood year ($P_{t,A}$) were modeled as random draws from a
 195 Dirichlet distribution:

196

$$197 \quad (4) \quad P_{t,A} \sim \text{Dirichlet}(\gamma_t)$$

198

199 Then, R_t was estimated as the sum of all natural-origin returns to the Hood River from brood
 200 year t that returned in years $t+2$ to $t+7$:

201

$$202 \quad (5) \quad R_t = \sum_{A=2}^7 P_{t,A} \times N_{A,t+A}$$

203

204 To account for interannual variation in recruitment from productivity covariates, we modeled α
 205 as a time-varying quantity:

206

$$207 \quad (6) \quad \alpha_t = \mu + \sum_{i=1}^k c_i X_{i,y} + h_i$$

208

209 where μ is the underlying mean productivity; c_i is the effect of a covariate ($X_{i,y+h_i}$) measured at
210 year y and adjusted for time lag h_i . Covariates are lagged by h_i to account for the life history
211 characteristics of Hood River steelhead.

212

213 Covariates fell into three categories: habitat conditions, predation, and hatchery influence (Table
214 3). All covariates were standardized by subtracting the mean and dividing by the standard
215 deviation of the data. Diffuse priors were specified for all coefficients using a normal distribution
216 centered about zero. In addition, we included the presence of Powerdale Dam as a binomial
217 effect to account for the dam's potential influence on steelhead survival (CTWS and ODFW
218 2019) as well as the change in adult abundance estimation methods that coincided with dam
219 removal.

220

221 *Habitat covariates.* — We evaluated several habitat metrics¹ as covariates in our productivity
222 model. Low summer flows can directly affect juvenile survival by limiting habitat availability
223 (Magoulick and Kobza 2003; May and Lee 2004), whereas high flows in the spring can be
224 associated with faster juvenile migration and greater survival (Courter et al. 2016). Accordingly,
225 we considered flow covariates for summertime lows, springtime highs and daily minimums
226 during juvenile rearing and outmigration using discharge data from a monitoring station on the
227 Hood River (rkm 9.5, U.S. Geological Survey gage #14120000). However, only minimum daily
228 flow was retained in the final model due to limited evidence of spring flow effects. Minimum
229 daily flow (MINq) was calculated as discharge in cubic feet per second (cfs) one year prior to
230 outmigration, adjusted by observed natural-origin age data:

231

232 (7)
$$\text{MIN}q_t = \sum_{A=1}^3 \text{MIN}q_{t+A-1} \times \bar{O}_{n,A}$$

233

234 where, q is flow in cfs and $\bar{O}_{n,A}$ is the mean proportion of natural-origin returns that outmigrated
235 after one, two, and three years in freshwater (Table 2).

236

237 In addition to stream flow, we also explored several possible ocean survival covariates to
238 account for conditions during marine rearing (Table 3). North Pacific Gyre Oscillation (NPGO)
239 in the month of May produced the best fit and was used during the covariate selection process.
240 NPGO is an index of ocean conditions including upwelling and phytoplankton concentrations
241 (DiLorenzo et al. 2008) and has been strongly correlated with ocean survival of coho salmon
242 (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*) (Kilduff et al. 2015), and steelhead
243 (Scheuerell et al. 2021). In our model, we included May NPGO to account for conditions
244 encountered upon ocean entry. May NPGO was offset using age-at-outmigration data to align
245 with the age of juvenile fish at the time of ocean entry (Table 2):

246

247 (8)
$$\text{NPGO}_t = \sum_{A=1}^3 \text{NPGO}_{t+A} \times \bar{O}_{n,A}$$

248

249 *Predation covariates.* — Pinniped and avian predators in the lower Columbia River consume
250 significant numbers of anadromous salmonids (Roby et al. 2021; Tidwell and van der Leeuw
251 2021) and are a major concern for fishery managers (Columbia River Inter-Tribal Fish
252 Commission (CRITFC 2014). To estimate their effects on Hood River steelhead productivity, we
253 fit our model with indices of predator abundance. These included annual estimates of brood pairs
254 for double-crested cormorants (*Phalacrocorax auritus*) and Caspian terns (*Hydroprogne caspia*)

255 located in the Columbia River estuary, as well as abundance of California (*Zalophus*
256 *californianus*) and Steller sea lions (*Eumetopias jubatus*) observed below Bonneville Dam on the
257 Columbia River (rkm 234). However, the effects of Caspian tern and double-crested cormorant
258 abundances did not meet inclusion criteria.

259

260 The pinniped predation covariate (PIN) included the combined abundance of California and
261 Steller sea lions observed by the U.S. Army Corp of Engineers downstream of Bonneville Dam.
262 These data were gathered (Tidwell et al. 2020) and weighted using natural-origin age-at-return
263 data (Table 2):

264

$$265 \quad (9) \quad PIN_t = \sum_{A=3}^6 PIN_{t+A} \times \bar{P}_{n,A}$$

266

267 where, $\bar{P}_{n,A}$ is the mean proportion of natural-origin returns at age A (Table 2).

268

269 *Hatchery covariates.* — To quantify the potential influence of hatchery supplementation on
270 natural-origin adult productivity, we examined three metrics: hatchery smolt releases, proportion
271 of hatchery-origin spawners (pHOS), and the proportionate natural influence (PNI) within the
272 spawning population. pHOS and PNI are common metrics used to measure gene flow and
273 contribution from hatchery-origin spawners (HSRG 2017). The intent of each covariate was to
274 incorporate three possible mechanisms for hatchery fish effects: (1) hatchery smolt releases
275 affect survival of natural-origin smolts, (2) hatchery-origin spawners influence natural-origin fish
276 production through genetic exchange and competition, and (3) the degree of hatchery fish
277 domestication influences the magnitude of pHOS effects. Data for these covariates were

278 collected from Hood River production reports, summarized in Olsen and French (2000) and
 279 CTWS and ODFW (2019).

280

281 Natural-origin juveniles from brood year t outmigrated in years $t+1$, $t+2$, and $t+3$. Therefore, the
 282 outmigration of hatchery smolts released (HSR) in year y coincided with natural-origin juveniles
 283 that were produced one to three years prior:

284

$$285 \quad (10) \quad HSR_t = \sum_{A=1}^3 HSR_{y+A} \times \bar{O}_{n,A}$$

286

287 pHOS for brood year t (pHOS_t) was calculated as hatchery-origin spawning escapement (HE)
 288 divided by total spawning escapement (SE). Spawning escapement was defined as the number of
 289 winter steelhead adults that passed the Powerdale Dam, and the East Fork Weir after dam
 290 removal (Figure 2).

291

$$292 \quad (11) \quad \text{pHOS}_t = \frac{HE_t}{SE_t}$$

293

294 PNI accounted for the parental origin of hatchery-origin fish as well as pHOS. Steelhead
 295 propagation in the Hood River relied on broodstock collected from hatchery returns and natural-
 296 origin fish collected at Powerdale Dam and the East Fork Weir. Therefore, to estimate the degree
 297 of “wildness” of hatchery-origin spawners, we began by calculating the proportion of natural-
 298 origin broodstock (pNOB) in the hatchery.

299

$$300 \quad (12) \quad \text{pNOB}_y = \frac{\text{Natural - origin broodstock}_y}{\text{Total spawned broodstock}_y}$$

301

302 pNOB in year y was then weighted to account for age at return of hatchery-origin spawners in303 brood year t :

304

305 (13)
$$pNOB_t = \sum_{A=2}^5 pNOB_{y-A} \times \bar{P}_{h,A}$$

306

307 where, $\bar{P}_{h,A}$ is the mean proportion of hatchery returns at age A (Table 2). Hatchery-origin returns

308 prior to 1996 that were from Big Creek stock were assigned a pNOB value of zero. PNI for

309 brood year t was then estimated annually for each natural spawning brood year (Figure 3).

310

311 (14)
$$PNI_t = \frac{pNOB_t}{pNOB_t + pHOS_t}$$

312

313 *Covariate selection.* — The influence of each covariate in the Ricker recruitment model was

314 determined by examination of the posterior distribution of effect size, associated 95% credible

315 interval, and the proportion of the posterior that was positive or negative (probability of

316 direction). Covariates were retained in the model if the posterior had a greater than 90%

317 probability of direction and inclusion was supported by cross-validation. We developed four

318 models for comparison, sequentially including covariates with well-established impacts on

319 productivity based on our literature review. We first developed the model without covariates,

320 then added habitat covariates and retained those that met inclusion criteria. Next, predation

321 covariates were added and examined for inclusion. Then, the hatchery effects covariates were

322 examined. In all model permutations, we assessed convergence with visual assessment of trace

323 plots and Gelman and Rubin scale reduction factors (Gelman and Rubin 1992) and estimated the

324 variance inflation factor (VIF) to monitor potential multicollinearity of predictors. Models were
325 compared using leave-one-out cross-validation with Pareto-smoothed importance sampling
326 (Vehtari et al. 2017) from the 'loo' R package (Vehtari et al. 2020). The final model was run
327 with three chains of 40,000 iterations with a thinning factor of 15, and burn-in and adaptation
328 periods of 1,000 samples to obtain Gelman and Rubin factors < 1.1 .

329

330 RESULTS

331 Model convergence and inspection of posteriors provided support for the state-space Ricker
332 stock-recruitment approach. Model parameter estimates converged appropriately (Gelman –
333 Rubin statistic < 1.1) and multicollinearity of covariates was not observed (VIF < 2.1 ; MCMC
334 cross-correlation < 0.3). Process error residuals centered about zero and did not display clear
335 autocorrelation until removal of Powerdale Dam in 2010 (Figure 4). Following dam removal and
336 subsequent spawner escapement estimation at the East Fork Weir, observation error increased by
337 approximately a factor of four (Table 4). The related binomial random effect for dam presence
338 had a 91% probability of being negative (median = -0.6543; 95% CI -1.581, 0.344), but dam
339 effects should not be directly inferred due to the causal relationship with the change in adult
340 enumeration methods.

341

342 Median spawning escapement estimates were reasonably aligned with observed values and 95%
343 credible intervals included observed escapement in 24 of 27 run years (Figure 5). Credible
344 intervals were substantially wider for spawning escapement estimates associated with the East
345 Fork Weir. Hood River winter steelhead were predicted to produce a density-independent
346 median of up to 2.03 recruits per spawner from the 1992 – 2016 brood years and recruitment was

347 maximized at 843 spawning adults (Table 4). The Ricker stock-recruitment curve indicated that
348 spawner abundance exceeded the escapement number necessary for maximum recruitment in 12
349 of the 27 years assessed, or 44% of brood years (Figure 6).

350

351 The final Ricker stock-recruitment model included four covariates that influence productivity at
352 three life stages: minimum Hood River flow, hatchery smolt releases, NPGO, and pinniped
353 abundance at Bonneville dam (Figure 7). These covariates were associated with clear effects on
354 productivity (Figure 8) and produced the model with the lowest leave-one-out information
355 criterion (LOOIC) (Table 5). Comparison of expected log-predictive densities (ELPD) indicated
356 that the final model formulation had significantly higher predictive accuracy than other candidate
357 models, given the assumption that ELPD was normally distributed with a 0.05 threshold for
358 significance. NPGO had the largest magnitude of effect with a median estimate of 0.3202 and a
359 97.5% probability of a positive relationship with productivity (Table 6). This effect size suggests
360 that an increase in NPGO of one standard deviation (SD) results in a 32% increase in
361 recruitment. Conversely, pinniped abundance had a high probability (95.2%) of a strong negative
362 effect on productivity (-0.273), suggesting a one SD increase in pinniped abundance predicts a
363 27.3% reduction in productivity. The effect of hatchery smolt releases was less pronounced
364 (0.1795), but almost certainly positive, with a 99.3% probability for positive effect and one SD
365 increase predicting an 18% increase in recruitment. Finally, the effect of minimum Hood River
366 flow was likely positive (91.3%) and one SD increase in flow from 248 to 299 cfs corresponded
367 with a 12.3% increase in predicted recruitment.

368

369 We did not find evidence that hatchery supplementation negatively affected natural-origin
370 steelhead recruitment during the 27-year period of record. The probability that pHOS negatively
371 influenced productivity was 18%, and the 95% credible interval for the pHOS effect straddled
372 zero (median = 0.1328; 95% CI = -0.1585, 0.3975). Similarly, the probability that PNI had a
373 positive effect was 20% and the 95% credible interval included zero (median = -0.0718; 95% CI
374 = -0.2802, 0.1103). Therefore, neither covariate was retained in the final productivity model.
375

376 DISCUSSION

377 We analyzed the influence of hatchery steelhead on natural-origin steelhead recruitment over a
378 27-year period of record within the Hood River basin and found that pHOS and PNI, the primary
379 metrics for inferring genetic risks of hatchery programs in the Pacific Northwest (Paquet et al.
380 2011), were not associated with changes in adult winter steelhead productivity. Given the
381 magnitude and immediacy of loss of reproductive success found by Araki et al. (2007a) (~40%
382 reduction in one generation), our results call into question how confidently individual relative
383 reproductive success studies can be extrapolated to infer impacts on population productivity. In
384 contrast, hatchery smolt releases, NPGO, minimum stream flow, and pinniped abundance were
385 associated with winter steelhead productivity.

386
387 Surprisingly, the number of juvenile hatchery steelhead released annually into the Hood River
388 was positively related to natural-origin steelhead recruitment. This finding is inconsistent with
389 previous work by Nickelson (2003) who found the number of juvenile hatchery coho salmon
390 released into streams reduced survival of natural-origin emigrants on the Oregon Coast.
391 Similarly, Scheuerell et al. (2021) found a negative relationship between the number of summer
392 steelhead smolts released and productivity of winter steelhead in the Skagit River, Washington.
393 However, “predator swamping” and preferential feeding on hatchery fish have also been shown
394 to improve the survival of naturally-produced emigrating salmonids. Furey et al. (2016)
395 demonstrated that predator swamping reduced predation of outmigrating sockeye salmon (*O.*
396 *nerka*) in British Columbia, and Collis et al. (2001) observed higher vulnerability of hatchery
397 steelhead to Caspian tern predation in the lower Columbia River because of their larger body size
398 and tendency to migrate higher in the water column. Juvenile hatchery-origin salmon and

399 steelhead are also known to be more susceptible to predation (Berejikian 1995), particularly
400 shortly after release (Muir et al. 2001). Our findings provide some evidence to suggest that
401 hatchery releases of winter steelhead smolts in the Hood River may have been insulating natural-
402 origin fish from predation, which could explain why we were unable to quantify a relationship
403 between abundance of avian predators and natural production despite well-documented predation
404 of juvenile steelhead by cormorants and other avian piscivores in the Columbia Basin (Roby et
405 al. 2021). It is also possible that hatchery supplementation increased density of natural-origin
406 spawners (Scheuerell et al. 2015) and diversified the population's demography as was observed
407 by Janowitz-Koch et al. (2019).

408

409 Pinniped predation is also known to impact anadromous salmonids in the Columbia Basin (Faley
410 2017). California and Stellar sea lions consume 6.8% of adult steelhead and 2.7% of spring
411 Chinook salmon arriving at Bonneville Dam in the lower Columbia River in an average year
412 (Tidwell and van der Leeuw 2021). Bite marks were observed on approximately 22% of adult
413 salmon and steelhead returns to the Hood River basin (Simpson et al. 2016). Consequently, we
414 observed a negative association between abundance of California and Stellar sea lions and Hood
415 River steelhead productivity. Nelson et al. (2019) also found a significant negative association
416 between pinniped density and the productivity of Chinook salmon in 14 of 20 populations
417 throughout British Columbia and Puget Sound. However, this study was designed to explore the
418 impact of harbor seals on survival of juvenile Chinook salmon and subsequent adult salmon
419 production.

420

421 Not surprisingly, we found that ocean conditions, modeled as NPGO, were positively associated
422 with Hood River steelhead production. Ocean conditions have a large influence on the
423 production of Pacific salmonids (Peterman et al. 1998; Pyper et al. 2002; Teo et al. 2009; Kilduff
424 et al. 2014; Zimmerman et al. 2015) primarily because early ocean growth affects their
425 susceptibility to predation (Friedland et al. 2014; Kendall et al. 2017). NPGO has also been
426 positively correlated with productivity of winter steelhead in the Skagit River, Washington
427 (Scheuerell et al. 2021). Similarly, Kilduff et al. (2015) observed a strong positive relationship
428 between NPGO and ocean survival of coho and Chinook salmon.

429
430 Our analysis included exploration of several stream flow metrics, but only minimum stream flow
431 one year prior to outmigration was associated with adult steelhead productivity. Minimum
432 stream flow one year prior to outmigration occurs when age 1+ juvenile steelhead, commonly
433 referred to as parr (50-80 mm in length), are actively rearing in freshwater. This is the life-stage
434 at which intraspecific competition and density-dependent survival is thought to be most intense
435 (Harvey and Nakamoto 1997; Hayes et al. 2008). The bottleneck for juvenile rearing habitat
436 availability in most interior Columbia Basin streams occurs in the summer when flows are at
437 their lowest and competition between rearing fish is high. Our findings support the hypothesis
438 that summer habitat availability limits juvenile steelhead production and subsequently adult
439 steelhead recruitment in the Hood River.

440
441 Araki et al. (2007a) reported that hatchery-reared steelhead experienced a significant loss in
442 reproductive success in the Hood River, thereby posing a risk to natural-origin steelhead
443 productivity through interbreeding. Fitness loss was also shown to be compounded with each

444 successive generation in the hatchery. This finding provided a mechanistic basis for genetic
445 impacts caused by an integrated natural broodstock fishery augmentation program. Numerous
446 publications followed, each concluding that reproductive success of Hood River steelhead
447 rapidly declined with successive generations in captivity (Araki et al. 2007b, 2009; Christie et al.
448 2012a, 2012b). Tissue samples prior to initiation of hatchery propagation in the Hood River are
449 not available, precluding a direct test of the influence of hatchery-origin spawners on genetic
450 ancestry within the population. However, we were able to explore the available long-term dataset
451 for evidence of reduced reproductive success (i.e. a reduction in population productivity). Since
452 we did not observe a decline in productivity related to the number of hatchery spawners, this
453 suggests that changes in relative reproductive success caused by captive rearing did not translate
454 directly into population-level effects. Therefore, the effect is either small, p_{HOS} and PNI are not
455 good surrogates for gene flow or hatchery ancestry, or other biological or genetic processes must
456 be mitigating or masking the influence of hatchery spawners.

457
458 There are several hypotheses useful for reconciling our findings with the work of Araki et al.
459 (2007a). First, without inheritance and retention of maladaptive traits, loss of fitness in hatchery-
460 origin fish would have limited consequences on the naturally spawning population. Our findings
461 could be explained by the notion that the fitness deficit was not incorporated and maintained
462 within the natural population, potentially due to plasticity of gene expression across
463 environments (Chittenden et al. 2010), independence of traits beneficial to survival in hatchery
464 and natural environments, or balancing selection (Charlesworth 2006), which preserves traits that
465 enhance or maintain fitness (Connallon and Chenoweth 2019).

466

467 Second, if the hatchery fish fitness deficit reported by Araki et al. (2007a) was indeed heritable,
468 it is possible that rapid feralization occurred. Captive-bred animals are phenotypically plastic and
469 can quickly adapt once introduced back into ancestral environments (Ho et al. 2020). Robust
470 naturally-reproducing fish populations derived from highly-domesticated hatchery-origin salmon
471 and steelhead stocks can be found throughout North and South America (Crawford 2001;
472 Pascual et al. 2001; Soto et al. 2007; DiPrinzio and Pascual 2008; Gomez-Uchida et al. 2018;
473 Keefer et al. 2018), indicating that anadromous hatchery-origin fish retain sufficient phenotypic
474 and genetic diversity to reestablish extirpated runs, expand spatial distribution, and populate
475 nonindigenous environments. Domestication selection favors traits that are advantageous in a
476 captive environment and can relax selection on traits that are advantageous in nature, but does
477 not necessarily select against such traits (Lahti et al. 2009). Domestication can also change gene
478 expression in the captive environment, which results in phenotypic changes to the fish but not
479 necessarily heritable changes (Chittenden et al. 2010). Reciprocal transplants and common
480 garden experiments are preferred when testing whether observed phenotypic differences between
481 hatchery and natural-origin fish have a heritable basis.

482
483 Finally, Araki et al. (2007a) estimated rates of reproductive success using a pedigree analysis,
484 but they did not demonstrate that the observed difference in reproductive success of hatchery and
485 natural-origin steelhead was due to genetic effects. Behavioral differences between hatchery and
486 natural-origin fish, such as spawning site selection, are also known to influence rates of
487 reproductive success (Williamson et al. 2010) and spawning site selection can influence fitness
488 of hatchery and natural-origin fish (Schroder et al. 2008; Ford et al. 2016). Steelhead exhibit
489 spawning site fidelity and, while some fish stray, most return to spawn proximate to natal rearing

490 areas. Araki et al. (2007a) collected tissue samples at Powerdale Dam on the lower Hood River,
491 roughly 16 km from primary spawning areas, and spatial overlap between hatchery and natural-
492 origin fish was undocumented. Therefore, if a portion of the hatchery-origin spawners utilized
493 suboptimal habitat, it follows that the relative reproductive success of those individuals would be
494 reduced. Coincidentally, from 1992-2012, approximately 50-70% of hatchery steelhead released in
495 the Hood River were acclimated in the East Fork at approximately rkm 10 and the remaining 30-
496 50% were acclimated at Parkdale Hatchery in the Middle Fork Hood River. Radio telemetry
497 monitoring of adult steelhead (Clabough et al. 2010) demonstrated that hatchery steelhead
498 spawner distribution differed substantially from natural-origin fish and closely resembled the
499 proportion of fish released at each acclimation site. Furthermore, acclimation in the East Fork
500 occurred adjacent to a large irrigation diversion. Juveniles produced by hatchery-origin spawners
501 in that area would have been exposed to artificially low summer flows. Therefore, the relative
502 reproductive success deficit estimated by Araki et al. (2007a) may have been caused by hatchery
503 acclimation and release practices. This is consistent with results observed in Chinook salmon in
504 the Wenatchee River, where first generation hatchery-origin fish have lower reproductive
505 success than natural-origin fish, but the progeny of these hatchery fish stray to spawn in locations
506 their first generation hatchery parents did not (Ford et al. 2015). The observation that second
507 generation fish spawning in nature produced roughly one adult recruit (Ford et al. 2012, Table 3)
508 suggests reduced reproductive success of hatchery-origin fish was due to selection of poor
509 spawning sites not maladaptive genetic traits.

510

511 Studies of hatchery fish effects on population productivity are relatively rare due to the need for
512 long-term time series data, but advancements in computing power have expanded opportunities

513 to utilize previously disregarded monitoring data (e.g. Scheuerell et al. 2021) and improve
514 quantification of statistical uncertainty in recruitment analyses (e.g. Fleischman et al. 2013).
515 Review of the few population productivity studies that have been published revealed inconsistent
516 outcomes concerning impacts of hatchery fish on natural-origin salmon and steelhead (Chilcote
517 2003; Buhle et al. 2009; Chilcote et al. 2011; Lister 2014; Courter et al. 2019; Nelson et al. 2019;
518 Scheuerell et al. 2021) owing to the complexity of factors that influence hatchery fish effects,
519 such as the size and type of hatchery program, rearing and release practices, broodstock source,
520 fish trapping and sorting facilities, and size of the population being supplemented.

521

522 Experimental design and methods used to analyze population census datasets can also influence
523 results of hatchery fish effects analyses. Chilcote (2003) and Chilcote et al. (2011) adopted an
524 approach whereby recruitment models were fit to adult salmon and steelhead abundance datasets
525 and the influence of the proportion of hatchery fish within the natural spawning population was
526 quantified. The authors found a negative association between the proportion of hatchery fish and
527 predicted productivity at low spawner abundance. Results of these evaluations may be attributed
528 to presence of hatchery fish within the spawning population (as interpreted by the authors),
529 inadequate explanatory variables to address process error in adult fish recruitment, uncertainty in
530 annual estimates of recruitment due to assumed constant age structure within each population, or
531 density-dependent population dynamics where increases in spawner abundance (i.e. addition of
532 hatchery fish) results in fewer recruits per spawner. The last explanation, if correct, would
533 address why the author's results were surprisingly consistent across a large number of
534 populations despite variation in type and size of hatchery programs. Lister (2014) provides an
535 explanation of why natural productivity estimated as recruits per spawner within supplemented

536 anadromous salmonid populations tends to reflect hatchery program scale, not productive
537 capacity of natal streams.
538
539 Buhle et al. (2009) also reported negative effects of hatchery fish on natural-origin anadromous
540 fish productivity. This study was more quantitatively rigorous than Chilcote (2003) and Chilcote
541 et al. (2011), but pre-dated the work of Fleischman et al. (2013) and Scheuerell et al. (2021), who
542 provided powerful analytical solutions to address well-documented bias in recruitment
543 estimation caused by overly-simplistic age-structure assumptions (Zabel and Levin 2002) and
544 observation error within population census datasets (Knape and de Valpine 2012). Therefore,
545 while it is possible there are localized differences between effects of hatchery fish on Oregon
546 Coast coho salmon and Hood River steelhead, inconsistency between our findings and those of
547 Buhle et al. (2009) may also be explained by dissimilarity in analytical methods. Perhaps more
548 importantly, changes in exploitation rates of Oregon Coast coho salmon could have confounded
549 the authors' analysis of hatchery fish effects. Buhle et al. (2009) relied on crude annual
550 approximations of fishing exploitation rates from Chilcote et al. (2005) ranging from a low of
551 0.07 to a high of 0.72 to estimate preharvest abundance of coho salmon within each
552 subpopulation over the period of record, 1990-2000. Exploitation rates of natural-origin fish
553 were high when hatchery fish returns were strong from 1990-1996 and declined precipitously
554 from 1997-2000, which is coincidentally when a regional restoration plan was implemented
555 (Nicholas 1997), and hatchery returns declined, harvest reforms occurred, and fishing effort
556 receded. Given the wide range in annual harvest rates, unknown level of accuracy of those
557 estimates, and coincident reductions in hatchery fish production and harvest, the authors' results
558 may have been biased by variation in fishing exploitation that could not be accurately quantified

559 and corresponded with other management actions. Analytical solutions, such as the recruitment
560 model developed by Fleischman et al. (2013) could be applied to determine how sensitive the
561 Oregon Coast coho salmon dataset is to harvest uncertainty.

562

563 Scheuerell et al. (2021) found that winter steelhead productivity in the Skagit River was
564 negatively affected by the number of juvenile hatchery steelhead released annually throughout
565 the basin. The authors developed a Bayesian hierarchical model that was similar to our approach
566 and addressed a number of important analytical challenges that were not addressed by Chilcote
567 (2003), Buhle et al. (2009), Chilcote et al. (2011), and Lister et al. (2014). However, there are
568 several key differences between our study and Scheuerell et al. (2021). Perhaps the most
569 significant difference is that the authors investigated the effects of a segregated hatchery
570 program, whereas we examined effects of an integrated natural-origin broodstock program.
571 Additionally, we used steelhead spawner abundance data derived from dam and trap counts that
572 provided reliable information on the origin of spawners and allowed us to estimate the effects of
573 pHOS and PNI on steelhead recruitment. Scheuerell et al. (2021) relied on redd counts from an
574 aggregate of winter and summer-run fish conducted in a small portion of the known spawning
575 area within the Skagit River basin and assumed all spawners were natural-origin due to
576 differences between hatchery- and natural-origin steelhead spawn timing. As a result, the authors
577 were only able to quantify the effect of hatchery production on natural-origin productivity using
578 counts of hatchery-origin smolts released each year. The authors attributed the observed negative
579 effect of hatchery steelhead releases to density-dependent interactions and loss of juvenile
580 rearing habitat in the Skagit River basin.

581

582 Clackamas River winter-run steelhead, as originally documented by Kostow and Zhou (2006)
583 and recently amended by Courter et al. (2019), also provide a valuable case study of population-
584 level effects of hatchery fish on natural-origin anadromous salmonids. Productivity of winter-run
585 steelhead in the Clackamas River was not impaired by the abundance of hatchery-origin
586 summer-run steelhead spawner escapement. However, these results are not directly compatible
587 with our findings because the Clackamas River study examined the effects of a segregated
588 hatchery program, whereas we examined effects of an integrated natural-origin broodstock
589 program.

590
591 Our analysis highlights the importance of directly testing theories about the influence of hatchery
592 fish on steelhead populations using abundance monitoring data. Hatchery steelhead effects
593 should also be examined in the context of other factors that influence natural-origin fish
594 recruitment to avoid overstating the expected conservation benefits of reducing or eliminating
595 hatchery programs. In the case of Hood River winter-run steelhead, interactions between
596 hatchery and natural-origin fish did not have a quantifiable negative impact on population
597 productivity, suggesting that an integrated broodstock program implemented to augment harvest
598 opportunity should not be expected to impair ecosystem-based efforts to enhance natural-origin
599 fish abundance.

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608

609 DATA AVAILABILITY

610 Data generated or analyzed during this study are provided in full within the published article and
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612

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948

949 FIGURE CAPTIONS

950 Figure 1. Map of the Hood River Basin and primary steelhead monitoring stations. Stream layer
951 source: USGS (2018).

952

953 Figure 2. Estimated adult spawner escapement of natural and hatchery-origin winter steelhead
954 upstream of Powerdale Dam prior to 2010 and upstream of the East Fork weir after dam
955 removal, indicated by the dashed vertical line.

956

957 Figure 3. Time series of Hood River winter steelhead proportion of hatchery-origin spawners and
958 proportionate natural influence by brood year.

959

960 Figure 4. Time series of estimated process error after accounting for model covariates and
961 density dependence. The solid line is the median estimate and the shaded area indicates the 95%
962 credible interval.

963

964 Figure 5. Observed and estimated natural-origin winter steelhead spawner escapement upstream
965 of Powerdale Dam prior to 2010 and upstream of the East Fork weir after dam removal,
966 indicated by the dashed vertical line. Points are observed values, the line is median model
967 estimates, and the shaded region is the associated 95% credible interval.

968

969 Figure 6. Ricker stock-recruitment model curve, fit at median posterior values and including the
970 estimated effect of Powerdale Dam weighted by the proportion of the period of record when it
971 was present. Points are annual estimates of Hood River winter steelhead recruitment are points
972 with associated 95% credible intervals for brood years 1992 to 2016.

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974 Figure 7. Hood River winter steelhead productivity model diagram depicting covariates applied
975 at each life stage. Grey text indicates model covariates.

976

977 Figure 8. Time series of covariate values by brood year and posterior distributions of covariate
978 effects. A: Northern Pacific Gyre Oscillation, B: hatchery smolt releases, C: minimum Hood
979 River flow, and D: pinniped abundance at Bonneville Dam.

Table 1. Data sources used in the Ricker stock-recruitment model.

Data type	Date range	Source
Spawner escapement by origin	1992 – 2018	CTWS and ODFW 2019
Age-at-return	1992 – 2014	ODFW and CTWS 2017
Age-to-smolt	1992 – 2014	ODFW and CTWS 2017
Broodstock collection and spawning	1992 – 2017	Olsen and French 2000 (1991 – 1996) and CTWS and ODFW 2019 (1997 – 2017)
Hatchery-origin smolts released	1994 – 2018	ODFW 2017 (1994 – 1996) and CTWS and ODFW 2019 (1997 – 2018)
Hood River flow at Tucker Bridge	1992 – 2020	USGS National Water Information System, station ID #14120000
May Northern Pacific Gyre Oscillation	1993 – 2020	Di Lorenzo 2020
Bonneville Dam pinniped abundance	2001 – 2018	Tidwell et al. 2020
Columbia River estuary double-crested cormorant abundance	1992 – 2019	Carter (1995), Anderson (2002), Roby et al. (2021)
Columbia River estuary Caspian tern abundance	1992 – 2019	Collis et al. (1999), Shuford and Craig (2002), Roby et al. (2021)

Table 2. Mean age at outmigration and return to Hood River for natural- and hatchery-origin winter steelhead observed from scale samples.

Origin		1	2	3	4	5	6	7
Natural	Outmigration age	0.03	0.82	0.15	-	-	-	-
	Return age	-	>0.01	0.05	0.64	0.28	0.03	>0.01
Hatchery	Return age	-	0.01	0.76	0.22	0.01	-	-

Table 3. Covariates tested in the stock-recruitment model. Covariates included in the final Ricker model are bolded.

	Life stage	Covariate
<i>Habitat</i>	Freshwater rearing	Minimum daily flow
	Smolt outmigration	Powerdale Dam spill during outmigration
	Ocean survival	North Pacific Gyre Oscillation (NPGO)
		Pacific Decadal Oscillation
		Coastal upwelling
		El Niño-Southern Oscillation
	Sea surface temperature	
<i>Predation</i>	Smolt outmigration	Columbia estuary double-crested cormorant abundance
		Columbia estuary Caspian tern abundance
	Adult returns	Bonneville Dam pinniped abundance (PIN)
<i>Hatchery</i>	Spawning	Proportion hatchery-origin spawners (pHOS)
		Proportionate natural influence (PNI)
	Smolt outmigration	Hatchery-origin smolt release abundance (HSR)

Table 4. Median estimates for stock recruitment model parameters and their associated 95% credible intervals.

Variable	Median	95% credible interval
β	0.0012	(0.0007, 0.0019)
$1/\beta$	843.72	(559.21, 1220.2)
α	2.0268	(0.854, 3.566)
φ	0.0347	(-0.6325, 0.9239)
<i>Estimated error</i>		
Process error	0.2494	(0.1271, 0.4205)
Observation error, dam counts	0.1327	(0.1327, 0.2688)
Observation error, weir estimates	0.5284	(0.2368, 0.9981)

Table 5. Differences in expected log-predictive density (ELPD) and leave-one-out cross-validation information criterion (LOOIC) with associated standard errors for four candidate models with covariates that met inclusion criteria. ELPD difference is calculated relative to the model with the highest predictive accuracy.

Model	Covariates	ELPD difference	Standard error	LOOIC	Standard error
Base Ricker	None	-5.2	1.4	21.4	7.6
Habitat	Minimum flow, NPGO	-3.2	1.3	17.6	8.4
Habitat and predation	Minimum flow, NPGO, pinniped abundance	-4.1	1.2	19.4	7.9
Habitat, predation, and hatchery	Minimum flow, NPGO, pinniped abundance, hatchery smolt releases	0.0	0.0	11.1	7.5

Table 6. Median effect estimates, associated 95% credible intervals, and probability of direction from the posterior distributions of covariates included in the final Ricker stock-recruitment model.

Covariate	Median	95% CI	Probability of direction
NPGO	0.3202	(0.0179, 0.5810)	97.5%
Hatchery smolts released	0.1795	(0.0452, 0.3194)	99.3%
Minimum Hood River flow	0.1230	(-0.0564, 0.2988)	91.3%
Pinniped abundance	-0.2730	(-0.5639, 0.0476)	95.2%

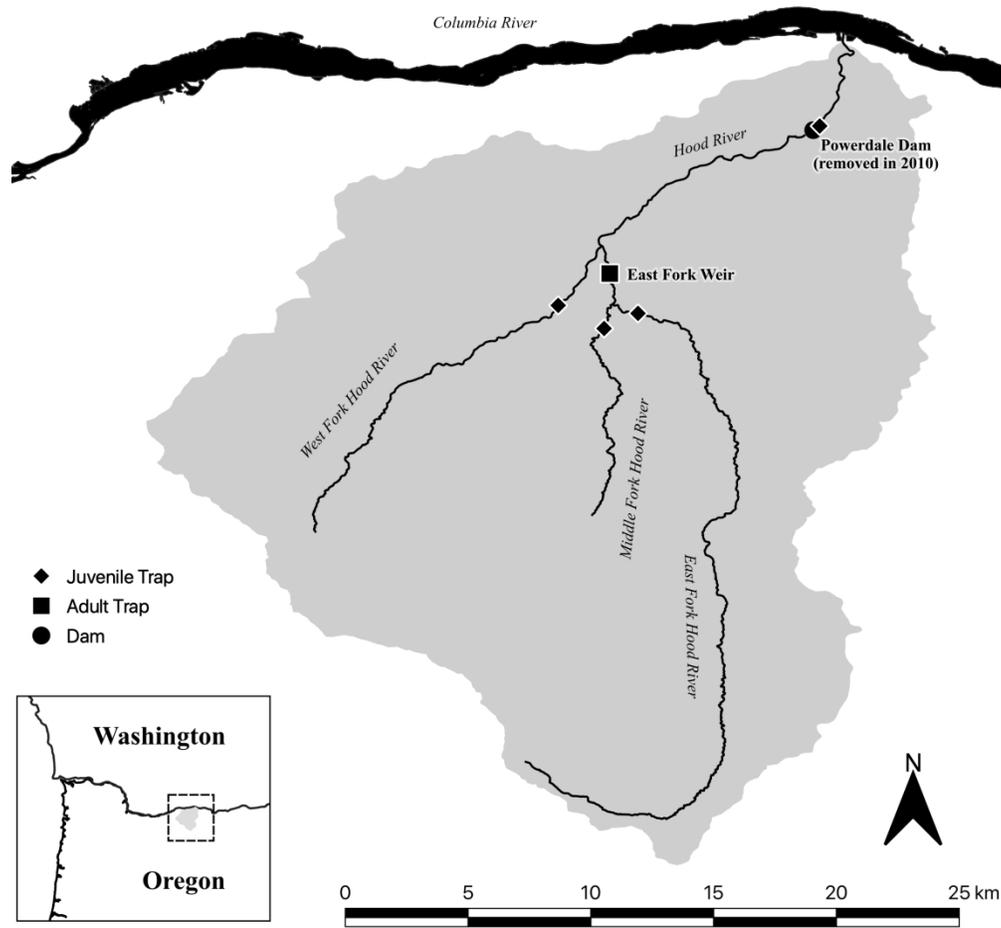


Figure 1. Map of the Hood River Basin and primary steelhead monitoring stations. Stream layer source: USGS (2018).

217x209mm (300 x 300 DPI)

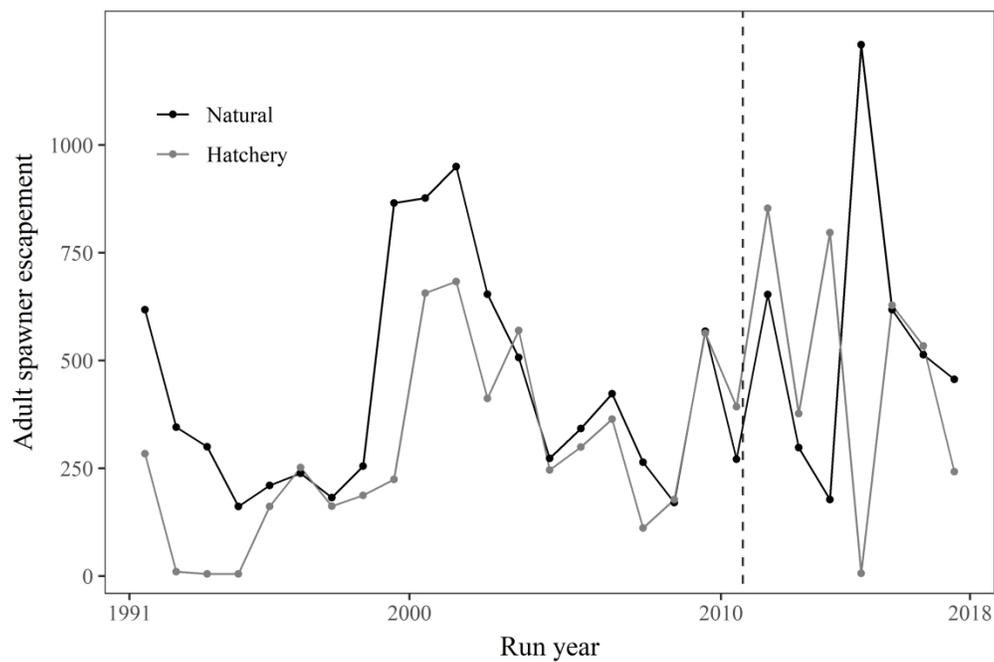


Figure 2. Estimated adult spawner escapement of natural and hatchery-origin winter steelhead upstream of Powerdale Dam prior to 2010 and upstream of the East Fork weir after dam removal, indicated by the dashed vertical line.

152x101mm (600 x 600 DPI)

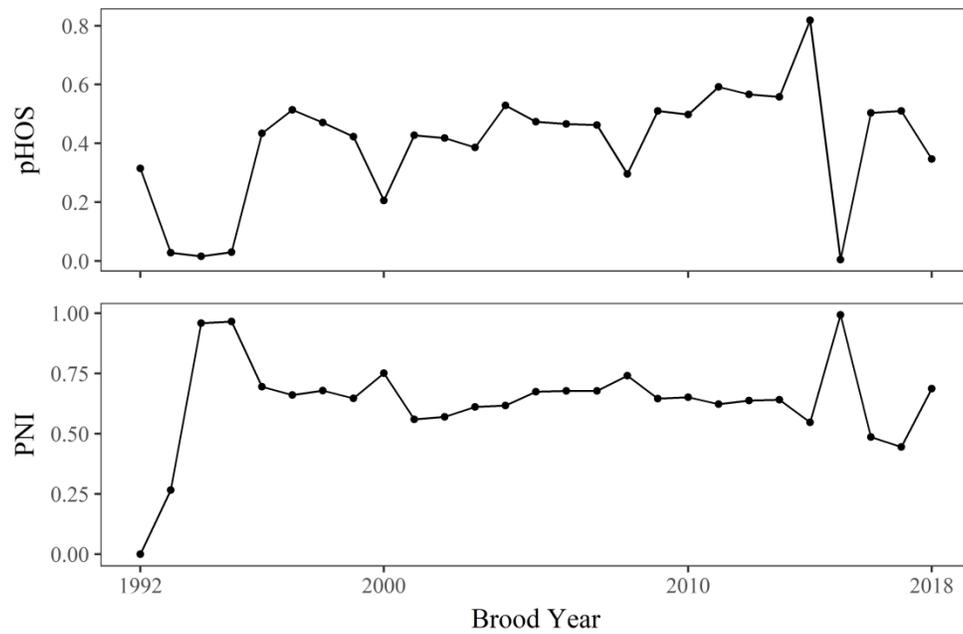


Figure 3. Time series of Hood River winter steelhead proportion of hatchery-origin spawners (pHOS) and proportionate natural influence (PNI) by brood year.

152x101mm (600 x 600 DPI)

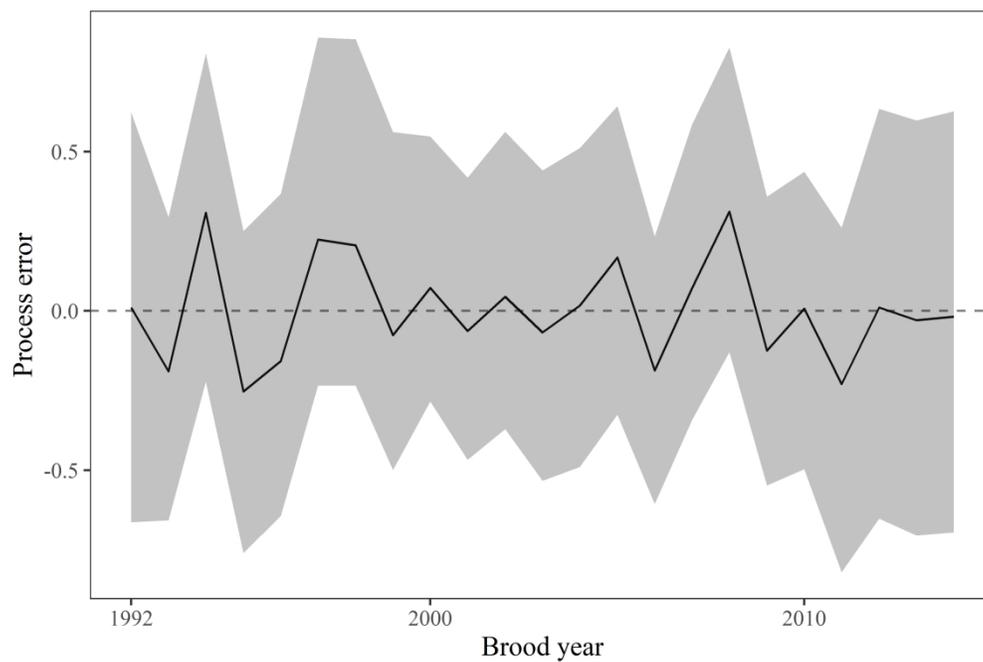


Figure 4. Time series of estimated process error after accounting for model covariates and density dependence. The solid line is the median estimate and the shaded area indicates the 95% credible interval.

152x101mm (600 x 600 DPI)

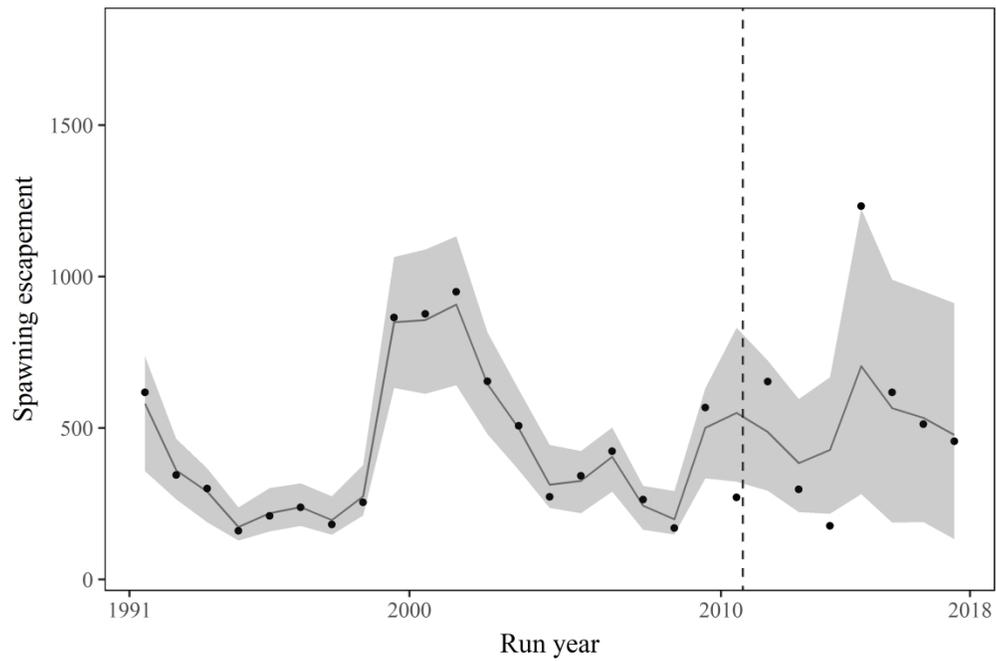


Figure 5. Observed and estimated natural-origin winter steelhead spawner escapement upstream of Powerdale Dam prior to 2010 and upstream of the East Fork weir after dam removal, indicated by the dashed vertical line. Points are observed values, the line is median model estimates, and the shaded region is the associated 95% credible interval.

152x101mm (600 x 600 DPI)

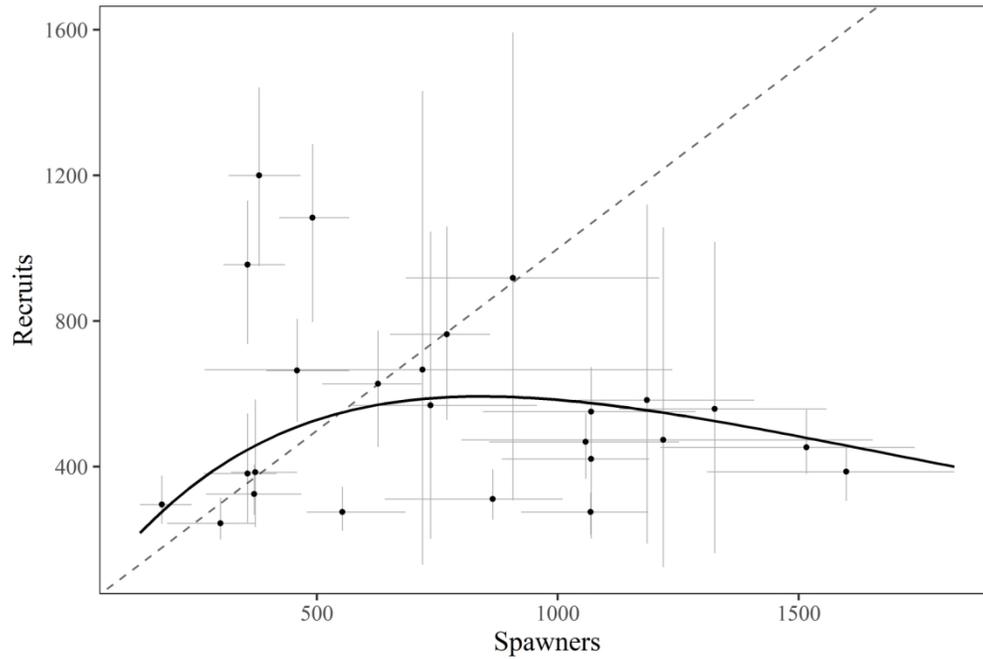


Figure 6. Ricker stock-recruitment model curve, fit at median posterior values and including the estimated effect of Powerdale Dam weighted by the proportion of the period of record when it was present. Points are annual estimates of Hood River winter steelhead recruitment are points with associated 95% credible intervals for brood years 1992 to 2016.

152x101mm (300 x 300 DPI)

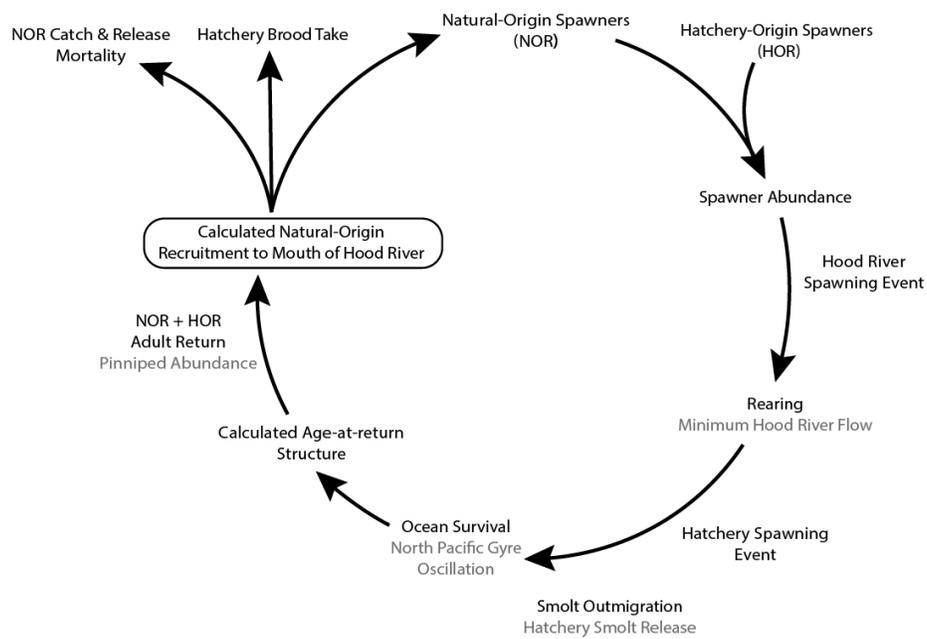


Figure 7. Hood River winter steelhead productivity model diagram depicting covariates applied at each life stage. Grey text indicates model covariates.

506x346mm (59 x 59 DPI)

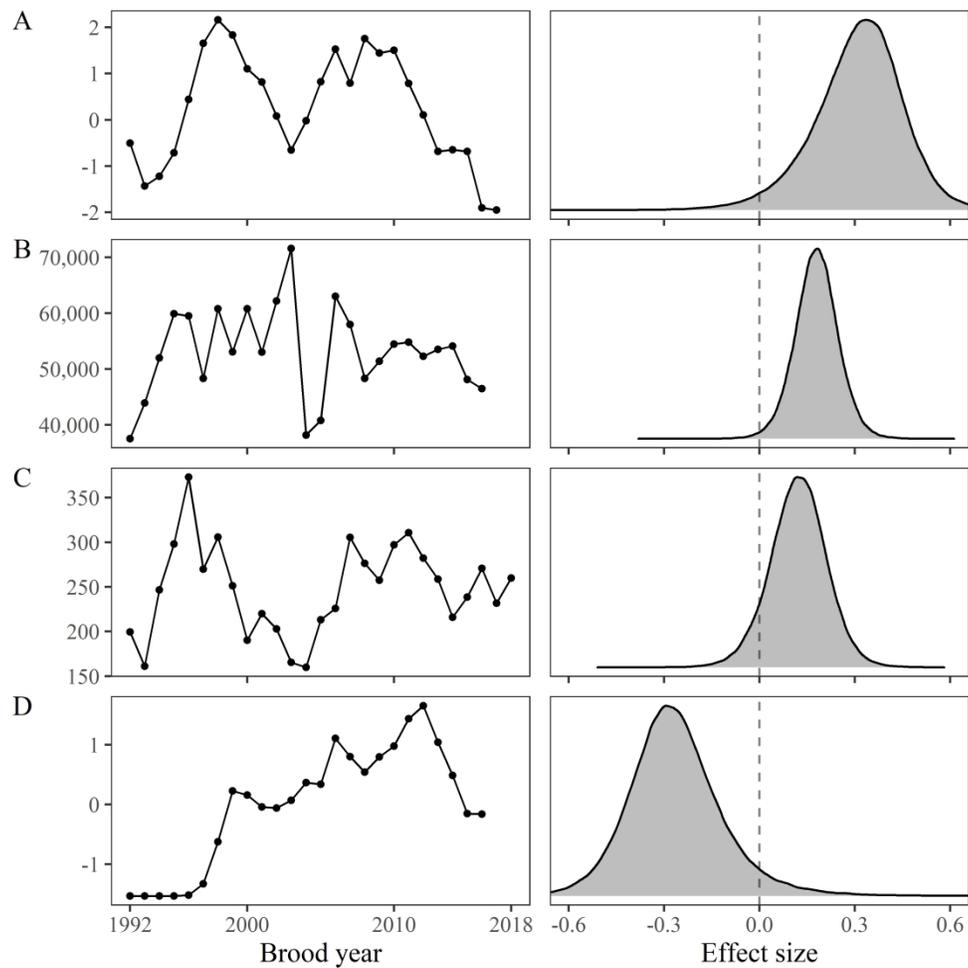


Figure 8. Time series of covariate values by brood year and posterior distributions of covariate effects. A: Northern Pacific Gyre Oscillation, B: hatchery smolt releases, C: minimum Hood River flow, and D: pinniped abundance at Bonneville Dam.

152x152mm (600 x 600 DPI)