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ARTICLE

A Natural-Origin Steelhead Population's Response to Exclusion of Hatchery Fish

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Abstract

It is asserted that reduction or elimination of hatchery stocking will increase natural-origin salmon *Oncorhynchus* spp. and steelhead *O. mykiss* production. We conducted an analysis of steelhead population census data (1958–2017) to determine whether elimination of summer steelhead stocking in the upper Clackamas River in 1998 increased the productivity of natural-origin winter steelhead. A Bayesian state–space stock–recruitment model was fitted to the adult steelhead data set, and productivity was estimated as a function of hatchery-origin spawner abundance as well as other environmental factors. When used as a predictive variable in our model, the abundance of hatchery summer steelhead spawners (1972–2001) did not have a negative effect on winter steelhead recruitment. However, spill at North Fork Dam (the gateway to the upper Clackamas River basin) and the Pacific Decadal Oscillation (an index of ocean conditions) were both negatively associated with winter steelhead recruitment. Moreover, winter steelhead abundance in the upper Clackamas River basin failed to rebound to abundances observed in years prior to the hatchery program, and fluctuations in winter steelhead abundance were correlated with those of other regional winter steelhead stocks. Our assessment underscores the need for studies that (1) directly quantify the effects of hatchery fish on the

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production of natural-origin salmon and steelhead, (2) empirically test published theories about mechanisms of hatchery fish impacts on natural-origin populations, and (3) document population responses to major changes in hatchery programs.

Throughout the Pacific Northwest, large-scale Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* hatchery programs have been used to mitigate for lost habitat and other anthropogenic impacts on natural fish production for over 100 years. Although hatcheries sustain large returns of adult fish for commercial and recreational harvest, regulatory protection of 28 genetically distinct Pacific salmon and steelhead stocks in the 1990s by the U.S. Endangered Species Act increased the scientific debate about the impacts of hatchery mitigation on natural-origin salmon and steelhead population viability. Hypothesized mechanisms of hatchery fish impacts on natural-origin salmon and steelhead production are numerous (e.g., Chilcote et al. 1986; Leider et al. 1990; Ford 2002; Weber and Fausch 2003; Berntson et al. 2011) and broadly categorized as genetic or ecological (Krueger and May 1991). Genetic interactions, such as those described by Araki et al. (2007), can be partially managed through use of locally derived stocks, through regular integration of natural-origin fish into the broodstock, and by limiting spawning interactions between natural- and hatchery-origin fish (Waples 1991). However, impacts from ecological interactions, such as increased predation or competition for available habitat (Harnish et al. 2014), are more difficult to control.

Theoretical mechanisms for ecological interactions abound in the literature (as reviewed by Kostow 2009), and observational evidence supports the validity of these theories (e.g., Harnish et al. 2014). However, relatively few direct empirical tests have demonstrated that these ecological interactions reduce natural-origin fish survival or production at a population scale (Pearsons et al. 2008). Moreover, studies have rarely considered the positive ecological effects of hatchery programs, such as increased importation of marine-derived nutrients (Scheuerell et al. 2005) or differences in habitat selection and rearing strategies of hatchery- and natural-origin fish (Davis et al. 2018), making it difficult to discern whether evidence of population-scale ecological impacts is lacking due to data shortfalls or to an incomplete understanding of the mechanisms affecting natural salmon and steelhead production.

One of the largest data sets available for examining this complex issue is maintained in the upper Clackamas River basin, Oregon, where a complete census of natural- and hatchery-origin adult steelhead abundance has been recorded since 1958. Analyzing this data set for adult return years 1958–2005, Kostow and Zhou (2006) concluded that a decline in productivity of the natural-origin winter steelhead population during return years 1972–1998 coincided with the presence of large numbers of hatchery-origin summer steelhead. Previous analyses indicated minimal spawning interaction between the two stocks (Kostow et al. 2003), and the authors concluded that deleterious genetic effects of domesticated hatchery fish spawning with natural-origin winter steelhead were not responsible for the observed productivity decline. Consequently, the authors posited that direct competition for freshwater resources between naturally produced offspring of hatchery summer steelhead and natural-origin winter steelhead was the most probable cause of the decline in productivity of the natural-origin population.

The findings of Kostow and Zhou (2006) received considerable attention due to the magnitude of the estimated decline in population productivity attributed to ecological effects of the hatchery program on natural-origin steelhead (~50% reduction in natural-origin adult recruitment during high hatchery return years). Concerns about ecological effects of hatchery fish on protected salmon and steelhead stocks, largely due to the results of that study, have led to numerous hatchery management changes throughout the Pacific Northwest (e.g., East Fork Lewis River steelhead, Puget Sound steelhead, Skagit River steelhead, Molalla River steelhead, Sandy River spring Chinook Salmon *O. tshawytscha*, Willamette River spring Chinook Salmon and steelhead, and Oregon coastal Coho Salmon *O. kisutch*). However, it remains uncertain whether these changes increased natural-origin salmon and steelhead production. Direct empirical demonstrations of the magnitude and directionality of hatchery fish impacts are needed. Therefore, we re-evaluated the upper Clackamas River winter steelhead data set for return years 1958–2017, expanding the production data time series in our analysis from 48 to 62 years, to determine whether trends in population productivity should be attributed to hatchery management or to other factors affecting steelhead productivity.

METHODS

Study area.— The Clackamas River basin (Figure 1) drains the western slopes of the Cascade Mountain Range near Olallie Lake, Oregon, between Mount Hood and Mount Jefferson—an area of roughly 2,435 km^2. The river is 133 km long and loses 1,370 m of elevation between its headwaters and its confluence with the Willamette River (river kilometer [rkm] 40.2), 2.4 km downstream of

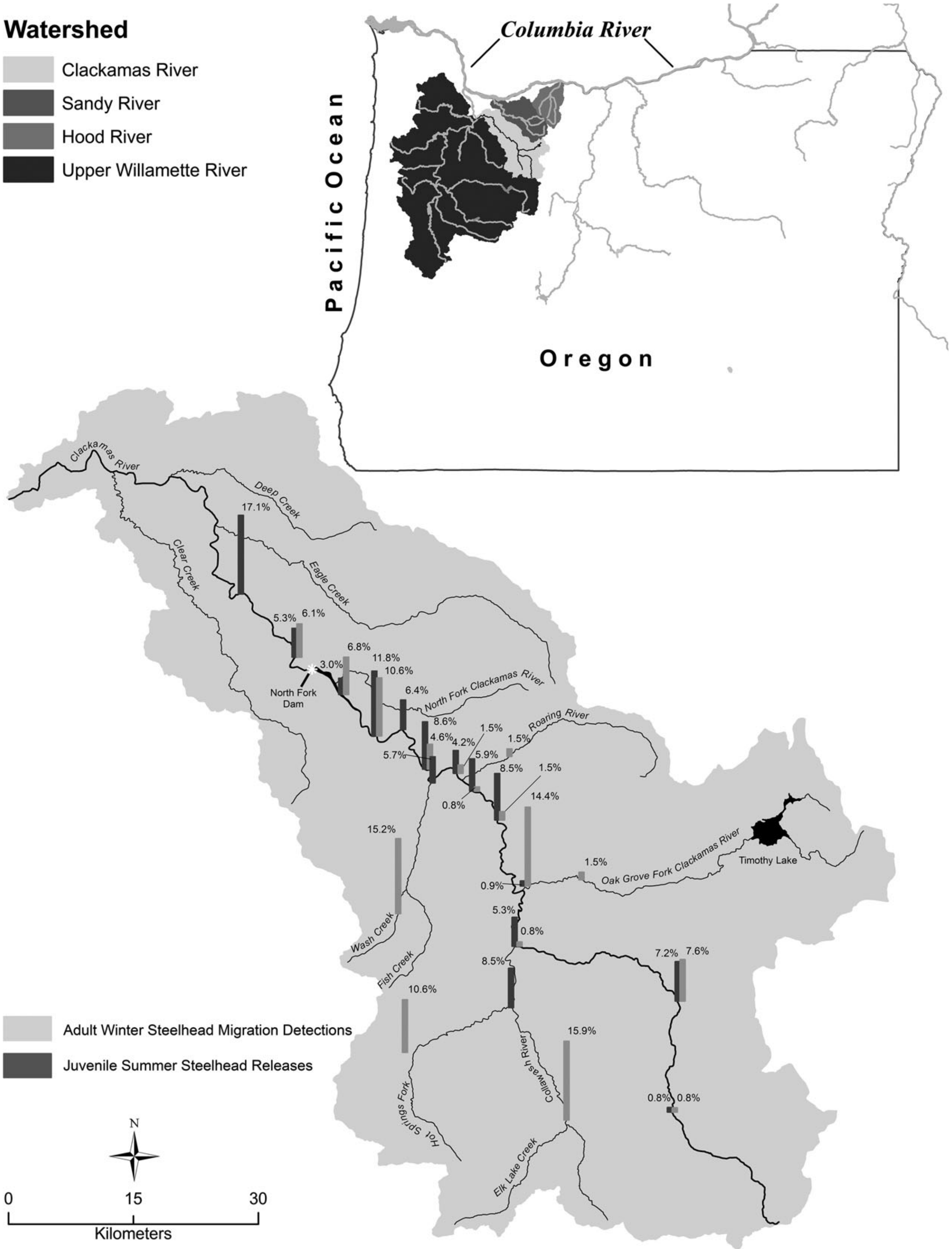

FIGURE 1. Map of the study area (upper Clackamas River basin, Oregon), depicting the location of North Fork Dam, the spawning distribution of natural-origin winter steelhead (David et al. 2018), and the proportion of hatchery-origin juvenile summer steelhead released at sites throughout the basin during 1970–1998 (Oregon Department of Fish and Wildlife, unpublished data).

Willamette Falls. The area of focus for this study includes the entire watershed upstream of North Fork Dam (rkm 46.5), often referred to as the upper Clackamas River basin, which supports populations of spring Chinook Salmon, Coho Salmon, and winter steelhead, all of which are listed as threatened under the U.S. Endangered Species Act.

Constructed in 1958, North Fork Dam serves as a counting station for upstream-migrating anadromous salmonids entering the upper Clackamas River basin and divides the basin into two management zones: a sanctuary for natural-origin fish upstream of the dam; and a large, hatchery-supported salmon and steelhead sport fishery downstream of the dam. However, this was not always the case. Planting of juvenile "Skamania" summer steelhead (a stock originally from the Washougal River, Washington) in the upper Clackamas River basin began in 1970, and the first adult return from these outplantings was recorded in 1972. By 1975, a robust summer steelhead fishery had emerged and was soon among the top summer steelhead retention fisheries in the state of Oregon (Oregon Department of Fish and Wildlife [ODFW], unpublished data), with a peak return exceeding 11,000 fish in 1984. In the late 1990s, due to concerns over possible negative effects of the hatchery program on viability of the natural-origin winter steelhead population, smolt release numbers upstream of North Fork Dam had subsided, and the last large return of adult hatchery-origin summer steelhead (>1,000) occurred in 1998. Releases of adult summer steelhead upstream of North Fork Dam were phased out after ODFW designated the upper Clackamas River basin a "Wild Fish Sanctuary" in 1999 (the last release of hatchery-origin fish upstream of North Fork Dam was 53 adult summer steelhead in 2001), and steelhead angling upstream of North Fork Dam was no longer permitted. In summary, annual summer steelhead supplementation practices in the upper Clackamas River basin can be categorized as follows: episodic or low (1958–1970 and 1999–2001), saturated (1970–1998), and excluded (2002–present). In addition to the summer steelhead hatchery program, early returning hatchery-origin winter steelhead from juvenile releases in the lower Clackamas River were also passed above North Fork Dam in relatively small numbers (averaged 2.9% of the winter steelhead return annually; range = 0–31%) over the period of record.

In concert with evolving fish management regimes, fish passage infrastructure and instream flows have also changed in the Clackamas River basin. As a result of the Federal Energy Regulatory Commission (FERC Number 2195) relicensing process, Portland General Electric (PGE) built, replaced, or modified most of the upstream and downstream migrant fish facilities to improve fish passage conditions through the Clackamas River Hydroelectric Project (hydrosystem) between 2006 and 2015 (Ackerman et al. 2014). Fish passage infrastructure, water flow, and temperature conditions present within the Faraday Dam diversion reach and North Fork Dam fish ladder adult sorting facilities changed considerably during that time. In addition, the installation of River Mill Dam and North Fork Dam juvenile fish collectors, combined with the North Fork Dam spillway exclusion net, has increased the percentage of downstream migrants captured and bypassed around the hydrosystem (Ackerman and Pyper 2018).

Analytical approach.— To examine the factors influencing abundance of natural-origin winter steelhead in the upper Clackamas River basin, including the presence of hatchery-origin summer steelhead, we obtained annual adult steelhead counts (Figure 2) and age data from PGE's database for the North Fork Dam fish collection and sorting facility (1958–2015). To ensure accuracy of the data set used in our analysis, we cross-referenced electronic records against archived data collection sheets. Adult winter steelhead counts were also obtained from three other neighboring subbasins in the lower Columbia River region: Willamette River (Willamette Falls, 1971–2015), Sandy River (Marmot Dam, 1978–2007), and Hood River (Powerdale Dam, 1992–2010; Figure 1). These three additional winter steelhead data sets were included in our assessment to serve as reference populations to examine whether trends in upper Clackamas River basin winter steelhead spawner abundance diverged from trends observed in other nearby basins.

Data handling.— In most contemporary Pacific Northwest hatcheries, juvenile salmon and steelhead are marked by removal of the adipose fin so that they can be differentiated from natural-origin fish after release. However, winter steelhead fisheries throughout Oregon's lower Columbia River basin were historically supplemented with unmarked Big Creek and Alsea River hatchery-origin steelhead. These coastal hatchery stocks have an earlier adult migration timing (November–January) compared with natural-origin winter steelhead stocks that are indigenous to the lower Columbia River (February–April). Therefore, we chose calendar dates as a means to exclude returning winter steelhead that were likely unmarked hatchery-origin fish (or the progeny of hatchery-origin fish) from each winter steelhead data set. Indigenous winter steelhead were assumed to be those that arrived at each counting station between February 15 and May 31. Additional data adjustments and assumptions were as follows:

- Natural-origin winter steelhead broodstock were historically collected in small numbers at North Fork Dam. Fish used as broodstock were deducted from dam counts when determining spawner abundance values for the upper Clackamas River.
- Harvest of natural-origin winter steelhead in all fisheries downstream of North Fork Dam was estimated as a

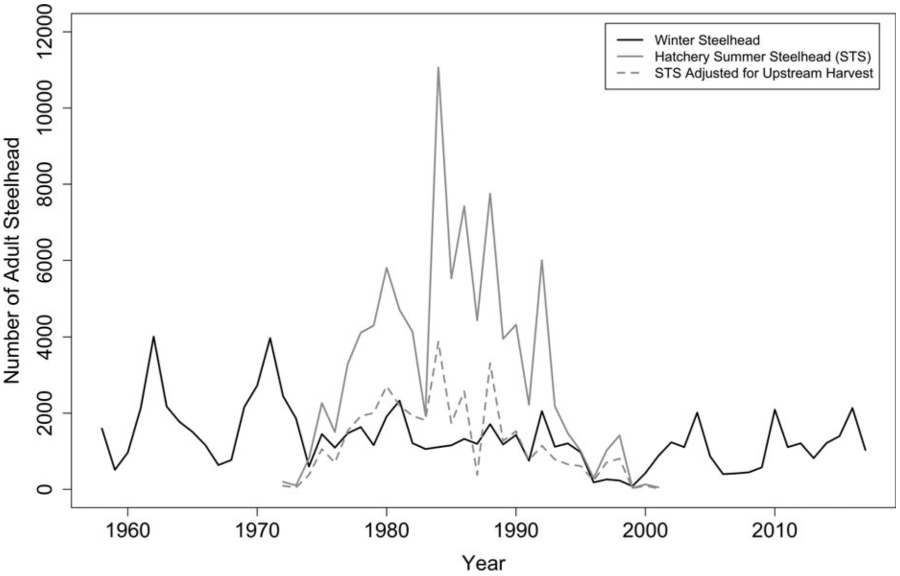

FIGURE 2. Annual abundance of natural-origin adult winter steelhead and hatchery-origin adult summer steelhead (STS) that passed upstream of North Fork Dam in the upper Clackamas River basin, 1958–2017.

composite of lower Columbia River commercial and recreational harvest rates (1958–2017) obtained from ODFW and Washington Department of Fish and Wildlife (WDFW) agency reports (ODFW and WDFW 2002) and ODFW creel survey data. Exploitation rates in the lower Columbia River averaged 9% between 1958 and 1974 and dropped to less than 2% thereafter due to harvest reforms. Harvest data for Columbia River tributaries are limited. Best estimates from creel survey data suggest that recreational fishery exploitation rates in the lower Willamette River and lower Clackamas River were approximately 15% on average between 1958 and 1991, ranging from 10% to 30% annually (ODFW 2017). Recreational harvest dropped substantially to less than 1.5% after 1991 due to the adoption of mark-selective fishery regulations, which required anglers to release all natural-origin fish. Unreported harvest is likely rare and would cause our productivity estimates to be biased low.

Estimation of hatchery fish influence on adult steelhead recruitment.— Reconstructing adult fish recruitment from their parental brood requires two types of data: an annual time series of the number of parent spawners and their age composition. Spawner escapement values were derived from census counts for winter steelhead that passed upstream of North Fork Dam, providing escapement values with little observation error. However, due to potential angling impacts and other factors affecting prespawn survival, as well as strays from other nearby populations, we did not know the precise number of natural-origin spawners and recruits. Moreover, age data were extremely limited because scale samples from adult steelhead were not collected annually, and sampling occurred intermittently within years. A common approach to overcome this obstacle is to assume a constant age structure when estimating recruitment for all brood years, but this can result in recruitment estimates that are biased high during low spawner return years and biased low during high spawner return years (Zabel and Levin 2002). Therefore, to approximate the most plausible annual age composition values for the upper Clackamas River basin winter steelhead data set and to account for observation error in our spawner and recruitment estimates, we developed a Bayesian state–space model following the methods of Fleischman et al. (2013). The state–space model allowed us to simultaneously estimate both process error (unexplained variation in recruitment and maturation) and observation error (incomplete accounting of spawner abundance, harvest, and age composition).

The age composition of returning adult winter steelhead was determined from scales collected from a subsample of fish over a 16-year period from 1982 to 1997 (n = 333; ODFW, unpublished data). Sample sizes differed between years and ranged from 5 to 65 fish annually. In total, 3 fish were estimated to be age 3; 198 were age 4; 109 were age 5; and 23 were age 6. Approximately 6% of winter steelhead returns to the Clackamas River are thought to be repeat spawners (Clackamas River Working Group, unpublished data), which would be expected to cause a small positive bias in our recruitment estimates. To account for uncertainty in annual estimates of age composition for the entire period of record (1958–2017), we assumed that the returns of age-A fish in brood year y ($N_{A,y}$) followed a multinomial distribution with sample size parameter $N_{\cdot,y}$ and proportion parameters as follows:

$$q_{A,y} = N_{A,y}/N_{\cdot,y}, \tag{1}$$

where $N_{A,y}$ is the total number of fish in each age-class observed each year; and $N_{\cdot,y}$ is the total subsample collected each year for age analysis.

Vectors of brood-year-specific age-at-return probabilities ($P_{i,y}$) were then modeled hierarchically as random draws from a Dirichlet distribution:

$$P_{i,y} \sim \text{Dirichlet}(\gamma_i). \tag{2}$$

The total number of recruits R from brood year y was then estimated as the sum of returns of age-A fish in year $y + A$ for all age-classes:

$$R_y = \sum\nolimits_{A=3}^{6} N_{A,y+A}. \tag{3}$$

To estimate the influence of hatchery-origin steelhead and other environmental covariates on winter steelhead recruitment, we fitted a stock–recruitment model to the reconstructed recruitment estimates in a manner similar to that described by Fleischman et al. (2013) and used a Ricker model (Ricker 1954) to describe density-dependent population dynamics. Both Beverton–Holt (Beverton and Holt 1957) and Ricker stock–recruitment models were explored; although these models revealed similar inferences about the influence of hatchery steelhead on winter steelhead production, the Beverton–Holt model provided productivity estimates that were biologically unreasonable. The formulation of the Ricker recruitment model used in our analysis can be described as

$$\log_e(R_y) = \log_e(S_y) + \log_e(\alpha_y) - \beta S_y + \phi\omega_{y-1} + \varepsilon_y, \tag{4}$$

where R_y is the number of natural-origin winter steelhead recruits produced from brood year y; S_y is the natural-origin winter steelhead spawner escapement in year y; α_y is the productivity parameter for brood year y, measuring the number of recruits per spawner at low spawner abundance; β is the capacity parameter; ϕ is the lag-1 autoregressive coefficient; ω_y is the model residual; and ε_y is the independent normally distributed process error with variance σ_p^2.

To further explain the year-to-year variability in recruitment, we modeled α as a time-varying process because steelhead survival varies annually and is driven by large-scale fluctuations in environmental conditions (M. Scheuerell, National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Seattle, personal communication). This approach allowed us to account for the interannual influence of survival covariates on recruitment as

$$\alpha = \mu + \sum\nolimits_{i=1}^{k} c_i X_{i,y+h_i}, \tag{5}$$

where μ is the underlying mean productivity; c_i is the effect of X_i, a covariate measured at year y and adjusted for time lag h_i, in accordance with the life history of Clackamas River winter steelhead. We included adult hatchery summer steelhead returns, North Fork Dam spill volume index (SVI), and May Pacific Decadal Oscillation (PDO) as covariates in our analysis (Figure 3). All covariates were standardized by subtracting the mean and dividing by the SD to allow for direct comparisons across estimated coefficients.

Bayesian inference was used to estimate all model parameters in R (R Core Team 2017) using the package "runjags" (version 4.2.0; Plummer 2003; Denwood 2016), specifying priors for all unknowns in the model (Table 1) and using Markov chain–Monte Carlo methods to generate posterior distributions for all unknowns. This process quantifies the uncertainty associated with each parameter estimate as well as the estimate of age composition drawn from the Dirichlet distribution. Our methods were similar to those of Fleischman et al. (2013) to determine posterior distributions of unknown parameters. Three parallel chains of 80,000 iterations were generated, with a burn-in period of 30,000 iterations, thinning each chain every 100 samples. Convergence of each parameter was checked visually with trace plots to ensure mixing of chains and was checked quantitatively by ensuring that the Gelman–Rubin statistic ($\hat{R}$) was less than 1.1. Model sensitivity to priors was assessed by the method of Fleischman et al. (2013), and diffuse priors were used for slope parameter estimates (i.e., c_1, …, c_3) so that priors had little influence on posterior distributions.

Hatchery summer steelhead spawner abundance.— Summer steelhead spawner abundance was estimated as the number of adult summer steelhead that passed upstream of North Fork Dam less the number of fish harvested by anglers in the upper Clackamas River (Figure 2). Since 1983, ODFW has maintained records of harvest cards submitted by anglers documenting the species and location of fish harvest. These records indicate substantial harvest of summer steelhead upstream of North Fork Dam during the period of record (mean = 1,886; SD = 2,182). We used annual counts of harvested fish obtained from ODFW's harvest card database to estimate potential summer steelhead spawner abundance in 1983–2001. An average value of 53% was used to predict harvest prior to 1983. Average estimated summer steelhead spawner abundance for the entire period of record was 637 (SD = 954). Submission of harvest cards by anglers is voluntary, and no adjustments were made for unreported harvest. Therefore, our

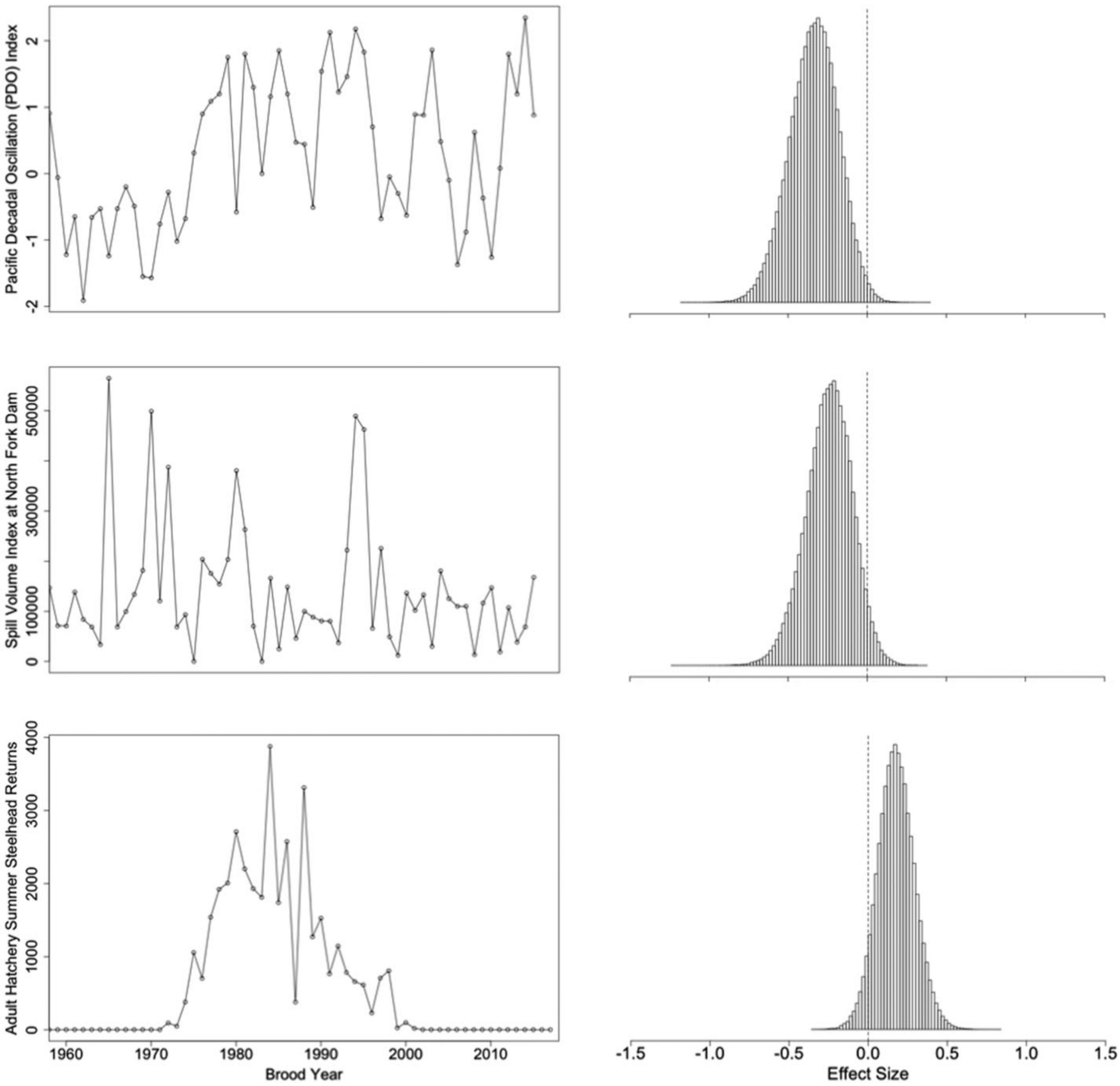

FIGURE 3. Time series of productivity covariates used in the upper Clackamas Basin winter steelhead recruitment model, 1958–2015 (left column) and posterior distributions of estimated effect size of each covariate (right column) on upper Clackamas Basin winter steelhead population productivity.

estimates of summer steelhead spawner abundance were likely negatively biased.

Ocean conditions.— To select the most appropriate ocean survival covariate in the model, we evaluated the influence of steelhead ocean survival indices identified by Petrosky and Schaller (2010) on steelhead recruitment in the upper Clackamas River basin. Petrosky and Schaller (2010) included May PDO, May upwelling indices, and March sea surface temperature (SST) and found that decreased smolt-to-adult survival and early ocean survival rates were mainly associated with warmer ocean conditions and reduced spring upwelling. Therefore, we evaluated the influence of May PDO (JISAO 2017) and May upwelling (PFEL 2017) on annual productivity estimates

TABLE 1. Prior distributions for parameters estimated in the Bayesian state–space Ricker stock–recruitment model for upper Clackamas River basin winter steelhead (JAGS = Just Another Gibbs Sampler; PDO = Pacific Decadal Oscillation; SVI = spill volume index at North Fork Dam; CSH = adult hatchery summer steelhead returns).

Text	JAGS	Prior
$\log_e(\alpha_y)$	lnalpha[y]	A function of covariates C0, . . ., C3
Intercept	C0	~Normal(0, 0.001)
PDO	C1	~Normal(0, 0.001)
SVI	C2	~Normal(0, 0.001)
CSH	C3	~Normal(0, 0.001)
β	beta	~Normal(0, 0.01) truncated [0,]
φ	phi	~Normal(0, 0.0001) truncated [−1, 1]
σ_R	sigma.R	~Gamma(0.001, 0.001)
π_1–π_4	pi[1:4]	~Dirichlet(0.2, 0.2, 0.2, 0.2)
R_1–R_6	R[1:6]	~Lognormal($\log_e[R_0]$, σ^2_{R0})
$\log_e(R_0)$	mean.log.R	~Normal(0, 0.0001) truncated [0,]
ω_0	log.resid	~Normal(0, $\sigma^2_R[1 - \varphi^2]$)
σ_{R0}	sigma.R0	~Gamma(0.001, 0.001)

for late-winter steelhead in the upper Clackamas River basin. March SST (Hadley Centre Sea Ice and SST Data Set: HadISST 2000) was excluded from our analysis because the time series for those data did not overlap completely with steelhead escapement estimates for the upper Clackamas River basin.

We fitted the Ricker production model for both May PDO and May upwelling. Model results were compared, and the most influential ocean condition variable was selected. Specifically, we examined the resulting covariate coefficient values to determine which metric best described the variability associated with steelhead production, and we found that May PDO had a stronger influence than May upwelling indices on model predictions of upper Clackamas River basin winter steelhead recruitment. Median coefficient values ranged from −0.5629 to −0.0892 for May PDO and from −0.2860 to −0.0359 for May upwelling indices. For the period of record, average May PDO was 0.28 (SD = 1.12).

Spill volume index.— Most juvenile steelhead are collected at North Fork Dam via a surface collection system and bypass the hydrosystem. When flows exceed the North Fork Dam powerhouse capacity (184 m^3/s), spill must occur, and the proportion of steelhead using the bypass declines dramatically in favor of the spillway (Ackerman and Pyper 2018). Steelhead passing North Fork Dam via the spillway have much lower survival than those in the bypass (Ackerman and Pyper 2018; P. G. Heisey, D. Mathur, J. L. Fulmer, S. W. Adams, and T. D. Brush, 2002 final report to Portland Gas and Electric and Clackamas River Project Fisheries and Aquatics Workgroup, on juvenile salmonid spillway passage survival at North Fork Dam). The SVI is a metric designed to provide an index of the quantity of spill that occurs during the smolt migration season. It was hypothesized that higher SVI values may be correlated with lower adult steelhead production due to lower smolt survival through the hydrosystem.

The SVI was calculated for each month (December–May) in each smolt migration year as the number of days spill occurred at North Fork Dam multiplied by the mean daily maximum spill volume for that month. The monthly SVI values were then summed across months within a migration year. Between 1958 and 2015, the SVI had a mean value of 141,308 (SD = 127,141).

Comparisons to reference populations.— We explored whether winter steelhead abundance in the upper Clackamas River basin during and after the period of hatchery stocking deviated from abundance trends for other winter steelhead stocks in the region. Correlations between returns of lower Columbia River basin winter steelhead from the upper Clackamas, upper Willamette, Sandy, and Hood River basins were examined using Pearson's product-moment correlation analysis and simple linear regression in program R. Pearson's product-moment correlation was used to quantify the extent to which each population's abundance was related to the others, while simple linear regression was used to visualize those relationships.

Summer steelhead stocking in Oregon was widespread in the 1990s, and the three reference populations in our analysis also had hatchery summer steelhead programs. We thought it was plausible that synchrony amongst returns of hatchery summer steelhead within each population could contribute to correlations between winter steelhead abundance if summer steelhead presence was a prominent driver of winter steelhead production. However, examination of the relative proportions of summer and winter steelhead spawners in each population revealed asynchronous hatchery management across basins.

RESULTS

The median estimated carrying capacity of the upper Clackamas River basin for natural-origin winter steelhead was 1,267 adult recruits, with a median density-independent productivity estimate of 4.48 recruits/spawner (Table 2). The population exhibited density-dependent recruitment across the full range of observed spawner abundances between 1958 and 2015 (Figure 4), suggesting that relatively few spawners are needed to fully seed the available habitat. We estimated that approximately 750 spawners are needed to maximize adult production potential. However, there was considerable uncertainty in our annual estimates of recruitment, which also led to a broad range of predicted carrying capacity and productivity parameter estimates. Ninety-five-percent credible intervals ranged between 1,182 and 1,931 recruits for carrying capacity and between 1.93 and 9.97 recruits/spawner for productivity.

Increases in both May PDO and the SVI had a negative influence on predicted upper Clackamas River basin winter steelhead recruitment (Table 2; Figure 4). However, there was little evidence to suggest a negative effect of hatchery summer steelhead abundance on winter steelhead productivity. In fact, the median of the posterior probability distribution for effects of hatchery summer steelhead abundance on winter steelhead productivity was positive, and more than 90% of the posterior probability effect sizes were greater than zero.

TABLE 2. Median Ricker stock–recruitment model parameter estimates, with 95% credible intervals in parentheses (PDO = Pacific Decadal Oscillation; SVI = spill volume index at North Fork Dam; CSH = adult hatchery summer steelhead returns). Parameters are defined in Methods (see equation 4).

Model parameter	Median
β	0.0013 (0.0006–0.0019)
α (recruits/spawner)	4.4772 (1.9279–9.9719)
Spawner capacity	749.58 (464.08–1,289.01)
ϕ	0.5839 (0.0130–0.9999)
Productivity covariates	
CSH	0.1738 (−0.0483 to 0.4108)
PDO	−0.3319 (−0.6400 to −0.0414)
SVI	−0.2365 (−0.5410 to 0.0308)
Estimated error	
Process error	0.4137 (0.1121–0.7074)
Observation error	0.3627 (0.1118–0.5930)

Returns of natural-origin winter steelhead have not increased since the hatchery fish exclusion period began (Figure 2). An average of 1,183 (range = 83–2,447) winter steelhead returned during the summer steelhead augmentation period from 1972 to 2001, and an average of 1,130 (range = 400–2,134) winter steelhead returned during the hatchery exclusion period from 2002 to 2017. There were positive and statistically significant correlations between winter steelhead returns to the upper Clackamas River basin and winter steelhead returns to the upper Willamette and Sandy River basins (Figure 5). Winter steelhead returns to the upper Willamette Basin were also highly correlated with returns to the Sandy and Hood River basins. Interestingly, steelhead returns to the Hood River basin were not highly correlated with returns to the Sandy and upper Clackamas River basins.

DISCUSSION

We tested whether the presence of hatchery-origin summer steelhead in the upper Clackamas River basin changed the productivity of the natural-origin winter steelhead population. Hatchery-origin summer steelhead spawner abundance did not have a negative effect on our estimates of upper Clackamas River basin adult winter steelhead productivity. Instead, the abundance of summer steelhead spawners was positively associated with winter steelhead productivity in our analysis, perhaps due to migration and ocean survival conditions common to both life history types. Our observation contradicts the previous assertion that negative ecological interactions between naturally

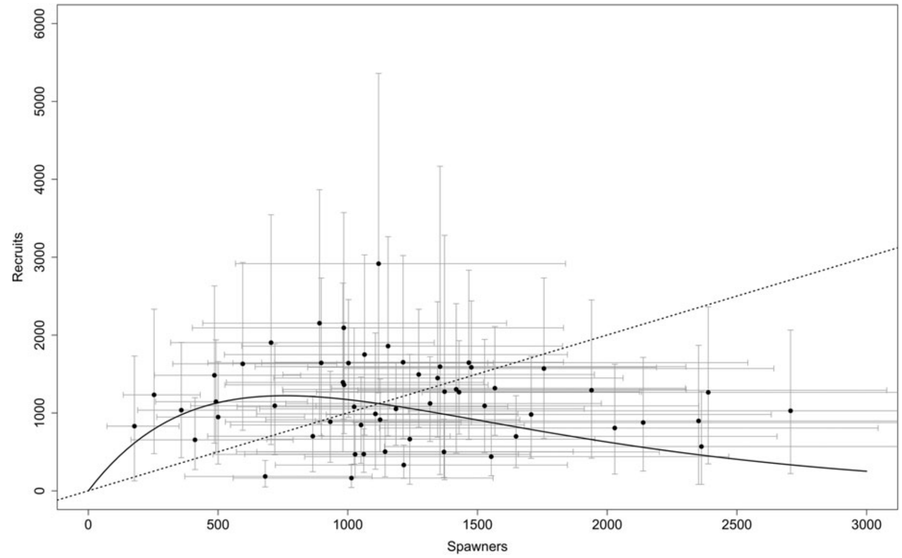

FIGURE 4. Annual estimates of upper Clackamas Basin winter steelhead recruitment (closed circles) with 90% credibility intervals (whiskers) for brood years 1958 to 2015. Ricker model relationship shown with all model parameters, including covariates, set to median estimates (black line).

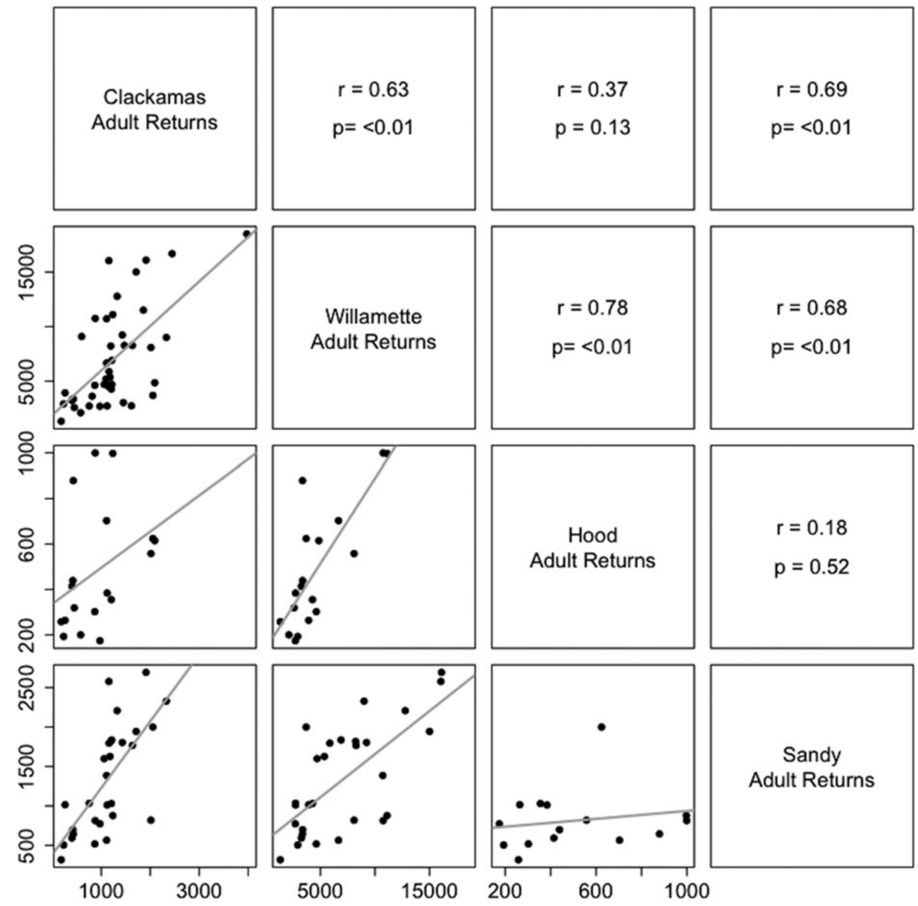

FIGURE 5. Relationships between counts of adult natural-origin late-winter steelhead returning to the upper Clackamas River (1971–2015), upper Willamette River (1971–2015), Hood River (1992–2004), and Sandy River (1978–2001), Oregon.

produced summer steelhead juveniles and winter steelhead juveniles reduced upper Clackamas River basin winter steelhead productivity between 1972 and 1998 (Kostow and Zhou 2006). If this causal mechanism was accurate, then productivity of the winter steelhead population would have increased with hatchery fish exclusion beginning in 2002; however, adult winter steelhead abundance failed to rebound (Figure 2), suggesting that the presence of hatchery fish was not driving the population dynamics.

The significance of an ocean effect (May PDO) on winter steelhead productivity in our recruitment model was consistent with previous research. Kendall et al. (2017) reported that ocean entry conditions are important for steelhead smolt-to-adult survival. For example, early ocean growth affects the susceptibility of steelhead to ocean predation (Friedland et al. 2014). More broadly, ocean conditions influence the production of other Pacific salmonid species, causing the abundance of contiguous populations to covary (Peterman et al. 1998; Pyper et al. 2002; Teo et al. 2009; Kilduff et al. 2014; Zimmerman et al. 2015). These findings are inconsistent with Kostow and Zhou (2006), who found a poor association between their ocean survival covariate (mean PDO during ocean residence) and steelhead productivity. In an effort to understand these findings, we truncated the data set to the same years (1958–2005) examined by Kostow and Zhou (2006) and found a negative association between May PDO and steelhead recruitment (median = −0.23; 95% confidence interval = −0.60 to 0.06), suggesting that their findings may have been driven by their choice of ocean survival covariate. A shift to a less-productive ocean phase coincident with the initiation of the summer steelhead hatchery program could have resulted in an apparent negative effect of hatchery fish on natural-origin fish in their analysis. Indeed, May PDO averaged 0.60 during the years of hatchery fish presence and dropped to an average of 0.40 during the exclusion period.

Productivity of anadromous fish populations is a function of both in-basin and out-of-basin survival factors. One approach to test for influence of the most influential factors is to compare annual abundance or productivity trends amongst neighboring populations (Pyper et al.

2001, 2002; Mueter et al. 2007; Lister 2014). When neighboring anadromous fish populations show divergent trends in spawner abundance, this may be an indicator that fine-scale factors, such as local changes in fisheries management or habitat conditions, are influencing fish production (Lawson et al. 2004; Pyper et al. 2005; Thompson and Beauchamp 2014). Conversely, regional synchronicity in salmon or steelhead abundance would indicate that broad-scale environmental factors, such as ocean conditions, are driving fish production (Mantua et al. 1997; Peterman and Dorner 2012; Stachura et al. 2014; Kendall et al. 2017). This "neighborhood effect" was reflected in our analysis, as we observed significant correlations in adult fish abundance in several of our pairwise comparisons between winter steelhead populations in the lower Columbia River region. This regional covariation lends support to our finding that ocean conditions, rather than the abundance of summer steelhead, have been the dominant driver of adult winter steelhead productivity in the upper Clackamas River basin.

Because our findings and conclusions differ from the analysis previously reported by Kostow and Zhou (2006), it is important to further elucidate the differences between our approach and theirs. One notable difference is that Kostow and Zhou (2006) estimated summer steelhead spawner abundance as the number of adult summer steelhead that passed annually upstream of North Fork Dam (Figure 2), less 15% prespawn mortality. Harvest records from ODFW indicate an average harvest of 53% on summer steelhead upstream of North Fork Dam (1983–2001), ranging annually from 6.9% to 66%. Therefore, a considerable difference existed between the available number of summer steelhead spawners assumed by Kostow and Zhou (2006; mean = 3,405; range = 249–9,403) and the actual number of potential summer steelhead spawners. In our analysis, we calculated maximum summer steelhead spawner abundances (mean = 1,359; range = 229–3,877) from returns to North Fork Dam and catch records upstream of the dam.

We were unable to obtain the data used by Kostow and Zhou (2006); therefore, direct comparisons between our data set and theirs were not possible. However, we noted at least one significant difference between the two winter steelhead data sets. Shortly after the hatchery exclusion period began, a return of 3,000 adult winter steelhead was reported in run year 2004 (see Kostow and Zhou 2006: their Figure 1A). This would have been a relatively large return for this population, and it was cited as an early indication that the declining trend in winter steelhead abundance reversed shortly after the hatchery fish exclusion period began. However, archived data sheets indicated an actual return of 2,110 winter steelhead that year, similar to escapement levels observed during the period of hatchery fish presence.

Finally, an important component of the findings reported by Kostow and Zhou (2006) involved calculations of juvenile steelhead recruitment from a smolt trap at the North Fork Dam juvenile bypass. We examined those data and found that juvenile fish counts at the dam did not provide a reliable measure of fish production because river flow conditions have a large impact on juvenile capture efficiency at the smolt trap (Ackerman and Pyper 2018). Unfortunately, the data required to account for variable juvenile collection efficiency across flows are not available for years prior to 2016. Given the large variability in flow conditions during the period of record, an analysis of the effects of summer steelhead on juvenile winter steelhead recruitment would be confounded by fluctuations in trap efficiency. Moreover, data are lacking to accurately proportion juvenile steelhead emigrants by life history type (early winter, late winter, and summer). We recommend that future studies investigate the utility of a state–space model for juvenile winter steelhead recruitment in the upper Clackamas River basin.

Separation in spawn timing and location may explain why the presence of large numbers of summer steelhead did not reduce the productivity of adult winter steelhead. Returning hatchery summer steelhead entered the basin in June–August and spawned in December–February, while natural-origin winter steelhead adults entered the basin in February–April and spawned in April–May. Additionally, releases of summer steelhead hatchery smolts tended to occur at lower elevations in the main-stem Clackamas River, while winter steelhead likely spawned further upstream in the basin and largely in tributaries to the main stem. David et al. (2018) found that 68% of winter steelhead spawners entered upper Clackamas River tributaries, but only 23% of hatchery summer steelhead were released in upper Clackamas River tributaries during the augmentation program (ODFW, unpublished data). If hatchery summer steelhead spawned at lower elevations proximate to their release sites, this may have limited their ecological interactions with winter steelhead because naturally produced juvenile summer steelhead were inhabiting areas downstream of the most productive winter steelhead rearing habitat.

Overall, environmental factors appear to have been more influential than the abundance of hatchery fish on winter steelhead productivity in the upper Clackamas River basin. In this case, the segregated summer steelhead hatchery program coexisted with the natural-origin winter steelhead population without negatively impacting adult winter steelhead recruitment. Our assessment of winter steelhead population response to changes in hatchery management in the upper Clackamas River basin underscores the need for studies that (1) directly quantify the effects of hatchery fish on the production of natural-origin salmon and steelhead, (2) empirically test published theories about mechanisms of hatchery fish impacts on natural-origin populations, and (3) document population responses to major changes in hatchery programs.

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REFERENCES

Ackerman, N., M. David, G. Wyatt, and D. Cramer. 2014. Upstream fish passage effectiveness monitoring 2014 annual report. Portland General Electric, Clackamas River Project Federal Energy Regulatory Commission 2195, Portland, Oregon.

Ackerman, N., and B. J. Pyper. 2018. Evaluation of juvenile salmonid passage through the North Fork hydro development. Portland General Electric, Clackamas River Project Federal Energy Regulatory Commission 2195, Portland, Oregon.

Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100–103.

Berntson, E. A., R. W. Carmichael, M. W. Flesher, E. J. Ward, and P. Moran. 2011. Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha basin, Oregon). Transactions of the American Fisheries Society 140:685–698.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Springer Science and Business Media, Dordrecht, The Netherlands.

Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Transactions of the American Fisheries Society 115:726–735.

David, M., N. K. Ackerman, G. Wyatt, and D. Cramer. 2018. Upstream fish passage effectiveness monitoring 2017 annual report. Portland General Electric, Clackamas River Project, Federal Energy Regulatory Commission 2195, Portland, Oregon.

Davis, M. J., I. Woo, C. S. Ellings, S. Hodgson, D. A. Beauchamp, G. Nakai, and S. E. W. De La Cruz. 2018. Integrated diet analyses reveal contrasting trophic niches for wild and hatchery juvenile Chinook Salmon in a large river delta. Transactions of the American Fisheries Society 147:818–841.

Denwood, M. J. 2016. Runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. Journal of Statistical Software [online serial] 71:9.

Fleischman, S. J., M. J. Catalano, R. A. Clark, and D. R. Bernard. 2013. An age-structured state–space stock–recruit model for Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 70:401–414.

Ford, M. J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16:815–825.

Friedland, K. D., B. R. Ward, D. W. Welch, and S. A. Hayes. 2014. Postsmolt growth and thermal regime define the marine survival of steelhead from the Keogh River, British Columbia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 6:1–11.

HadISST (The Hadley Centre Global Sea Ice and Sea Surface Temperature). 2000. March sea surface temperature data obtained using the University Corporation for Atmospheric Research web portal and originated from the Hadley Centre Global Sea Ice and Sea Surface Temperature. Available: https://rda.ucar.edu/. (February 2019).

Harnish, R. A., E. D. Green, C. R. Vernon, and G. A. McMichael. 2014. Ecological interactions between hatchery summer steelhead and wild *Oncorhynchus mykiss* in the Willamette River basin, 2014. Pacific Northwest National Laboratory, Richland, Washington.

JISAO (Joint Institute for the Study of the Atmosphere and Ocean). 2017. May Pacific Decadal Oscillation data obtained from the University of Washington. Available: http://research.jisao.washington.edu/pdo/PDO.latest. (February 2019).

Kendall, N. W., G. W. Marston, and M. M. Klungle. 2017. Declining patterns of Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. Canadian Journal of Fisheries and Aquatic Sciences 74:1275–1290.

Kilduff, D. P., L. W. Botsford, and S. L. H. Teo. 2014. Spatial and temporal covariability in early ocean survival of Chinook Salmon (*Oncorhynchus tshawytscha*) along the west coast of North America. ICES Journal of Marine Science 71:1671–1682.

Kostow, K. 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. Reviews in Fish Biology and Fisheries 19:9–31.

Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Transactions of the American Fisheries Society 132:780–790.

Kostow, K. E., and S. Zhou. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. Transactions of the American Fisheries Society 135:825–841.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48(S1):66–77.

Lawson, P. W., E. A. Logerwell, N. J. Mantua, R. C. Francis, and V. N. Agostini. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest Coho Salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61:360–373.

Leider, S. A., P. L. Hulett, J. J. Loch, and M. W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. Aquaculture 88:239–252.

Lister, D. B. 2014. Natural productivity in steelhead populations of natural and hatchery origin: assessing hatchery spawner influence. Transactions of the American Fisheries Society 143:1–16.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Mueter, F. J., J. L. Boldt, B. A. Megrey, and R. M. Peterman. 2007. Recruitment and survival of northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. Canadian Journal of Fisheries and Aquatic Sciences 64:911–927.

ODFW (Oregon Department of Fish and Wildlife). 2017. Clackamas River winter steelhead hatchery and genetic management plan. ODFW, Salem.

ODFW (Oregon Department of Fish and Wildlife) and WDFW (Washington Department of Fish and Wildlife). 2002. Status report: Columbia River fish runs and fisheries 1938–2002; tables only. ODFW, Salem.

Pearsons, T. N., G. M. Temple, A. L. Fritts, C. L. Johnson, and T. D. Webster. 2008. Ecological interactions between non-target taxa of concern and hatchery supplemented salmon. Washington Department of Fish and Wildlife, Project 1995-063, Annual Report, Olympia.

Peterman, R. M., and B. Dorner. 2012. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. Canadian Journal of Fisheries and Aquatic Sciences 69:1255–1260.

Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan Sockeye Salmon (*Oncorhynchus nerka*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:2503–2517.

Petrosky, C. E., and H. A. Schaller. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook Salmon and steelhead. Ecology of Freshwater Fish 19:520–536.

PFEL (Pacific Fisheries Environmental Laboratory). 2017. May upwelling indices data obtained from NOAA Pacific Fisheries Environmental Laboratory. Available: https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html. (February 2019).

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *In* K. Hornik, F. Leisch, and A. Zeileis, editors. Proceedings of the Third International Workshop on Distributed Statistical Computing. Technische Universität Wien, Vienna.

Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of northeast Pacific salmon. Transactions of the American Fisheries Society 134:86–104.

Pyper, B. J., F. J. Mueter, R. M. Peterman, D. J. Blackbourn, and C. C. Wood. 2001. Spatial covariation in survival rates of northeast Pacific Pink Salmon (*Oncorhynchus gorbuscha*). Canadian Journal of Fisheries and Aquatic Sciences 58:1501–1515.

Pyper, B. J., F. J. Mueter, R. M. Peterman, D. J. Blackbourn, and C. C. Wood. 2002. Spatial covariation in survival rates of northeast Pacific Chum Salmon. Transactions of the American Fisheries Society 131:343–363.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Scheuerell, M. D., P. S. Levin, R. W. Zabel, J. G. Williams, and B. L. Sanderson. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 62:961–964.

Stachura, M. M., T. E. Essington, N. J. Mantua, A. B. Hollowed, M. A. Haltuch, P. D. Spencer, T. A. Branch, and M. J. Doyle. 2014. Linking northeast Pacific recruitment synchrony to environmental variability. Fisheries Oceanography 23:389–408.

Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in Coho Salmon (*Oncorhynchus kisutch*) survival, from California to Southeast Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 56:2570–2578.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910–925.

Waples, R. S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 48(S1):124–133.

Weber, E. D., and K. D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60:1018–1036.

Zabel, R. W., and P. S. Levin. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia 133:349–355.

Zimmerman, M. S., J. R. Irvine, M. O'Neill, J. H. Anderson, C. M. Greene, J. Weinheimer, M. Trudel, and K. Rawson. 2015. Spatial and temporal patterns in smolt survival of wild and hatchery Coho Salmon in the Salish Sea. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 7:116–134.