

Constable RJ, Sabal MC. 2026. An evaluation of spawner-to-parr productivity for coho salmon in Western Oregon Evolutionarily Significant Units. *Northwest Science* 99(2): *in press*.

Ronald J. Constable Jr.¹ and **Megan C. Sabal**, Oregon Department of Fish and Wildlife,
Corvallis Research Lab, 28655 Hwy 34, Corvallis, OR 97333

**An evaluation of spawner-to-parr productivity for coho salmon in Western Oregon
Evolutionarily Significant Units.**

Running footer: coho salmon productivity in Oregon

3 tables, 5 figures

¹Author to whom correspondence should be addressed. Email: ron.constable@oregonstate.edu

Accepted Article

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*.
Copy-editing may lead to differences between this version and the final published version.

Abstract

Coho salmon (*Oncorhynchus kisutch*) populations in Western Oregon coast are culturally and economically valuable, and agencies employ conservation measures to increase freshwater productivity. The limiting factor to freshwater productivity is posited to be the capacity of the habitat to support overwinter survival, but survival rates at earlier life stages may be co-limiting and are relatively understudied. If density-dependence limits productivity at spawner-to-parr life stages, it could inform conservation efforts. We examined patterns in coho salmon parr productivity across the Oregon Coast Coho (OCC) and Lower Columbia River (LCR) Evolutionarily Significant Units (ESUs) using Oregon Plan for Salmon and Watersheds (OPSW) monitoring data. OPSW monitoring has been continuous in the OCC since 1997 and in the LCR since 2005, producing annual abundance estimates of parr and parental adults in 1st–3rd order streams on the stratum (clusters of similar populations within ESUs) scale. Using these estimates, we fit three Bayesian stock-recruit models with strata-specific parameters to evaluate evidence for density-dependence across strata at the spawner-to-parr life stage. We found the strongest evidence for the Beverton-Holt model, which provided a substantially better fit compared to the density-independent model, suggesting strong evidence for density-dependence. Density-dependent effects were variable among strata and ESUs. Rearing capacity was highest in the Mid-South Coast stratum of the OCC, while intrinsic productivity was lowest in the LCR. All strata exhibited density-dependence at spawner abundances below recovery goals, suggesting freshwater habitat conditions in 1st–3rd order streams may be limiting coho salmon recovery at this early life stage.

Introduction

Coho salmon (*Oncorhynchus kisutch*) are a keystone species that provide significant environmental, economic, cultural, and recreational benefits (Rahr et al. 2025) including tourism, recreational fishing, ceremonial uses by tribes, and cycling nutrients that link freshwater, marine, and terrestrial ecosystems (Wainwright et al. 2008). After population declines in the 1980s, coho salmon were federally listed as a threatened species under the U. S. Endangered Species Act (ESA). Populations in the coastal region of Oregon were listed in 1998 and populations in the Lower Columbia River region were listed in 2005. These regions are considered two distinct Evolutionarily Significant Units (ESUs) under the ESA; the Oregon Coast Coho ESU (hereafter OCC) and the Lower Columbia River ESU (hereafter LCR) (Figure 1). ESUs are aggregations of populations that are reproductively isolated from other populations and contain evolutionary characteristics that contribute to the genetic diversity of the species (Waples 1991).

To restore coho salmon in these ESUs, actions were taken to reduce harvest, improve hatchery practices, restore habitat, and develop recovery plans. Coho salmon fisheries were closed by the Oregon Department of Fish and Wildlife (ODFW) in 1993, and exploitation rates have remained under 20%, down from peak rates of 80–90% in the 1970s (NWFSC 2015). Hatchery coho salmon releases were reduced to < 1% of their historical peak (Jones et al. 2018) and improved hatchery practices have increased coho salmon productivity (Buhle et al. 2009, Jones et al. 2018). As part of the Oregon Plan for Salmon and Watersheds (OPSW), millions of dollars have been invested in habitat restoration projects related to coho salmon since the 1998 ESA listing (Bernhardt et al. 2005, Katz et al. 2007). Federal and state recovery plans established narrow sense recovery goals, that set criteria for ESA delisting (ODFW 2007, ODFW 2010, NWFSC 2015), and broad sense recovery goals, that exceed delisting criteria and strive to restore self-sustaining populations that are healthy enough to provide additional ecological, economic,

recreational, and cultural benefits (ODFW 2021). These actions, along with improved marine survival rates, have resulted in some progress toward recovery (Chilcote et al. 2005), but have been insufficient so far to delist coho salmon, given the ongoing threats of habitat degradation and climate change (Stout et al. 2012).

Limits in the productivity of freshwater habitat continue to prevent the delisting of coho salmon (NWFSC 2015) and impede progress toward recovery goals (Chicote et al. 2005, Falcu and Suring 2018). Coho salmon productivity in freshwater habitats exhibits density-dependence. Productivity rates (the number of smolts per parental adult) increase when parental abundance is low and decrease when parental abundance is high (Bradford et al. 1997, Nickelson and Lawson 1998, Nickelson 2003). Density dependence can be driven by habitat capacity—including limitations in suitable space, food, or consequently increases in competition (Gibson et al. 2008, Ebersole et al. 2009). However, it has been posited that the primary limitations of freshwater habitat productivity for coho salmon are related to the capacity of the habitat to support parr in the winter months (Nickelson et al. 1992, Beechie et al. 1994, Nickelson and Lawson 1998, Solazzi et al. 2000, Chilcote et al. 2005). Coho salmon overwinter survival requires habitats insulated from main channel flows or low-velocity pools with complex submerged habitat, much of which has been lost due to land use changes and development (Beckham 1990, Quinn and Peterson 1996, Gallagher et al. 2012). Recovery plans focus on restoring overwinter habitat (e.g., ODFW 2007, NMFS 2013) and these efforts often involve adding complexity, such as large woody debris, to streams (Johnson et al. 2005, Jones et al. 2014a, Bair et al. 2019). However, the survival of coho salmon during the summer months may be limited by low flows, high temperatures, and stream connectivity (Ebersole et al. 2006, Obedzinski et al. 2018).

If density-dependence occurs at or before the summer parr rearing stage of the life cycle, habitat restoration designs that provide cooler stream temperatures, sustained spring/summer flows, and closer proximities of spawning and rearing habitats could improve freshwater productivity. We investigated patterns of density-dependence during the life cycle period from parental adults (spawners) to summer parr. We specifically asked (1) is there further evidence for density dependence in coho salmon populations specific to the spawner-to-summer parr life stage, (2) is density dependence evident on the stratum scale at this life stage and, if so, does the strength of density dependence vary by ESU or stratum, and (3) at what spawner abundance is density dependence occurring and how does this relate to recovery goals?

Methods

The data used to address our questions were provided by OPSW monitoring (Stevens 2002). The OPSW is the state's approach to restore native fish populations and their ecosystems (State of Oregon 1997). OPSW monitoring has produced annual abundance estimates of coho salmon in 1st-3rd order streams at two life stages, starting with OCC spawners in 1997 (Sounhein et al. 2023) and OCC parr in 1998 (Constable and Suring 2025). This monitoring was extended to the LCR starting with spawners in 2005 and parr in 2006. Spawner monitoring was conducted on the population, strata, and ESU scales. Parr monitoring was conducted on the strata and ESU scales. Strata are contiguous clusters of 3-6 geographically or ecologically similar but independent populations (typically 4th Field HUCs) and their associated dependent populations (Lawson et al. 2007). OPSW monitoring also included habitat conditions (Anlauf-Dunn and Jones 2012) and the calculation of marine and freshwater survival rates in select basins (Suring et al. 2015). Using OPSW spawner and parr abundance data, we examined density dependent patterns across the OCC and its strata and the LCR. The OCC was defined in 1997 and extends from the Sixes

River north to the Necanicum River. It contains 13,044 km of coho salmon freshwater habitat, the majority of which (11,678 km) is in 1st–3rd order streams (USGS 2019) that are accessible to coho salmon (i.e. below barriers to the upstream migration of spawners) and upstream of tidal influence. The OCC is composed of four monitoring strata: the North Coast, Mid Coast, Mid-South Coast, and Umpqua (Weitkamp et al. 1995). A fifth stratum, the Lakes, encompasses 308 km of freshwater stream habitat and, due to this small size relative to the other strata and similarities to the Mid-South Coast, it was incorporated into the Mid-South Coast for juvenile monitoring (Weitkamp et al 1995). The LCR was established in 2005 and includes the Columbia River tributaries downstream of, and including, the Hood River and the Willamette River downstream of Willamette Falls (NMFS 2013). OPSW monitoring only takes place in the Oregon portion of the ESU. This portion contains 1,793 km of coho salmon freshwater habitat, the majority of which (1,493 km) is in 1st–3rd order streams that are accessible to coho salmon and upstream of tidal influence. (USGS 2019).

Life cycle

Coho salmon have a relatively fixed life cycle in Western Oregon (Nickelson and Lawson 1998). The majority spend 1.5 years in freshwater during the egg-to-smolt phase of the life cycle and 1.5 years in the ocean during the smolt to adult phase of the life cycle (reviewed by Sandercock 2003). Eggs that are fertilized in the fall-winter (October-January) mature into age-1 fry, which emerge in the spring. Fry transition into age-1 parr (which we define as the life stage between the absorption of the yolk sac and transformation to smolt and when dark vertical bars i.e., “parr marks”, are apparent on the body of the fish) by June (Nickelson and Lawson 1998). After overwintering, parr develop into smolts and migrate to the ocean in the subsequent spring (February to June) at age-2 (Weitkamp et al. 1995), though age-1 fall migrants have been shown

to be a common life history variant in other systems (Roni et al. 2012, Rebenack et al. 2015).

The majority (> 90%) of adults return to spawn in the second fall-winter after ocean entrance at age-3 with the remaining (< 10%) returning to spawn as precocial males (jacks) in the first fall-winter after ocean entrance at age-2. Scale analyses indicate that > 95% of spring smolts in Western Oregon were age-2 (Moring and Lanz 1975, Lorion et al. 2018, Jones et al. 2021, Strobel 2024). The dominance of age-2 smolts indicates that summer parr are predominantly of the same age-1 cohort.

Parr estimates of relative abundance

Parr relative abundance at the stratum and ESU scales was estimated by snorkel surveys at selected sites, following the methods described by Constable and Suring (2025). Sites were selected using a Generalized Random Tessellation Stratified (GRTS) design which produced a random, spatially balanced sample within our sampling frame (Stevens 2002). The sampling frame consisted of the putative coho salmon spawning and rearing distribution upstream of tidal influence and within 1st–3rd order streams. Previous work from 2002–2008 in the OCC and from 2006–2011 in the LCR indicated small portions (mean = 8.4%, SD = 0.085, n = 34) of total coho salmon abundance estimates were in 4th–6th order streams and that these portions were not correlated with abundances in 1st–3rd order streams (ODFW, unpublished data). The sampling frame used a 1:100,000 stream hydrography layer prior to 2007 and a 1:24,000 stream hydrography layer beginning in 2007. Selected sites were incorporated into a rotating panel system, which emulated the coho salmon three-year life cycle; a quarter of selected sites were placed on an annual survey rotation, a quarter were placed on a three-year survey rotation, a quarter were placed on a nine-year survey rotation, and the final quarter were surveyed only once

(Stevens 2002). Using the GRTS and rotating panel design, sites were selected, assigned to a panel and apportioned among the coho salmon ESUs and strata.

The GRTS design produces geographic coordinates on our hydrography layer (GRTS points) that determine site locations. Sites were surveyed by daytime snorkel surveys during the base flow period (July 15-September 30). Daytime snorkeling was appropriate because most sample sites (94%) had stream temperatures that were between 10° to 20°C (Hillman et al. 1992; Roni and Fayram 2000). Field crews were trained in species identification and snorkel survey protocols described by Constable and Suring (2025). Crews began at the downstream end of the site and proceeded upstream, measuring the site length and identifying habitat types. Pools were identified as a habitat type where the water surface slope is zero and where the substrate was scoured or the stream was impounded by a blockage in the channel (Frissell et al. 1986). Site lengths and pool dimensions were measured using a combination of depth staff, range finder, or hip chain. All pools ≥ 20 cm deep and ≥ 6 m² in surface area were snorkeled with a single pass where coho salmon parr were identified and counted. Dive lights were used to improve visibility in shaded areas such as undercut banks. Sites with poor water clarity or quality ($< 9\%$ each year) were not sampled. Target site length was 1,000 meters, but this varied slightly depending on barriers to anadromy and landowner permissions; the mean site length was 989 meters (SD = 133.4, n = 4711). Parr count and site length were used to determine estimates of parr/km (linear density) at each site. Site length was the sum of the lengths of all habitat units within the site, including those that were not sampled (i.e., habitats that did not meet criteria for snorkeling). Estimates of parr/km at each site were then extrapolated to an annual relative abundance of parr in 1st-3rd order streams at the stratum and ESU scales by multiplying by site weight. Site weight was calculated by dividing the length of the sampling frame by the number of sites that were

surveyed within the frame, respective to each stratum and ESU. A mean of 38 sites per stratum (1.4% of the sampling frame) were surveyed per year in the OCC. A mean of 68 sites (4.7% of the sampling frame) were surveyed per year in the LCR. Parr estimates represent relative abundance because (i) snorkelers observe an average of 63% of mark-recapture estimates of parr in pools and (ii) an average of 23% of the total number of parr in a snorkel survey reach (also determined by mark-recapture) are distributed into habitats that are not snorkeled (Faley and Constable 2024). We did not adjust relative to absolute abundance to avoid introducing more uncertainty and assumptions and because our focus was on the shape of density-dependence and strata-level comparisons, which would be unaffected (Supporting Information). This also assumes snorkel detection patterns were similar among strata as data was not available to investigate otherwise.

Female spawner abundance estimates

Spawner abundance, within 1st–3rd order streams that were upstream of tidal influence and within the putative coho salmon distribution, was obtained from spawning ground surveys following Oregon Adult Salmonid Inventory and Sampling Project (OASIS) protocols (OASIS 2024). Like parr site selection, spawning survey sites were chosen using the GRTS design (Stevens 2002) and incorporated into the rotating panel system. From 1998 to 2005, only moderate and high productivity spawning habitats were sampled; starting in 2006, all habitat types were targeted (Lewis et al. 2010). Areas above established counting stations (e.g., fish ladders) are not surveyed; passage counts at these stations were added to the survey-based abundance estimates. Target site length was 1.6 km, but this could vary based on landowner restrictions and the upstream extent of accessible coho salmon habitat. (OASIS 2024). Each site was surveyed once every ten days by making counts of live fish for the duration of the spawning season. Estimates

of spawners were used to obtain Area-Under-the-Curve (AUC) estimates of spawners/km (linear density) at each survey site (Jacobs et al. 2002). Spawners/km was then used to estimate spawner abundance by extrapolating to the extent of spawning habitat within the ESUs and strata (Stevens and Olsen 2004). Coho salmon abundance estimates from these methods are the accepted abundance estimates for the OCC and LCR in conservation planning and ESA status reviews (Stout et al. 2012, PFMC 2015, ODFW 2021). Protocols included determining the sex of each carcass, from which an annual proportion of females was determined in each stratum. The proportion of females was multiplied by total spawner abundance to estimate female spawner abundance. A mean of 77 sites per stratum were surveyed each year in the OCC. A mean of 89 sites were surveyed each year in the LCR.

Female Spawner to Parr Recruit Analysis

We used Bayesian stock-recruit models with stratum-specific parameters to examine whether there was evidence for density-dependence between spawner and summer parr life stages within our sampling frame and whether the shape of density-dependence varied among strata or ESUs. We compared statistical fits among density-independent, Ricker, and Beverton-Holt density-dependent model forms, which included strata-level density-dependent parameters.

Model forms included:

$$R_{t,p} = \alpha_p S_{t,p} e^{\epsilon_t} \quad (\text{Density-independent})$$

$$R_{t,p} = \alpha_p S_{t,p} e^{-\frac{\beta_p S_{t,p}}{H_p}} e^{\epsilon_t} \quad (\text{Ricker})$$

$$R_{t,p} = \frac{\alpha_p S_{t,p}}{1 + \frac{\beta_p S_{t,p}}{H_p}} e^{\varepsilon_t} \quad (\text{Beverton-Holt})$$

where $R_{t,p}$ indicates the relative abundance of parr recruits (in millions) in year t for stratum p , $S_{t,p}$ is the total female spawners, α_p represents intrinsic productivity (the relative abundance of parr recruits per female spawner per habitat unit occurring with no density-dependence), and β_p controls the curvature and height of the function representing the strength of density-dependence per unit of habitat area. We scaled spawner abundance by stratum-level habitat (distribution in river km) H_p to improve model convergence and allow for comparison of parameters across strata. We also estimated parameters $Rmax_p$ and $S50_p$, which indicate the expected maximum recruitment at high spawner abundances and the number of spawners at half of $Rmax_p$, respectively:

$$Rmax_p = \frac{\alpha_p H_p}{\beta_p}$$

and

$$S50_p = H_p / \beta_p.$$

To account for temporal autocorrelation in process error, we assumed multiplicative, lognormal, error ε_t where φ captures the strength of autocorrelation and σ_ε^2 represents unexplained process variance:

$$\varepsilon_t \sim \text{Normal}(\varphi \varepsilon_{t-1}, \sigma_\varepsilon^2).$$

Initial error conditions were drawn from a stationary normal distribution of the AR(1) process:

$$\varepsilon_{t=1} \sim \text{Normal}\left(0, \frac{\sigma_\varepsilon^2}{(1 - \varphi^2)}\right)$$

We further incorporated observation error σ_s , assuming that observed parr recruits arose from a lognormal distribution:

$$\hat{R}_{t,p} \sim \text{Lognormal}(\log(R_{t,p}), \sigma_s^2),$$

where $\hat{R}_{t,p}$ denotes the observed parr recruits and $R_{t,p}$ denotes the true (latent) recruits predicted

Models were compared based on efficient approximate leave-one-out cross-validation and Leave-One-Out Information Criterion (LOOIC), which is appropriate for Bayesian models, where smaller LOOIC values indicate stronger out-of-sample statistical fit to the data (Vehtari et al. 2017). Using the best-supported model form, we compared strata-level parameters (α_p , β_p) by calculating posterior contrasts from the Gibbs Markov Chain Monte Carlo (MCMC) samples. For each posterior draw, we computed all pairwise differences between strata and summarized these contrasts using posterior means, 95% credible intervals, and the posterior probability that one parameter exceeds another.

We chose moderately informative priors for the density-dependent parameters to achieve model convergence. We first used Maximum Likelihood Estimation (MLE) to fit Ricker and Beverton-Holt model forms on each stratum separately. Priors for α_p and β_p followed normal distributions on the log-scale with means near the MLE estimated values (α : $\log(0.00016)$, β : $\log(0.3)$) and standard deviation of 1. Remaining priors were weakly informed. The autoregressive parameter φ was bounded uniformly between -0.99 and 0.99, while unexplained process (σ_ε^2) and observation (σ_s^2) errors were bounded uniformly between 0 and 5.

Our models were fit using Just Another Gibbs Sampler (JAGS) software and MCMC sampling implemented with the R package “jagsUI”. We ran three chains each with 500,000 iterations with 5,000 considered as burn-in, and a thinning rate of 10, which resulted in 148,500 posterior

samples. We evaluated model convergence by confirming that traceplots showed no trends and had similar dynamics among chains and that Gelman-Rubin convergence statistics (Rhat) were < 1.1 for all estimated parameters.

Results

We observed strong evidence for density-dependence between the spawner and summer parr life stages for coho salmon in our sampling frame. Bayesian models successfully converged with all parameter Rhat values < 1.1 (Table 1). Both density-dependent model forms exhibited substantial improvements over the density-independent model (Table 2). Vehtari et al. (2017) suggest benchmarks based on expected log pointwise predictive density (ELPD) where for $\Delta\text{ELPD}/\Delta\text{ELPD SE}$ values 0–2 indicate negligible, 2–5 small, 5–10 moderate, and > 10 strong differences between pairwise models. Thus, the density-independent model was moderately worse than both Beverton-Holt and Ricker forms ($\Delta\text{ELPD}/\Delta\text{ELPD SE}$: 6.1, 5.2, respectively), while the Beverton-Holt model exhibited a slight improvement over the Ricker ($\Delta\text{ELPD}/\Delta\text{ELPD SE}$: 1.8).

All strata showed a decline in parr recruits per female as female spawner abundance increased (Figure 2; Figure 3). However, the shape of the curves, as influenced by α_p , β_p , $Rmax_p$, and $S50_p$ parameters, varied among strata and ESUs. The Lower Columbia ESU exhibited the lowest intrinsic productivity (α_p) with over 97% probabilities that it was significantly different from other strata (Figure 4; Figure 5). This is evident in the Lower Columbia ESU exhibiting the most gradual increase in parr recruits at low spawner abundances (Figure 2; Figure 3). The Umpqua and Mid Coast had the largest α_p estimates, which were larger than those of the North Coast with

82% and 86% probabilities, respectively (Figure 5). This is represented by the Umpqua and Mid Coast having the steepest increases in parr recruits at low spawner abundances (Figure 2; Figure 3).

The estimated maximum capacity of recruits (R_{max_p}) was highest for the Mid-South Coast stratum in terms of both raw abundance units (1.47 parr per million; Figure 2) and when scaled by habitat area (Figure 4). The maximum recruits per habitat area for the Mid-South Coast was greater than all other strata with over 82% probability (Figure 5). Maximum recruits per habitat area were similar and in the middle for the North Coast and Mid Coast, while the Umpqua and Lower Columbia strata had substantially lower estimates of R_{max} (Figure 4). The Lower Columbia, therefore, had both the lowest absolute estimate of relative parr capacity (0.17 million parr; Figure 2) and the lowest estimate of R_{max} per habitat area (Figure 4) with > 0.99% probability (Figure 5).

As expected from the Beverton-Holt parameterization, β_p and $S50_p$ parameters showed inverse among strata patterns and describe how quickly habitat capacity is reached. The Umpqua stratum had the largest β_p value and smallest $S50_p$ value, indicating lower habitat capacity per km, which was substantially (> 74% probability) larger than β_p parameters for other strata (Figure 4; Figure 5). Strata with the highest habitat capacity (smallest β_p values; largest $S50_p$ values) were the North Coast and Mid-South Coast and these estimates were significantly different than those for the Mid Coast and Umpqua (Figure 4; Figure 5). High habitat capacity in the North Coast and Mid-South Coast is visualized by a more gradual approach to the asymptote at high spawner abundances, while low habitat capacity can be seen in the quicker saturation of summer parr recruits at relatively lower spawner abundances in the Umpqua and Mid Coast (Figure 2; Figure 3).

The higher rearing habitat capacity in the Mid-South Coast can also be seen in the OPSW monitoring data. Though the Mid-South Coast had the fewest stream kilometers within the sampling frame, it included six of the ten highest summer parr relative abundance estimates (Table 3). Mean summer parr relative abundance per kilometer (parr/km) of habitat in the Mid-South Coast was 516; over double the mean parr/km (257) of the other strata. Mean female spawner density (females/km) in the Mid-South Coast was 12.3, also over double the mean females/km of the other strata (5.9).

The Lower Columbia ESU exhibited lower abundances of spawners, parr, and habitat area compared to OCC strata (Figure 1; Figure 2; Figure 3; Table 3). In the LCR, mean parr per kilometer was 81, 25% of the mean parr per kilometer in the OCC, and mean females per kilometer was 3.7, 49% of the mean for the OCC. Furthermore, mean parr/female (relative parr abundance divided by parental female spawner abundance) was 30.7 with a 95% CI of ± 8.6 , significantly lower than the mean parr/female in the OCC strata (Table 3). Cumulatively, this suggests that density-dependence became limiting at low absolute female spawner abundances in the LCR with lower total habitat capacity compared to the OCC, reflecting both low intrinsic productivity and reduced habitat capacity.

Discussion

To conserve coho salmon it is valuable to know which life stages limit productivity. Many studies have documented density-dependence for coho salmon in the spawner-to-smolt stage of the life cycle and recognize the capacity of habitat to support overwinter survival as the primary limiting factor (Nickelson et al. 1992, Nickelson and Lawson 1998, Solazzi et al. 2000, Bell et al.

2001). Evidence of density dependence and summer carrying capacities has also been found at early (fry and parr) freshwater life stages (House 1996, Roni and Quinn 2001). Our study indicated broad-scale patterns of density dependence within our sampling frame at the spawner to parr life stage over our 26-year dataset in the OCC and over our 19-year dataset in the LCR. These density-dependence patterns varied in strength and onset among the strata in these ESUs. Stock-recruit curves also indicated that female spawner abundances, at which density-dependence occurred, were lower than targets for broad sense recovery goals stated in coho salmon recovery plans (e.g., ODFW 2021). These results suggest that freshwater conditions within our sampling frame during the spawner-to-summer parr life stage limited productivity and impeded recovery goals across this large spatial scale and at spawner abundances over the timespan of OPSW monitoring.

Strata-specific patterns suggested that the LCR supported the lowest coho salmon productivity. Low productivity was especially evident in the 2015, 2016, and 2019 brood years when low female spawner abundance was accompanied by low estimates of parr/female. In these years, mean spawner linear density was near or below 2.5 fish per kilometer, at which the probability of demographic effects (i.e., fish of opposite sex not encountering each other) leading to depensation increases (Sharr et al. 2000, Rupp et al. 2012). Lower rates of productivity are often attributed to lower habitat quality (Bradford et al. 1997), and summer habitat in LCR has been shown to be lower quality than in the OCC (Strickland and Constable 2022). These findings were based on the Habrate model, which uses critical habitat variables to score coho salmon summer habitat as poor, fair, or good (Burke et al. 2001). Releases of hatchery coho salmon in the LCR have been larger than in the OCC (ODFW 2010), which could also lower freshwater productivity rates by increasing competition (Nickelson 2003, Jones et al. 2018) and reducing the fitness of

populations (Chilcote et al. 2011). Measuring the individual impacts of habitat quality and hatchery influences on overall productivity is difficult (Hoekstra et al. 2007) and beyond the scope of this study, but both are likely to impact freshwater productivity in the LCR (ODFW 2010).

The Mid-South Coast had the highest modeled habitat capacity and the highest OPSW parr and spawner linear densities (fish/km). Mechanisms controlling habitat capacity and productivity are likely related to habitat and environmental conditions (e.g., Lawson et al. 2004, Ebersole et al. 2009), but specific drivers in our study were unknown. OPSW habitat monitoring data has indicated a larger proportion of high-quality habitat in the Mid-South Coast relative to the other strata (Anlauf-Dunn and Jones 2012). However, later assessments (Strickland et al. 2018) have shown the amount of high-quality habitat in the stratum to be below the mean for the OCC and lower than that estimated by Anlauf-Dunn and Jones (2012). Environmental variables, like temperature and flow, have been relatively uniform across the OCC, apart from the Umpqua stratum (Weitkamp et al. 1995). Large coastal lakes (Tenmile, Siltcoos, and Tahkenitch) have historically produced high spawning densities (Jacobs et al. 2000) and may have influenced productivity. However, parr and spawners were sampled in tributaries of the lakes and not within the lakes; therefore, lake productivity would not be reflected in our dataset. Other factors that are not monitored as part of the OPSW, such as freshwater seasonal habitat connectivity (Flitcroft et al. 2012) or the proximity of spawning and rearing habitats (Anlauf-Dunn et al. 2014) may have played roles in the higher habitat capacity of the Mid-South Coast. Determining the drivers of higher habitat capacity in the Mid-South Coast is a primary research question arising from this study.

Understanding patterns in density-dependence is critical to coho salmon monitoring and recovery planning (Shea 2006). Analyses of strata-level patterns in density-dependence allow managers to tailor coho salmon management and research and improve population models (Kendall et al. 2022; Shea et al. 2006, Jones et al. 2021). Accounting for density dependence and variability in parr/female rates can inform our comprehension of how populations resist further declines when spawner abundance is low and, conversely, help our understanding of limiting factors to juvenile production when spawner abundance is high (Wainwright et al. 2008). While overwinter survival rates are vital to understanding coho salmon productivity (Nickelson et al. 1992, Beechie et al. 1994, Chilcote et al. 2005), dynamics occurring during the spawner-to-summer parr period can also limit productivity (Ebersole et al. 2009, Obedzinski et al. 2018) and may be co-limiting or the primary limiting factor for populations in warmer, drier climates (ODFW 2021). Continued evaluation and modeling of productivity from adult spawners to freshwater life stages will inform managers charged with conserving coho salmon and restoring habitats and could improve productivity metrics in decision support systems used to assess narrow sense recovery goals

Our models indicated that strong density dependence occurred at spawner abundances that were below broad sense recovery goals. This result suggests freshwater habitat conditions may continue to impede progress toward recovery goals, even if marine survival rates improve. Broad sense recovery goals define a desired status for the OCC where naturally produced populations of coho salmon are self-sustaining and sufficiently healthy to provide significant ecological, cultural, and economic benefits (ODFW 2021). Spawner abundances for broad sense goals are derived from and evaluated by the same OASIS data set that we used to calculate our spawner abundance estimates (ODFW 2021). These goals are scaled to marine survival rates and the OCCCCP recognizes that achieving this status may require more than 50 years of sustained

conservation actions. Federal recovery plans also recognize the need for freshwater habitat to support high juvenile productivity at high parental abundances to have confidence in the health of an ESU, which is consideration for delisting (NWFSC 2015). The minimum annual abundance target for broad sense goals in the OCC was 400,000 total (male and female) spawners (ODFW 2021). We defined strong density dependence as reaching 80% of R_{max} and summed the corresponding number of spawners for each OCC strata and multiplied by two to account for males and females. This resulted in our models indicating a strong approach to carrying capacity at a median OCC total of 196,029 spawners – only 49% of broad sense recovery goals. This approximation is illustrative of the additional habitat restoration and time required for the benefits of process-oriented restoration work to take effect to meet recovery goals. Our results suggest that restoration work may require additional focus on streamflow enhancement (May and Lee 2004, Obedzinski et al. 2018), water temperature (reviewed by Richter and Kolmes 2005), and the accessibility and proximity of seasonal habitats (Ebersole et al. 2006, Flitcroft et al. 2012, Anlauf-Dunn et al. 2014, Jones et al. 2014b). We would also expect that as spawner abundance increases, correspondingly larger portions of fish may spawn in sub-optimal habitats (Anlauf-Dunn et al. 2014), and factors such as redd superimposition (Butler et al. 2021) and spawning substrate availability (Pulg et al. 2019) to influence productivity.

Our study describes density-dependent patterns at the strata-scale but includes limitations. A primary limitation was the unknown abundance of parr and spawners in 4th order or larger streams and unknown rates of migration between these larger streams and 1st–3rd order streams. Coho salmon could move between warmer mainstem sections into cooler mainstem sections or tributaries (Kaylor et al. 2025) or migrate from tributaries into larger order (mainstem) streams

or estuaries (Ebersole et al. 2006, Jones et al. 2014b, Jones et al. 2021; Flitcroft et al. 2014).

Though it is uncertain how dynamics in 4th order or larger streams could have affected overall productivity rates in our study, 1st–3rd order streams represent the majority (90% of the OCC and 83% of the LCR) of stream kilometers of coho salmon freshwater habitat, contain the majority of high-quality freshwater habitat (Burnett et al. 2007), and typically have cooler temperatures than larger streams (Fullerton et al. 2015). Previous surveys occurring in the OCC and the LCR indicated small portions (<10%) of total coho salmon abundance estimates were in 4th–6th streams (ODFW, unpublished data). Furthermore, these previous surveys and additional sampling in the Smith River Basin (Douglas County, Oregon) both showed no pattern of density-dependent movements among tributary and mainstem streams (ODFW, unpublished data; Constable and Suring 2023). Therefore, we postulate that productivity in 1st–3rd order streams is likely a strong driver of overall productivity in the OCC and LCR, but we caution that our results apply only to these streams and not the entire population within a stratum or ESU.

Our results were also limited by uncertainties in snorkel survey estimates and inadequate data on overwinter (parr-to-smolt) survival rates. We assumed that parr/female productivity rates and modeled density dependence were not significantly impacted by parr moving from pools into less optimal habitats (such as riffles or rapids) when abundances were high. This assumption is supported by mark-recapture estimates, which suggest density in pools (that meet snorkel survey criteria) does not influence the portion of total abundance estimates distributed in habitats that do not meet snorkel survey criteria (Falcy and Constable 2024). This same study determined that the mark-recapture portion of coho salmon observed by snorkelers declined with increasing abundances of coho salmon; however, this relationship is difficult to apply in practice because true abundance is unknown when counts are made as discussed in Falcy and Constable (2024).

Furthermore, our own examination of the same data showed a strong linear relationship between snorkel pool counts and mark-recaptures estimates, which suggests that any calibration would be applied consistently and not change the shape of our density-dependent patterns or among population comparisons (Supporting Information). Future directions could incorporate overwinter (parr to smolt) survival rates for a thorough comparison of relative strength of density dependence throughout the freshwater portion of the life cycle. Unfortunately, data on overwinter survival rates is limited to two sub-watersheds (12-digit HUCs) in the Mid Coast (Lance et al. 2020, Suring et al. 2015) and for a 7-year period in the Salmon River watershed (Jones et al. 2021) and could not be reasonably applied to strata across the entire OCC and LCR on our timescale. Additional data on overwinter survival rates and parr abundances in 4th order or larger streams represent a research need for coho salmon monitoring.

Our results can inform population models, future monitoring, restoration efforts, and recovery planning. While monitoring the ability of freshwater habitats to support overwinter survival is vital to coho salmon management and recovery, our analysis suggests monitoring conditions during the spawner-to-parr life cycle period may become increasingly important with predicted increases in summer temperatures and drought frequencies (Isaak and Rieman 2012, Brunner et al. 2021, Dalton and Fleishman 2021). Our results were illustrative of the disparity between freshwater habitat conditions and recovery goals and indicate this disparity may persist even with increased marine survival rates. A continued evaluation of parr/female spawner rates will be useful for managers charged with conserving coho salmon. Conservation and restoration plans should consider winter and summer habitat conditions (ODFW 2021) and the connections between these habitats.

Acknowledgements

Thank you to the many hard-working crews who spent long hours in the field collecting this data. Thank you, Matt Weeber, Peggy Kavanagh, Julie Firman, Erik Suring, Jamie Anthony, and Morgan Davies for your helpful reviews of this manuscript.

Author Statements

Fish sampling in this study was done in an ethical manner and in accordance with Oregon Administrative Rule 635-011-0066 and within the confines of ODFW's permitted fisheries research programs. Our most recent National Marine Fisheries Service permit number is 27654.

Funding: This research was supported by the Oregon Department of Fish and Wildlife and the Oregon Plan for Salmon and Watersheds, as funded by the NOAA Coastal Salmon Recovery Fund (OWEB Contract #216-904 and #218-904), the State of Oregon Lottery Fund, and the State of Oregon General Fund.

Competing interests: The authors declare there are no competing interests.

Data Availability: Juvenile data is available in annual report appendices. The most recent annual report can be found at <https://odfw-aqi.forestry.oregonstate.edu/juvenile-salmonid-monitoring>.

Adult data is available at <https://odfw-oasis.forestry.oregonstate.edu/coho-salmon-data>.

Author contributions: RC conceptualized the study, supervised data collection and management, contributed to data analysis, and led the writing. MS led the data analysis and contributed to the writing.

References Cited

Anlauf-Dunn KJ, Ward EJ, Strickland M, Jones KK. 2014. Habitat connectivity, complexity, and quality: predicting adult coho salmon occupancy and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1–13.

Anlauf-Dunn KJ, Jones KK. 2012. Stream habitat conditions in Western Oregon, 2006–2010. OPSW-ODFW-2012-5. Oregon Department of Fish and Wildlife, Salem, OR.

Bair RT, Segura C, Lorion CM. 2019. Quantifying the restoration success of wood introductions to increase coho salmon winter habitat. *Earth Surface Dynamics* 7:841–857.

Beckham D. 1990. *Swift flows the river: log driving in Oregon*. Arago Books, Coos Bay, OR.

Beechie T, Beamer E, Wasserman L. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for restoration. *North American Journal of Fisheries Management* 14:797–811.

Bell E, Duffy WG, Roelofs TD. 2001. Fidelity and survival of juvenile coho salmon in response to a flood. *Transactions of the American Fisheries Society* 130:450–458.

Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J, Galat D, Gloss S, Goodwin P, Hart D, Hassett B, Jenkinson R, Katz S, Kondolf GM, Lake PS, Lave R, Meyer JL, O'Donnell TK, Pagano L, Powell B, Sudduth E. 2005. Synthesizing U. S. river restoration efforts. *Science* 308:636–637.

Bradford MJ, Taylor GC, Allen JA. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. *Transactions of the American Fisheries Society* 126:49–64.

Brunner MI, Swain DL, Gilleland E, Wood AW. 2021. Increasing importance of temperature as a contributor to the spatial extent of streamflow drought. *Environmental Research Letters* 16, article 024038.

Buhle ER, Holsman KK, Scheuerell MD, Albaugh A. 2009. Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. *Biological Conservation* 142:2449–2455.

Burnett KM, Reeves GH, Miller DJ, Clarke S, Vance-Borland K, Christainse K. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecological Applications* 17:66–80.

Burke JL, Jones KK, Dambacher JM. 2001. Habrate: A limiting factors model for assessing stream habitat quality for salmon and steelhead in the Deschutes River basin. Information Report 2010-03. Oregon Department of Fish and Wildlife, Corvallis, OR.

Butler MB, Flitcroft RL, Guillermo G. 2021. The relationship between hydroregime and coho salmon (*Oncorhynchus kitsutch*) redd construction in the Smith River, Oregon. *Ecology of Freshwater Fish* 30:519–530.

Chilcote MW, Goodson KW, Falcu MR. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 68:511–522

Chilcote M, Nickelson T, Moore K. 2005. Oregon Coastal Coho Assessment, Part 2: Viability criteria and status assessment of Oregon coastal coho. Oregon Department of Fish and Wildlife, Salem, OR.

Constable RJ, Sabal MC. 2026. An evaluation of spawner-to-parr productivity for coho salmon in Western Oregon Evolutionarily Significant Units. *Northwest Science* 99(2): *in press*.

Constable RJ Jr, Suring E. 2023. Implications of metrics and methodology for juvenile salmonid monitoring in Western Oregon streams. *Northwest Science* 96:63–79.

Constable RJ Jr, Suring E. 2025. Juvenile salmonid monitoring in Coastal Oregon and Lower Columbia streams, 2024 Field Season. Monitoring Program Report Number OPSW-ODFW-2025-1. Oregon Department of Fish and Wildlife, Salem, OR.

Dalton M, Fleishman E (editors). 2021. Fifth Oregon climate assessment. Oregon Climate Change Research Institute, Oregon State University, Corvallis, OR.

Ebersole JL, Colvin ME, Wigington PJ Jr, Leibowitz SG, Baker JP, Church MR, Compton JE, Cairns ME. 2009. Hierarchical modeling of late-summer weight and summer abundance of juvenile coho salmon across a stream network. *Transactions of the American Fisheries Society* 138:1138–1156.

Ebersole JL, Wigington PJ Jr, Baker JP, Cairns MA, Church MR, Hansen BP, Miller BA, LaVigne HR, Compton JE, Leibowitz SG. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. *Transactions of the American Fisheries Society* 135:1681–1697.

Falcy MR, Constable RJ Jr. 2024. Quantifying uncertainty when extrapolating the relationship between snorkel counts and mark-recapture estimates of juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 81:1279–1291.

Falcy MR, Suring E. 2018. Detecting the effects of management regime shifts in dynamic environments using multi-population state-space models. *Biological Conservation* 221:34–43.

Flitcroft RL, Burnett K, Reeves G, Ganio L. 2012. Do network relationships matter? Comparing network and instream habitat variables to explain densities of juvenile coho salmon

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

(*Oncorhynchus kisutch*) in Mid-coastal Oregon, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22:288–302.

Flitcroft RL, Burnett K, Snyder J, Reeves G, Ganio L. 2014. Riverscape patterns among years of juvenile coho salmon (*Oncorhynchus kisutch*) in Mid-coastal Oregon: Implications for conservation. *Transactions of the American Fisheries Society* 143:2638.

Frissell CA, Liss WJ, Wissmar RC, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:AA199–124.

Fullerton AE, CE Torgerson, JL Lawler, RN Faux, EA Steel, TJ Beechie, JL Ebersole, SG Leibowitz. 2015. Rethinking the longitudinal stream temperature paradigm: region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. *Hydrological Processes* 29:4719-4737.

Gallagher SP, Thompson S, Wright DW. 2012. Identifying factors limiting coho salmon to inform stream restoration in coastal Northern California. *California Fish and Game* 98:185–201.

Gibson AJF, Bowlby HD, Amiro PG. 2008. Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science* 65:1667–1680.

Hillman TW, Mullan JW, Griffith JS. 1992. Accuracy of underwater counts of juvenile Chinook Salmon, coho salmon, and steelhead trout. *North American Journal of Fisheries Management* 12:598–603.

Hoekstra JM, Bartz KK, Ruckelshaus MH, Moslemi JM, Harms TK. 2007. Quantitative threat analysis for management of an imperiled species: Chinook salmon (*Oncorhynchus tshawytscha*). *Ecological Applications* 17:2016–2073.

House R. 1996. An evaluation of stream restoration structures in a Coastal Oregon stream, 1981–1993. *North American Journal of Fisheries Management* 16:272–281.

Isaak DJ, Rieman BE. 2012. Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology* 19:742–751.

Jacobs S, Firman J, Susac G, Brown E, Riggers B, Temple K. 2000. Status of Oregon coastal stocks of anadromous salmonids. Monitoring Report Number OPSW-ODFW-2000-3. Oregon Department of Fish and Wildlife, Portland, OR.

Jacobs S, Firman J, Susac G, Stewart D, Weybright J. 2002. Status of Oregon coastal stocks of anadromous salmonids 2000-2001 and 2001-2002. Monitoring Report Number OPSW-ODFW-2002-3. Oregon Department of Fish and Wildlife, Portland, OR.

Johnson SL, Rodgers JD, Solazzi MF, Nickelson TE. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus spp.*) in an Oregon coastal stream. *Canadian Journal of Fisheries and Aquatic Science* 62:412–424.

Jones KK, Anlauf-Dunn KJ, Jacobson PS, Strickland M, Tennant L, Tippery SE. 2014a. Effectiveness of instream wood treatments to restore stream complexity and winter rearing habitat of juvenile coho salmon. *Transactions of the American fisheries society* 143:334–345.

Jones KK, Cornwell TJ, Bottom DL, Campbell LA, Stein S. 2014b. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology* 85:52–80.

Jones KK, Cornwell T, Bottom D, Stein S, Anlauf-Dunn KJ. 2018. Population viability improves following termination of coho salmon hatchery releases. *North American Journal of Fisheries Management* 38:39–55.

Jones KK, Cornwell TJ, Bottom DL, Stein S, Starcevich S. 2021. Interannual variability in life-stage specific survival and life history diversity of coho salmon in a coastal Oregon basin. *Canadian Journal of Fisheries and Aquatic Science* 78:1887–1899.

Katz SL, Barnas K, Hicks R, Cowen J, Jenkinson R. 2007. Freshwater habitat restoration actions in the Pacific Northwest: a decade's investment in habitat improvement. *Restoration Ecology* 15:494–505.

Kaylor MJ, Ciepiela LR, Feden M, Lemanski JT, Justice C, Staton BA, Armstrong JB, Kelly S, Narum SR, Tattum IA, White S. 2025. Watershed-scale dispersal patterns of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) revealed through genetic parentage analysis. *Movement Ecology* 13:6

Kendall NW, Unrein J, Volk C, Beauchamp DA, Fresh KL, Quinn TP. 2022. Life cycle model reveals sensitive life stages and evaluates recovery options for a dwindling Pacific Salmon population. *North American Journal of Fisheries Management* 43:203–230.

Lance M, Suring E, Biederbeck R. 2020. Summary of habitat and fish monitoring data from East Fork and Upper Mainstem Lobster Creeks: 1988-2020. *Salmonid Life Cycle Monitoring Project*. Oregon Department of Fish and Wildlife, Salem, OR.

Lawson PW, Bjorkestedt EP, Chilcote MW, Huntington CW, Stout JS, Wainwright TC, Weitkamp LA. 2007. Identification of historical populations of coho salmon (*Oncorhynchus kisutch*) in the Oregon coast coho evolutionarily significant unit. U. S.

Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-79.
Northwest Fisheries Science Center, Seattle, WA.

Lawson PW, Logerwell EA, Mantua NJ, Francis RC, Agostini VN. 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.

Lewis M, Sounhein B, Weeber M, Brown E. 2010. Status of Oregon stocks of coho salmon, 2009. Monitoring Program Report Number OPSW-ODFW-2010-3. Oregon Department of Fish and Wildlife, Salem, OR.

Lorion CM, Suring E, Gerding JL, Leonetti ET. 2018. Abundance and life history characteristics of steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) smolts in two direct ocean tributaries on the central Oregon coast. Oregon Department of Fish and Wildlife Information Report Number 2018-07. Oregon Department of Fish and Wildlife, Salem, OR.

May CL, Lee DC. 2004. The relationships among in-channel sediment storage, pool depth, and summer survival of juvenile coho salmon in Oregon Coast Range streams. *North American Journal of Fisheries Management* 24:761–774.

Moring JR, Lantz RL. 1975. The Alsea watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part I. Biological studies. Oregon Department of Fish Wildlife Fish Division Fisheries Research Report 9.

Nickelson TE. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1050–1056.

Nickelson TE, Lawson P. 1998. Population viability of coho salmon (*Oncorhynchus kisutch*) in Oregon coastal basins: application of a habitat-based life cycle model. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2383–2392.

Nickelson TE, Rodgers JD, Johnson SL, Solazzi MF. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:783–789.

[NMFS] National Marine Fisheries Service. 2013. ESA Recovery plan for Lower Columbia River coho salmon, Lower Columbia River Chinook Salmon, Lower Columbia River chum salmon, and Lower Columbia River steelhead. National Marine Fisheries Service. <https://repository.library.noaa.gov/view/noaa/16002>.

[NWFSC] Northwest Fisheries Science Center. 2015. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. US Department of Commerce, Northwest Fisheries Science Center, Seattle, WA.

[OASIS] Oregon Adult Salmonid Inventory and Sampling Project 2024. Salmon spawning survey procedures manual. Oregon Department of Fish and Wildlife. Corvallis, OR.

Obedzinski M, Nossaman-Pierce S, Horton GE, Deitch MJ. 2018. Effects of flow-related variables on oversummer survival of juvenile coho salmon in intermittent streams. *Transactions of the American Fisheries Society* 147:588–605.

- [ODFW] Oregon Department of Fish and Wildlife. 2007. Oregon coast coho salmon conservation plan for the State of Oregon. Oregon Department of Fish and Wildlife, Salem, OR.
- [ODFW] Oregon Department of Fish and Wildlife. 2010. Lower Columbia River conservation and recovery plan for Oregon populations of salmon and steelhead. Oregon Department of Fish and Wildlife, Salem, OR.
- [ODFW] Oregon Department of Fish and Wildlife. 2021. Oregon coast coho conservation plan; 2019 12-year plan assessment. Oregon Department of Fish and Wildlife, Salem, OR.
- [PFMC] Pacific Fishery Management Council. 2015. Review of 2014 Ocean Salmon Fisheries: Stock Assessment and Fishery Evaluation Document for the Pacific Coast Salmon Fishery Management Plan. Pacific Fishery Management Council. Portland, OR.
- Pulg U, Vollset KW, Lennox RJ. 2019. Linking habitat to density-dependent population regulation: How spawning gravel availability affects abundance of juvenile salmonids (*Salmo trutta* and *Salmo salar*) in small streams. *Hydrobiologia* 841:13–29.
- Quinn TP, Peterson NP. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef creek, Washington. *Canadian Journal of Fisheries and Aquatic Science* 53:1555–1564.
- Rahr GR III, Sloat MR, Atlas WI, Hart JL. 2025. Strongholds for pacific salmon: A proactive conservation strategy for ecosystem health, food security, biodiversity, and climate resilience. *Fisheries* 50:399–415.

- Rebenack JJ, Ricker S, Anderson C, Wallace M, Ward DM. 2015. Early emigration of juvenile coho salmon: implications for population monitoring. *Transactions of the American Fisheries Society* 144:163–172.
- Richter A, Kolmes SA. 2005. Maximum temperature limits for Chinook, coho, chum salmon and steelhead trout in the Pacific Northwest. *Reviews in Fisheries Science* 13:23–49.
- Roni P, Bennett TR, Holland R, Pess GR, Hanson KM, Moses R, McHenry M, Ehinger W, Walter J. 2012. Factors affecting migration timing, growth, and survival of juvenile coho salmon in two Coastal Washington watersheds. *Transactions of the American Fisheries Society* 141:890–906.
- Roni P, Fayram A. 2000. Estimating winter salmonid abundance in small Western Washington streams: a comparison of three techniques. *North American Journal of Fisheries Management* 20:682–691.
- Roni P, Quinn TP. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in Western Oregon and Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:282–292.
- Rupp DE, Wainwright TC, Lawson PW. 2012. Effect of forecast skill on management of the Oregon coast coho salmon (*Oncorhynchus kisutch*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1016–1032.
- Sandercock FK. 2003. Life history of coho salmon (*Oncorhynchus kisutch*). In C Groot and L Margolis (editors), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver. Pp. 397–445.

Sharr S, Melcher C, Nickelson T, Lawson P, Kope R, Coon J. 2000. 2000 review of amendment 13 to the Pacific Coast salmon plan. Exhibit B.3.b. ONC workgroup report. Pacific Fisheries Management Council, Portland, OR.

Shea K, Wolf N, Mangel M. 2006. Influence of density dependence on the detection of trends in unobserved life-history stages. *Journal of Zoology* 269:442–450.

Solazzi MF, Nickelson TE, Johnson SL, Rodgers JD. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. *Canadian Journal of Fisheries and Aquatic Science* 57:906–914.

Sounhein B, Brown E, Weeber M, Nott J, Neerman A. 2023. Western Oregon adult coho salmon, 2022 spawning survey data report. Monitoring Program Report Number OPSW-ODFW-2023-3. Oregon Department of Fish and Wildlife, Salem, OR.

State of Oregon. 1997. The Oregon plan (Oregon Coastal Salmon Restoration Initiative). Oregon Governor's Office, Salem, OR.

Stevens DL Jr. 2002. Sampling design and statistical analysis methods for the integrated biological and physical monitoring of Oregon streams. Monitoring Program Report Number OPSW-ODFW-2002-7. Oregon Department of Fish and Wildlife, Portland, OR.

Stevens DL Jr, Olsen AR. 2004. Spatially-balanced sampling of natural resources. *Journal of the American Statistical Association* 99:262–278.

Stout HA, Lawson PW, Bottom DL, Cooney TD, Ford MJ, Jordan CE, Kope RG, Kruzic LM, Pess GR, Reeves GH, Scheuerell MD, Wainwright TC, Waples RS, Ward E, Weitkamp LA, Williams JG, Williams TH. 2012. Scientific conclusions of the status review for Oregon coast coho salmon (*Oncorhynchus kisutch*). U.S. Department of Commerce,

NOAA Technical Memorandum NMFS-NWFSC-118. Northwest Fisheries Science Center, Seattle, WA.

Strickland MJ, Anlauf-Dunn K, Jones K, Stein C. 2018. Winter habitat condition of Oregon coast coho salmon Populations, 2007-2014. Information Report 2018-01. Oregon Department of Fish and Wildlife, Salem, OR.

Strickland MJ, Constable RJ Jr. 2022. Stream habitat conditions in the Lower Columbia ESU, 2007-2016. Science Bulletin 2022-05. Oregon Department of Fish and Wildlife, Salem, OR.

Strobel B. 2024. Sandy River Basin Smolt Monitoring, Appendix C. 2024. Portland Water Bureau, Portland, OR.

Suring E, Burns P, Constable RJ Jr, Lorion CM, Wiley DJ. 2015. Salmonid life cycle monitoring in Western Oregon streams, 2012-2014. Monitoring Program Report Number OPSW-ODFW-2015-2. Oregon Department of Fish and Wildlife, Salem, OR.

[USGS] United States Geological Survey. 2019. National Hydrography Dataset (Version USGS National Hydrography Dataset Best Resolution (NHD)), September, 2019.

Vehtari A, Gelman A, Garby J. 2017. Practical Bayesian model evaluation using leave-one-out cross validation and WAIC. *Statistics and Computing* 27:1413–1432.

Wainwright TC, Chilcote MW, Lawson PW, Nickelson TE, Huntington CW, Mills JS, Moore KMS, Reeves GH, Stout HA, Weitkamp LA. 2008. Biological recovery criteria for the Oregon Coast coho salmon evolutionarily significant unit. US Department of Commerce,

Constable RJ, Sabal MC. 2026. An evaluation of spawner-to-parr productivity for coho salmon in Western Oregon Evolutionarily Significant Units. *Northwest Science* 99(2): *in press*.

NOAA Technical Memorandum NMFS-NWFSC-91. Northwest Fisheries Science Center, Seattle, WA.

Waples RS. 1991. Pacific salmon, *Oncorhynchus spp.*, and the definition of a “species” under the Endangered Species Act. *Marine Fisheries Review* 53:11–22.

Weitkamp LA, Wainwright TC, Bryant GJ, Milner GB, Teel DJ, Kope RG, Waples RS. 1995. Status review of coho salmon from Washington, Oregon, and California. US Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-24. Northwest Fisheries Science Center, Seattle, WA.

Submitted 12 May 2025

Accepted 30 January 2026

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

Table 1. Summary of posterior samples (mean, SD, and 95% credible intervals) and model convergence statistics (Rhat) for all model parameters.

| Parameter | Posterior mean | Posterior SD | 2.5% CI | 97.5% CI | Rhat |
|-----------------------------------|----------------|--------------|---------|----------|------|
| $\alpha_{\text{Lower Columbia}}$ | 0.0001 | 0.0000 | 0.0000 | 0.0002 | 1.00 |
| $\alpha_{\text{Mid Coast}}$ | 0.0003 | 0.0001 | 0.0001 | 0.0004 | 1.00 |
| $\alpha_{\text{Mid South Coast}}$ | 0.0002 | 0.0001 | 0.0001 | 0.0005 | 1.00 |
| $\alpha_{\text{North Coast}}$ | 0.0002 | 0.0000 | 0.0001 | 0.0003 | 1.00 |
| α_{Umpqua} | 0.0003 | 0.0001 | 0.0001 | 0.0005 | 1.00 |
| $\beta_{\text{Lower Columbia}}$ | 0.71 | 0.43 | 0.24 | 1.80 | 1.00 |
| $\beta_{\text{Mid Coast}}$ | 0.68 | 0.26 | 0.32 | 1.32 | 1.00 |
| $\beta_{\text{Mid South Coast}}$ | 0.34 | 0.19 | 0.13 | 0.82 | 1.00 |
| $\beta_{\text{North Coast}}$ | 0.38 | 0.14 | 0.18 | 0.71 | 1.00 |
| β_{Umpqua} | 1.05 | 0.51 | 0.42 | 2.29 | 1.00 |
| $R_{\text{maxLower Columbia}}$ | 0.29 | 0.07 | 0.20 | 0.45 | 1.00 |
| $R_{\text{maxMid Coast}}$ | 1.26 | 0.15 | 1.01 | 1.61 | 1.00 |
| $R_{\text{maxMid South Coast}}$ | 1.50 | 0.23 | 1.15 | 2.04 | 1.00 |
| $R_{\text{maxNorth Coast}}$ | 1.81 | 0.29 | 1.35 | 2.48 | 1.00 |
| $R_{\text{maxUmpqua}}$ | 0.37 | 0.05 | 0.28 | 0.49 | 1.00 |
| $S_{50\text{Lower Columbia}}$ | 4277 | 2235 | 1281 | 9787 | 1.00 |
| $S_{50\text{Mid Coast}}$ | 5568 | 2103 | 2397 | 10508 | 1.00 |
| $S_{50\text{Mid South Coast}}$ | 8058 | 3795 | 2669 | 17145 | 1.00 |
| $S_{50\text{North Coast}}$ | 11351 | 4007 | 5383 | 20930 | 1.00 |
| $S_{50\text{Umpqua}}$ | 1668 | 724 | 628 | 3416 | 1.00 |
| σ_{ϵ} | 0.28 | 0.10 | 0.03 | 0.39 | 1.03 |
| σ_s | 0.15 | 0.11 | 0.006 | 0.37 | 1.02 |
| ϕ | 0.07 | 0.38 | -0.76 | 0.84 | 1.00 |

Table 2. Summary of leave-one-out cross-validation comparison among model forms ranked by descending LOOIC where the lowest value indicates the top model.

| Model form | Δ ELPD | Δ ELPD SE | LOOIC | LOOIC SE |
|---------------------|---------------|------------------|-------|----------|
| Beverton-Holt | 0 | 0 | -43.7 | 21.7 |
| Ricker | -8.8 | 4.9 | -26.2 | 20.4 |
| Density-independent | -60.1 | 9.8 | 76.4 | 19.4 |

Table 3. Estimates of coho salmon female spawners abundance, relative parr abundance, and parr produced per parental female in 1st-3rd order streams in the four strata of the Oregon Coast Coho ESU and the Lower Columbia River ESU for brood years 1998-2023. Female estimates were from spawning ground surveys and parr estimates were from snorkel surveys. Surveys were not conducted in the Lower Columbia River ESU before brood year 2005.

| Brood Year | North Coast Stratum | | | Mid Coast Stratum | | | Mid-South Stratum | | | Umpqua Stratum | | | Lower Columbia River ESU | | |
|------------|---------------------|---------|-----------------|-------------------|---------|-----------------|-------------------|-----------|-----------------|----------------|---------|-----------------|--------------------------|------|-----------------|
| | Females | Parr | Parr/ Female | Females | Parr | Parr/ Female | Females | Parr | Parr/ Female | Females | Parr | Parr/ Female | Females | Parr | Parr/ Female |
| 1998 | 1,171 | 61,228 | 52 | 1,221 | 201,765 | 165 | 8,971 | 358,029 | 40 | 4,876 | 263,907 | 54 | | | |
| 1999 | 4,047 | 513,448 | 127 | 4,809 | 636,561 | 132 | 10,377 | 763,557 | 74 | 4,288 | 947,507 | 221 | | | |
| 2000 | 9,109 | 650,882 | 71 | 7,781 | 803,171 | 103 | 12,659 | 998,651 | 79 | 7,297 | 516,299 | 71 | | | |
| 2001 | 16,343 | 728,083 | 45 | 10,538 | 717,782 | 68 | 36,396 | 1,057,355 | 29 | 17,542 | 852,391 | 49 | | | |
| 2002 | 26,292 | 976,142 | 37 | 46,942 | 873,357 | 19 | 34,909 | 946,047 | 27 | 21,965 | 837,345 | 38 | | | |

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

| | | | | | | | | | | | | | | | |
|-------------|---------------|----------------|-----------|---------------|----------------|-----------|---------------|------------------|-----------|---------------|----------------|-----------|--------------|----------------|-----------|
| 2003 | 27,278 | 842,367 | 31 | 35,636 | 672,677 | 19 | 35,321 | 880,565 | 25 | 17,979 | 923,622 | 51 | | | |
| 2004 | 14,304 | 853,247 | 60 | 21,071 | 610,126 | 29 | 41,429 | 1,114,794 | 27 | 14,796 | 508,369 | 34 | | | |
| 2005 | 7,101 | 1,406,547 | 198 | 25,614 | 1,187,999 | 46 | 25,097 | 1,176,018 | 47 | 22,279 | 514,918 | 23 | 2,182 | 113,374 | 52 |
| 2006 | 11,128 | 1,017,969 | 91 | 10,679 | 857,588 | 80 | 43,096 | 1,285,252 | 30 | 7,652 | 960,097 | 125 | 3,535 | 115,289 | 33 |
| 2007 | 8,989 | 370,797 | 41 | 6,094 | 805,066 | 132 | 15,041 | 1,329,052 | 88 | 5,356 | 593,066 | 111 | 3,390 | 214,467 | 63 |
| 2008 | 12,187 | 829,855 | 68 | 38,822 | 1,345,667 | 35 | 29,236 | 1,691,157 | 58 | 20,612 | 1,075,136 | 52 | 2,535 | 136,558 | 54 |
| 2009 | 20,593 | 775,036 | 38 | 48,711 | 834,439 | 17 | 39,240 | 1,141,767 | 29 | 27,943 | 752,199 | 27 | 5,991 | 179,989 | 30 |
| 2010 | 24,127 | 742,914 | 31 | 30,027 | 802,427 | 27 | 61,459 | 1,733,106 | 28 | 36,740 | 1,115,480 | 30 | 3,810 | 103,458 | 27 |
| 2011 | 22,924 | 577,017 | 25 | 64,268 | 1,009,801 | 16 | 56,018 | 1,595,194 | 28 | 51,366 | 716,040 | 14 | 4,641 | 72,323 | 16 |
| 2012 | 4,077 | 459,220 | 113 | 17,974 | 1,117,548 | 62 | 21,064 | 2,192,920 | 104 | 10,973 | 666,602 | 61 | 1,766 | 117,372 | 66 |
| 2013 | 5,478 | 337,136 | 62 | 22,045 | 1,025,977 | 47 | 25,265 | 963,062 | 38 | 16,865 | 617,845 | 37 | 3,456 | 84,705 | 25 |
| 2014 | 31,666 | 618,560 | 20 | 65,915 | 1,335,493 | 20 | 58,340 | 1,415,931 | 24 | 36,192 | 959,413 | 27 | 14,271 | 97,896 | 7 |
| 2015 | 3,851 | 485,460 | 126 | 11,407 | 1,019,727 | 89 | 7,165 | 812,154 | 113 | 7,753 | 751,757 | 97 | 1,655 | 21,627 | 13 |
| 2016 | 8,839 | 690,210 | 78 | 13,178 | 1,173,889 | 89 | 12,016 | 1,198,942 | 100 | 2,645 | 556,851 | 211 | 2,258 | 61,780 | 27 |
| 2017 | 5,519 | 784,995 | 142 | 12,571 | 959,394 | 76 | 5,095 | 855,895 | 168 | 9,133 | 713,140 | 78 | 5,897 | 90,675 | 15 |
| 2018 | 4,165 | 588,926 | 141 | 12,515 | 1,151,923 | 92 | 10,248 | 809,809 | 79 | 18,101 | 682,272 | 38 | 2,201 | 112,044 | 51 |
| 2019 | 10,288 | 521,331 | 51 | 12,423 | 982,718 | 79 | 18,264 | 1,636,225 | 90 | 10,092 | 619,890 | 61 | 2,881 | 80,242 | 28 |
| 2020 | 7,518 | 716,662 | 95 | 15,721 | 835,531 | 53 | 15,109 | 574,107 | 38 | 14,803 | 476,275 | 32 | n/a | 72,295 | n/a |
| 2021 | 16,696 | 602,660 | 36 | 46,079 | 1,759,535 | 38 | 34,437 | 1,191,902 | 35 | 20,692 | 1,316,727 | 64 | 7,823 | 147,215 | 19 |
| 2022 | 28,067 | 971,987 | 35 | 38,844 | 1,146,185 | 30 | 15,257 | 929,708 | 61 | 4,045 | 363,109 | 90 | 11,219 | 233,268 | 21 |
| 2023 | 20,028 | 614,145 | 31 | 23,409 | 937,635 | 40 | 24,926 | 644,252 | 26 | 17,347 | 804,849 | 46 | 15,186 | 107,542 | 7 |
| Mean | 13,530 | 682,186 | 71 | 24,781 | 953,999 | 62 | 26,786 | 1,126,748 | 57 | 16,513 | 734,812 | 67 | 5,261 | 116,101 | 31 |

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

Figures

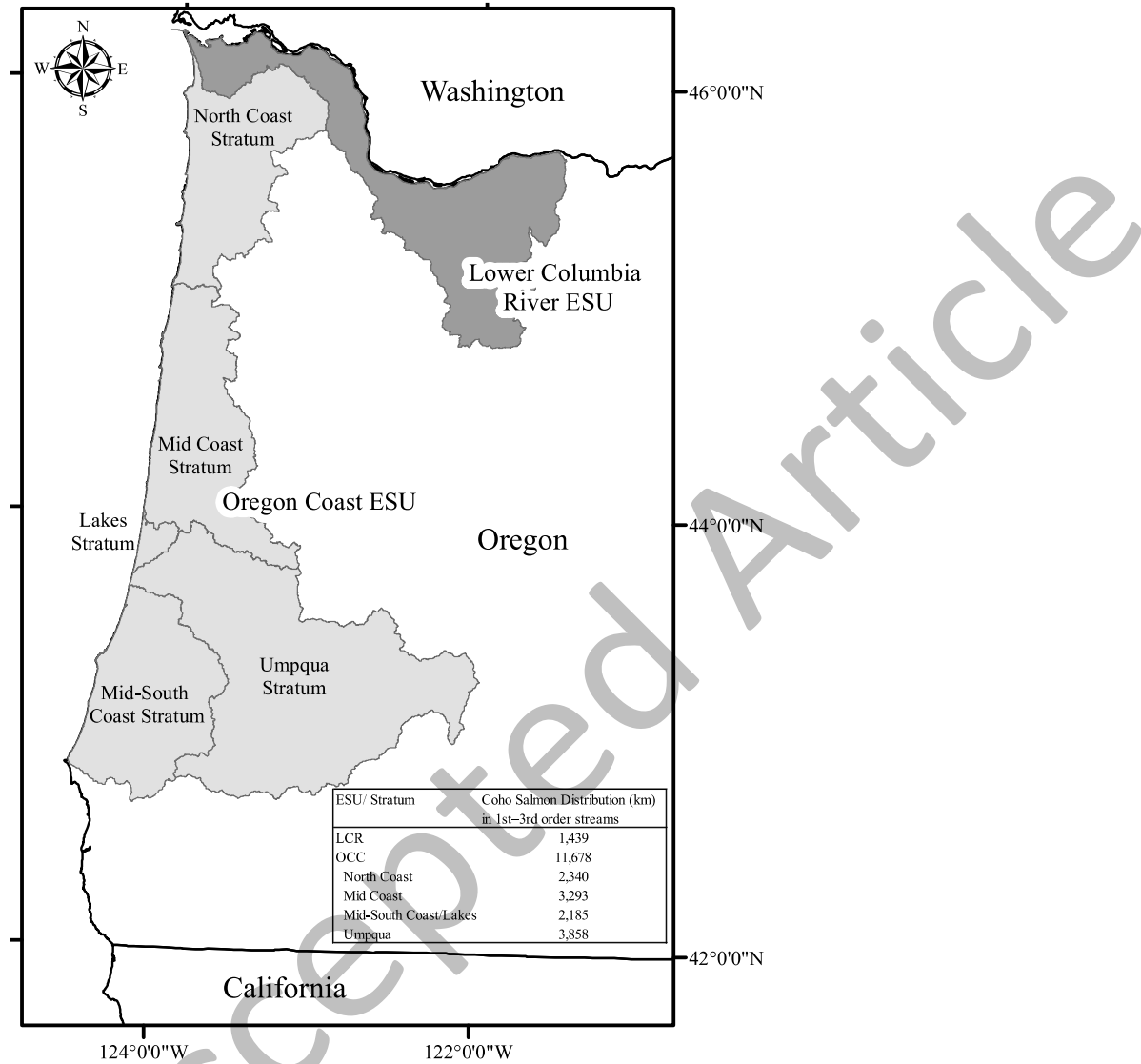


Figure 1. Evolutionarily Significant Units (ESUs) and their strata in Western Oregon that included both parr and adult monitoring for the Oregon Plan for Salmon and Watersheds; the Oregon Coast Coho ESU is shaded in light gray and the LCR Coho ESU is shaded in dark gray. The table shows the length of coho salmon habitat in 1st-3rd order streams (sampling frame length) for the two ESUs and strata.

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

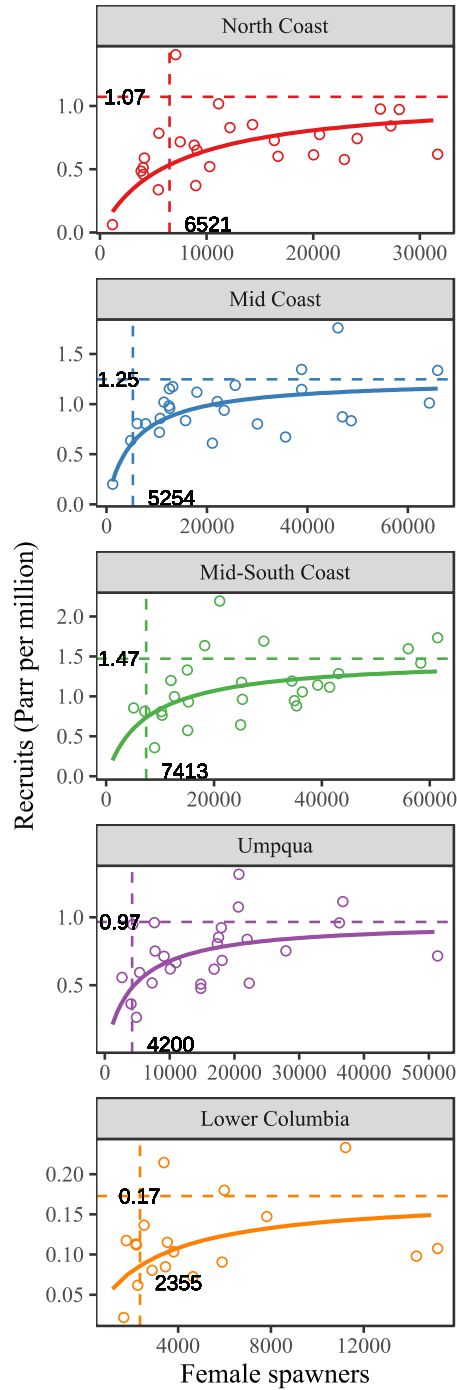


Figure 2. Beverton-Holt model predictions (solid lines) with 95% credible intervals (shaded areas) plotted over observations (circles) by strata. The dashed lines represent R_{max} (horizontal) and S_{50} (vertical) parameters with the values in absolute abundance near the respective axis.

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

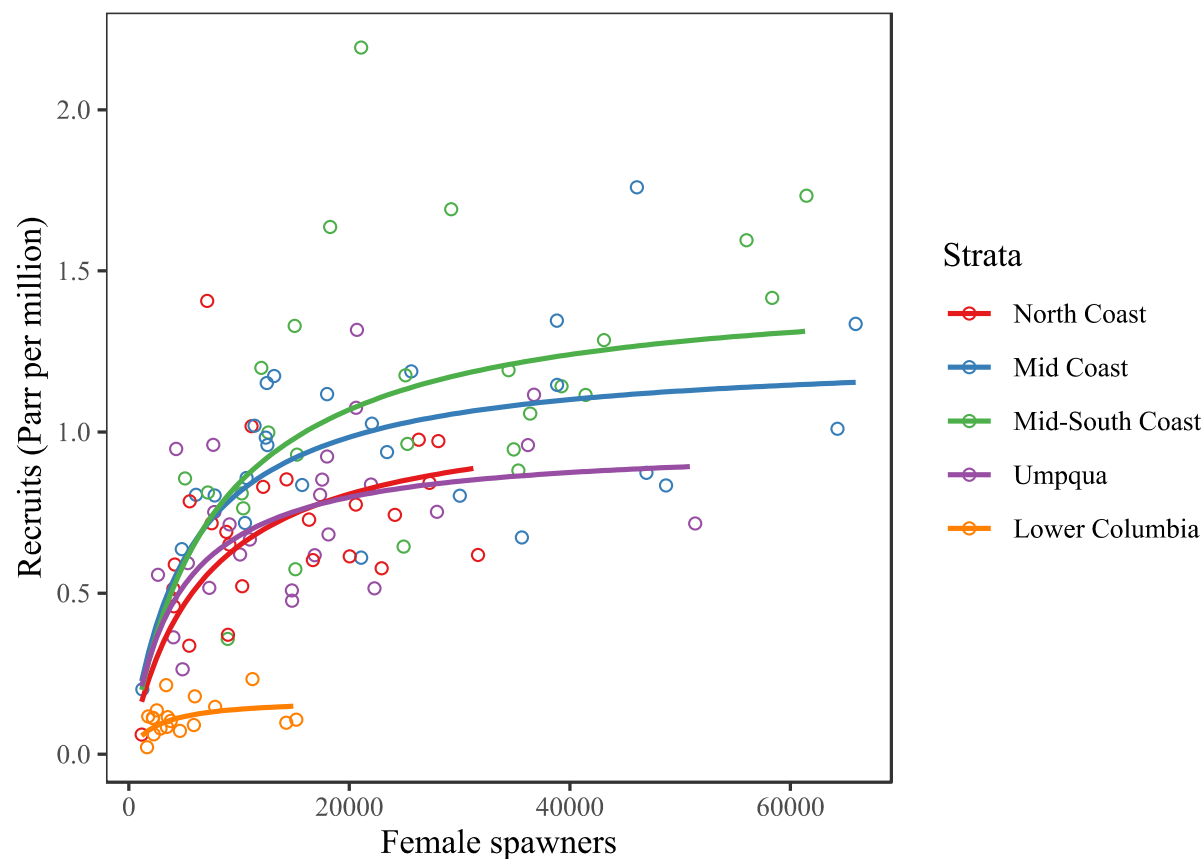


Figure 3. Beverton-Holt model predictions (solid lines) plotted over observations (circles) by strata.

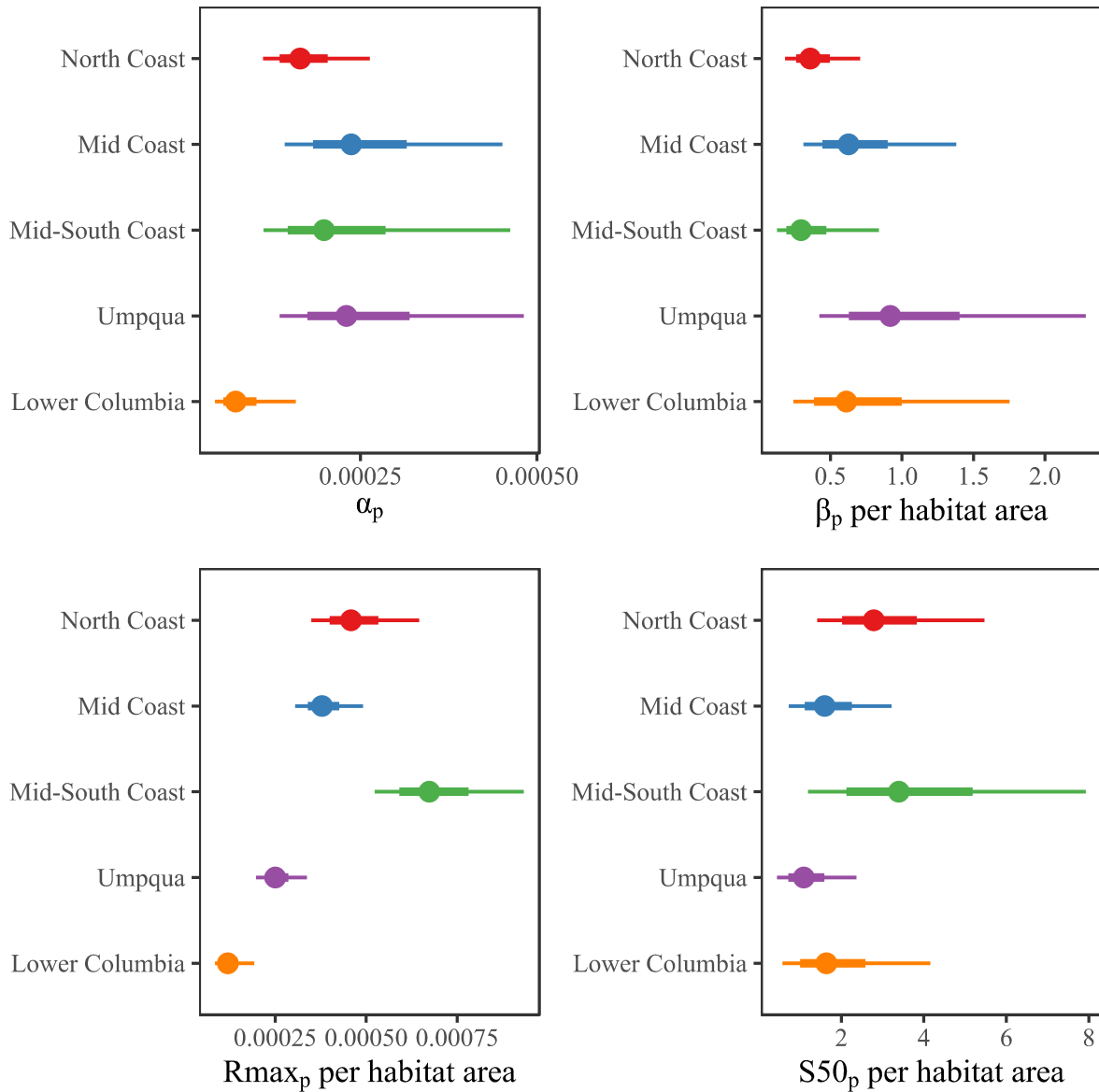


Figure 4. Beverton-Holt posterior probability summaries for α , β , $Rmax$, and $S50$ parameters by strata with points representing the median and thick and thin lines indicating 50% and 95% credible intervals, respectively.

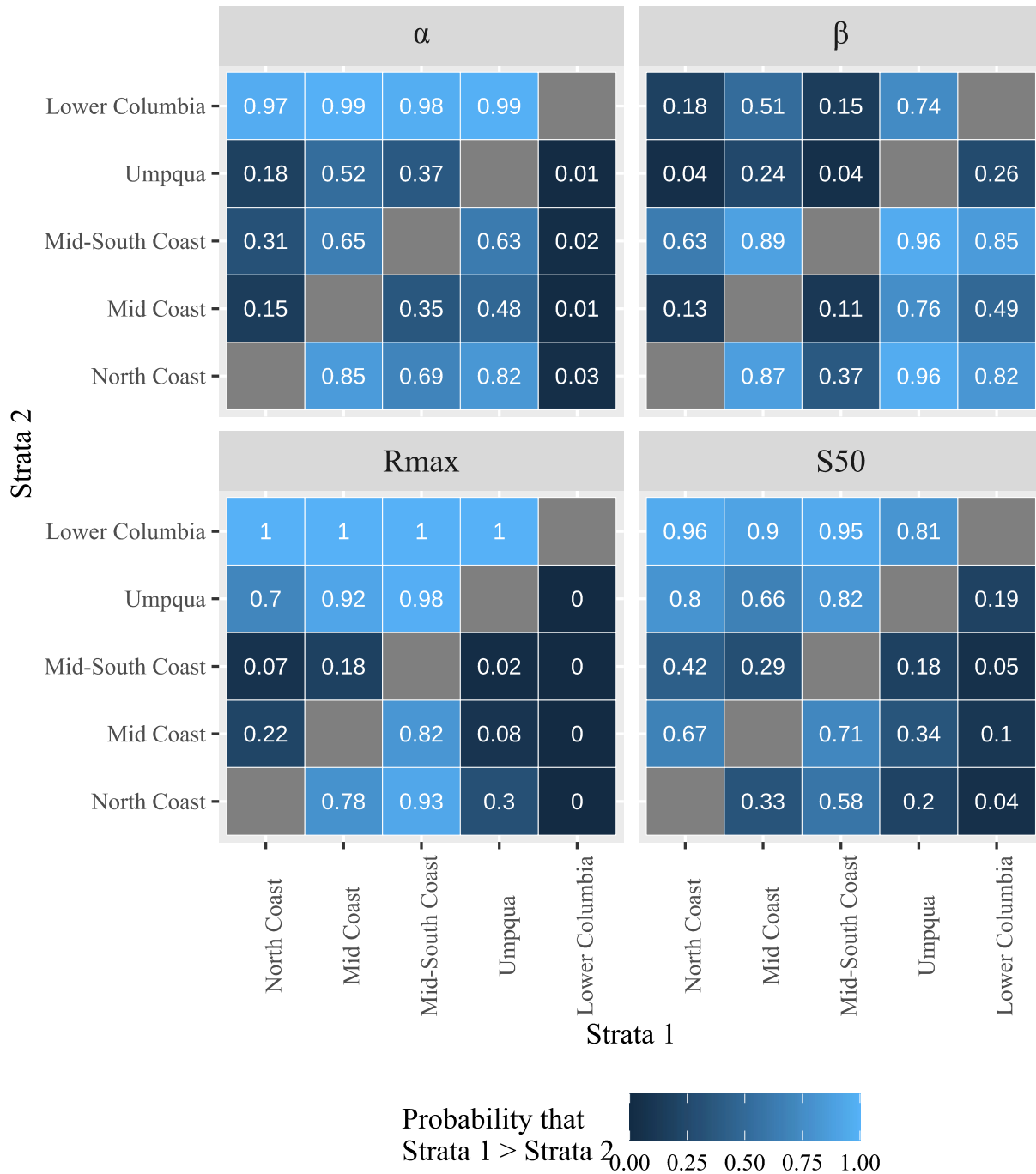


Figure 5. Beverton-Holt posterior contrasts between pairs of strata for α , β , R_{max} , and S_{50} parameters. Colors and white text indicate the probability that strata 1 (x-axis) is larger than strata 2 (y-axis).

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

Supplemental Material

Bias in snorkel counts

Goal: Evaluate whether possible density-dependent bias in snorkel detections could have impacted the shape of our Beverton-Holt models or qualitative differences among strata.

Analysis: We fit models to data collected for a previous study (Falcy and Constable 2024). We examined the relationship between snorkel pool counts and mark-recapture pool estimates. We fit three candidate models: (1) generalized linear model (GLM) with a Gamma distribution and identity link function, (2) generalized additive model (GAM), and (3) linear model with an intercept of zero and additional polynomial term.

All three models resulted in extremely similar shapes and predictions (Figure S1). The correlations among the models' predictions were greater than 0.998 and each with R^2 values of 0.9 (range: 0.899 – 0.904). When models were compared using Akaike Information Criterion (AIC), the GLM exhibited the lowest value indicating the greatest statistical support (AIC values: 515 [GLM], 528 [GAM], 529 [Polynomial]).

The top model (GLM) describes a linear relationship between snorkel counts and mark-recapture estimates where snorkel counts represented 59% of mark-recapture estimates (model coefficient 1.69) across snorkel pool count abundances.

Conclusion: Despite the data here and in (Falcy and Constable 2024) showing a negative relationship between mark-recapture abundance estimates and the proportion of fish seen by snorkelers, we do not see support for a non-linear (i.e., density-dependent) relationship between snorkel counts and mark-recapture estimates. Therefore, any calibration to snorkel pool counts would apply a consistent relationship and consequently would not change the relative shape of Beverton-Holt curves or population-specific comparisons.

Figure S1. Observations (black points) and smoothed model predictions for three candidate models: polynomial (dotted green), GLM (solid blue), and GAM (dashed red). Yellow line indicates 1:1 line.

References Cited

Falcy MR, Constable RJ. 2024. Quantifying uncertainty when extrapolating the relationship between snorkel counts and mark-recapture estimates of juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 81:1279–1291. doi:10.1139/cjfas-2023-0085.