# Conservation hatchery effects on the abundance and spawn timing of natural steelhead populations: A replicated, before-after-control-impact experiment in the Hood Canal Watershed.

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## Abstract

A 17-year, replicated, before-after-control-impact experiment involving seven natural steelhead populations from the same geographic region compared three conservation hatchery-supplemented populations to four non-supplemented (control) populations. Spawn timing varied among the populations with the average median spawn day ranging from late February to the middle of May. Among-population diversity in spawn timing persisted throughout the study period, and there was no evidence for changes in spawn timing across the study period for either the control or supplemented populations. For the supplemented populations, releases of hatchery-reared smolts and adults from the conservation hatcheries caused a substantial increase in the number of redds constructed. After supplementation ended, redd abundance returned to levels only slightly greater than before supplementation. In contrast, the control populations that received no hatchery steelhead had moderately lower redd abundance in the after period compared to the before period. Taken together, the results suggest that the conservation hatcheries contributed to a marginal improvement in adult abundance relative to the control populations. This and the few previous studies that have included non-supplemented reference populations suggest that neutral-to-positive population-level demographic benefits should be expected for carefully planned conservation hatchery programs.

Keywords: steelhead, Oncorhynchus mykiss, conservation, hatchery, before-after-control impact, BACI, supplementation, redd, salmonid

# Introduction

Anadromous salmonid hatcheries have been used to augment natural populations for over a century and have proven effective at increasing the abundance of sexually maturing adults available for harvest (Waples et al. 2007; Jaeger and Scheuerell 2023). In fact, the continued human demand for hatchery-produced salmon to support harvest combined with widespread human-caused declines in natural populations contributed to increasing reliance on hatcheries (Lichatowitch 1999), which reached a peak around the 1980’s with over 500 million salmon released annually (Naish et al. 2008). Since then, refinements to hatchery operations evident across broad geographic areas suggest collective knowledge and experience of the public salmon hatchery system has converged on improved approaches that reduce the ranges of size and timing of release (Nelson et al. 2019). Experimental studies have also contributed to improvements in hatchery operations by identifying strategies to favor physiological and behavioral traits that maximize survival rates and production of returning adults. (Johnsson et al. 2014; Larsen et al. 2019; Tatara et al. 2021). But, the use of hatcheries as a strategy to conserve and rebuild depleted natural populations is far less certain. Therefore, it’s important to carefully evaluate the effectiveness of conservation hatcheries on key indicators of population viability.

Several lines of investigation have shed light on the effects of hatcheries on natural anadromous salmonid populations. Hatcheries may inadvertently select for traits conducive to survival and growth in the hatchery environment (Reisenbichler et al., 2004; Wessel et al. 2006; Howe et al. 2024) with unknown consequences on fitness` in the natural environment (Naish et al. 2008). Estimating the reproductive success of comingled hatchery and natural-origin salmon has proven useful in determining whether hatchery rearing can affect fitness, and in some cases leading to reasonable inferences about genetic and environmental (rearing) mechanisms (Christie et al. 2014; Ford et al. 2016; Theriault et al. 2011; Williamson et al. 2010) causing reduced fitness (or not) in hatchery populations. However, estimating the effect of hatchery inputs on population-level productivity is difficult without a control or reference point (Hess et al. 2012). Hatchery effects can be estimated by incorporating hatchery production (e.g., the number of smolts released or hatchery adults spawning naturally) as an explanatory variable into models attempting to explain changes in productivity or abundance, but the importance of hatchery effects are relative to other factors selected for the analysis, such as streamflow, marine conditions, climate, habitat, hydropower, or other factors. Before-after-control impact (BACI) experimental designs provide perhaps the most rigorous approach to assessing human impacts (in this case, hatcheries) on ecological responses in the face of natural temporal and spatial variability (Stewart-Oaten and Bence 2001; Underwood 1994). A pre-planned replicated, BACI design would provide a more direct comparison of supplemented to non-supplemented populations experiencing similar broad-scale ecological conditions, such as regional precipitation and temperature patterns, and perhaps most importantly, early marine survival (Moore et al. 2010) and ocean conditions affecting smolt-to-adult survival (Welch et al. 2000) for steelhead (Kendall et al. 2017). The lack of BACI-type investigations of hatchery effectiveness stem from a number of factors including: insufficient monitoring of ‘control’ populations, the unavailability of comparable reference populations (because hatchery releases are so widespread), the absence of baseline data before hatchery programs are initiated, and difficulties with terminating hatchery programs once they have started (ISAB 2005, AHSWG 2008).

While the majority of published information indicates that anadromous hatcheries have negative consequences, broadly considered, on fish reared in captivity or co-mingling natural populations (McMillan et al. 2023), few studies have been designed, *a priori*, to specifically test the effects of conservation hatcheries on key measures of population viability, such as abundance and life history diversity. Populations at low abundance face greater risk of extinction from environment fluctuations, chance events that can reduce productivity, and destabilizing depensatory mechanisms (McElhany et al. 2000). A key, largely unanswered, question is whether increases in abundance from the addition of hatchery-reared adults (Waples et al. 2007) will persist in subsequent generations, given the generally lower reproductive success of hatchery-origin fish in natural rivers (Christie et al. 2014). Spawn timing is a trait with generally high heritability (Tillotson et al. 2019; Abadía-Cardoso et al. 2013) and among the most important life history traits known to be altered by hatcheries, both intentionally and unintentionally (McLean et al. 2005; Quinn 2018). Spawn timing in natural populations probably reflects trade-offs between a number of survival factors including hydrologic conditions that affect risks to embryos from scour during high flows or dewatering during declining flows. Together with incubation temperatures, spawn timing will determine emergence timing and the ecological conditions experienced by young offspring (Baldock et al. 2023), the temporal (and thermal) opportunity for growth before the first winter, and therefore possibly age-at-smoltification, which is a threshold trait in steelhead (Arriaza et al. 2017).

There are good reasons to distinguish between the effects of hatcheries intended to support harvest and those designed for conservation. Conservation programs often take large portions of small natural populations into captivity, which may require non-conventional techniques, such as collecting adults from spawning grounds or collecting embryos or juveniles for rearing to sexual maturity (Ford et al. 2015; Venditti et al. 2013). Spawning practices have been designed to mitigate genetic risks that are amplified in small populations, including low effective population size, inbreeding, drift and domestication selection (Fisch et al. 2015). Rearing and release strategies may also incorporate more experimental techniques that have less of a track record (Johnson et al. 2020; Berejikian et al. 2004; Carr et al. 2004) than increasingly uniform strategies implemented by production-oriented programs (e.g., Nelson et al. 2019) where maximizing in-hatchery survival and smolt-to-adult returns are the primary goals. Paradoxically, in many cases, conservation hatchery programs designed to support the most imperiled anadromous salmonid populations implement strategies that are more experimental in nature than production-oriented hatchery programs, and it’s reasonable to expect that the effects of hatcheries operated in disparate manners should manifest in differential impacts on natural populations.

The ‘Hood Canal Steelhead Project’, was a pre-planned experiment to study the effects of conservation hatchery programs on natural populations of steelhead in rivers flowing into the Hood Canal in Washington State. The project was designed and carried out as a replicated BACI experiment wherein all populations were simultaneously monitored for key metrics of population viability, including abundance and life history and genetic diversity before, during and after supplementation. The present study estimates changes in abundance and spawn timing in supplemented and control populations. A subsequent analysis and manuscript will estimate effects on juvenile life history traits, life history transitions, and measures of genetic variability.

# Methods and materials

## Study populations and design

The study included seven steelhead populations and spanned the years 2007-2023. Four of the populations were designated as “controls” and were not supplemented throughout the study. The other three populations were designated experimental populations and received both smolt and adult supplementation. Throughout all three phases of the study, we conducted redd surveys to estimate spawner abundance and spawn timing. The “before” period consisted of the first four years (2007-2010) where only naturally produced steelhead were spawning in each of the populations. The “during” period consisted of the years 2011-2019 when adults returning from age-2 smolt releases would have been present on the spawning grounds along with age-4 and age-5 captively reared adults released into the experimental streams (Figure 1; Table S1). This accounts for smolts last released in 2014 that may have matured at age-4 or 5 or age-4 and age-5 captively reared adults that may have survived and spawned a second time, even though repeat spawning is rare in steelhead. The “after” period consisted of the years

2020-2023 when all of the adult steelhead were of natural-origin. Throughout the study, no adults were collected and artificially spawned. Rather, eyed embryos were collected from nests naturally produced by the populations selected for supplementation beginning in 2007. Releases of age-2 smolts, the modal age-at-smoltification in the natural populations, began in 2009, and releases of age-4 captively reared adults began in 2011 (Figure 1). As planned at the outset of the study, smolt releases were terminated in 2016 and adult releases in 2019 (Figure 1). Endangered Species Act (ESA) permitting was obtained through the National Marine Fisheries Service (NMFS) Evaluation of Hatchery and Genetic Management Plans for Hood Canal Salmon under Limit 6 of the ESA Section 4(d) Rule (NMFS Consultation Number: WCRO-2021-03133), and animal care in accordance with NMFS Policy 04-112.

The Hood Canal is a glacial-carved fjord approximately 100 km long, and the surrounding watersheds range from the steep western slopes of the Olympic Mountains to the lowlands on the Kitsap Peninsula (Figure 2) creating a range of temperature and hydrologic regimes and other macro-scale habitat features in the study streams (Berejikian et al. 2013). All of the steelhead populations included in this study were listed as Threatened under the US Endangered Species Act (ESA) in 2007 (Federal Register/Vol. 72, No. 91/Friday, May 11, 2007/Rules and Regulations), which is the same year we began collecting data on redd abundance and spawn timing. The seven populations included in the study represent a single Major Population Group (MPG) and four Demographically Independent Populations (DIPs) as defined in the recovery plan for the Puget Sound Steelhead distinct population segment (NMFS 2019). Only one of the major steelhead-producing watersheds in Hood Canal was excluded (Dosewallips River) because flow and turbidity conditions during the spawning season precluded consistently complete redd counts. The remaining seven populations included in the study represented the most productive steelhead watersheds in Hood Canal. The three populations designated for supplementation (Dewatto River, South Fork Skokomish River, Duckabush River) and the four that were monitored as experimental ‘controls’ (Tahuya River, Big Beef Creek, Union River, and Little Quilcene River) were selected so that both treatments would encompass a mix of hydrological regimes (rain dominant and snow-rain transitional), habitat types (high and low gradient), and geographic distribution throughout Hood Canal (Figure 2; Berejikian et al. 2013).

Hatchery-reared winter-run hatchery steelhead, derived initially from the Chambers Creek hatchery population in South Puget Sound were periodically released into all of the Hood Canal populations until release year 2002, with one additional release into the Duckabush River in 2003 and in the Mainstem Skokomish River in 2003 and 2004 (Hard et al. 2015). Releases were terminated largely because survival rates were poor and reproductive success of the source hatchery population (Chambers Creek) had been found to be very low relative to natural populations (Berejikian and Ford 2004, (Araki et al. 2007). Genetic analyses conducted in the 1990's (Phelps et al 1997) and again during the pre-supplementation phase of this project (Van Doornik and Berejikian 2015) have indicated no evidence of introgression from the Chambers Creek stock into any of the study populations, perhaps because of their low fitness and very early spawn timing, which peaks in January (NMFS 2019). Therefore, at the onset of the study, all populations were presumed to represent the endemic, self-sustaining, natural populations, with only natural-origin steelhead spawning each year.

## Redd surveys

Female steelhead construct and spawn in a series of nests, contiguously referred to as a 'redd' (Berejikian et al. 2020). Redds provide a more precise measure of spawn timing than run timing, especially for steelhead which can spend days to months in freshwater prior to spawning. Redds also serve as a critical indicator of female abundance in situations where returning adults cannot be captured at a weir or trap, and redd counts closely approximate adult abundance in small populations (Gallagher et al. 2010). Typically, females will construct either one or two redds with each containing between one and eight individual nests with each nest containing eggs from a single spawning event; the average number of redds constructed per female has been estimated at about 1.5 (Gallagher and Gallagher

2005; Kuligowski et al. 2005). Spawning events involve one or more anadromous (steelhead) males and may involve participation by one or more non-anadromous (‘resident’) males (McMillan et al. 2007). Redds are visually identified from a number of characteristics, including:  a large area of ‘clean’ gravel, a crescent shaped mound at the downstream end, and a pit at the upstream end (Gallagher et al. 2007). The shape is typically oblong (from downstream to upstream), but can be as wide as they are long in some cases. Streambed position, gradient, and substrate size and composition, are also evaluated in order to distinguish from flow generated scour.

Redd surveys were conducted in all streams every year from 2006 through 2023 by experienced, trained surveyors operating from the same set of shared protocols (Gallagher et al. 2007). Surveyors were aware of the streams that were being supplemented, which could introduce unconscious bias, but the survey effort and redd identification methodologies were clearly defined, shared among all groups, and re-visited annually, as were detailed discussions to help ensure unbiased counts. Each stream was surveyed, from the mouth of each stream to the upstream-most point accessible to adult steelhead (Table S1) with the exception of the Duckabush River where two reaches (river km 4.3-7.7 and 9.6-11.7) were too difficult to survey on higher flows and were not surveyed regularly. Surveys commenced as early in the spawning season as flow conditions would allow, which varied among watersheds, and were conducted weekly except where high flow events precluded a survey. Individual redds were marked with flagging attached to vegetation at the nearest point on shore indicating the date of detection and channel location to prevent duplicate counting. Redds were also often marked with a weighted piece of flagging placed near the pit and tailspill of the redd. Redds under construction that were enlarged within a week were counted as one redd. Redds separated by more than 1 m, or a redd that was enlarged after 1 week of no new activity, were considered separate because redd construction takes approximately 3-4 days (Berejikian et al. 2020). Surveys continued until no new redds (i.e, not previously observed) were detected in a given stream. Surveyors were highly experienced, working together across watersheds, and several surveyors conducted surveys throughout the entire duration of the 18-year study, providing consistency in the implementation of methodologies. We assumed that variation in redd counts caused by natural variability in flows that affected visibility or access were uniform across drainages and did not affect the comparison of redd counts or timing between supplemented and control populations.

## Embryo collections, hatchery rearing, and release strategies

The following briefly describes the approach to supplementation in treatment streams. Redds identified during approximately weekly redd surveys were precisely located by triangulating to two points on shore (Berejikian et al. 2011). Accumulated temperature units (ATU; daily average temperature x number of days) were monitored for each redd to determine when the embryos would have developed externally visible eyes, which occurred between approximately 210-250 ATU, and could be collected from each redd and transported without harm. A hydraulic process was used to remove ‘eyed’ embryos from portions of the redds (Berejikian et al. 2011). The embryos from the Dewatto and Duckabush Rivers were transferred to the USFWS Quilcene National Fish Hatchery, incubated on pathogen free water and ponded into small circular rearing vessels for rearing to approximately 30 days. Juveniles were transferred to the Long Live the Kings, Lilliwaup Hatchery for rearing to smolt and adult stages (Table S2, Fig 1). Embryos from the SF Skokomish River were transferred to the McKernan salmon hatchery within the SF Skokomish watershed and incubated then subsequently reared on pathogen free spring water supplies for rearing to the same ages as the other two populations (Table S2, Fig 1).

Rearing conditions to the smolt release stage, similarities and differences in smolt characteristics between the two hatcheries, and some measures of post-release performance are well documented in (Berejikian et al. 2012; Moore et al. 2012). In short, temperature-based feeding regimes were developed to regulate growth rates to produce smolts of a similar size to natural-origin smolts in two years to match the modal age-at-smoltification in natural populations. Smolts were loaded into transport tanks and trucked and released in late April, which is near the peak outmigration timing, in the lower to middle reaches of each of the three rivers (Figure 2, Supplementary Table S3).

A portion of the smolt release groups were retained, reared to the adult stage (hereafter, the adult release groups), and released at either age-4 or age-5 (Figure 2, Supplementary Table S4). The Duckabush and Dewatto smolts were reared to the adult stage in freshwater at the Lilliwaup Hatchery. The SF Skokomish smolts were transferred to the Manchester Research Station for rearing in seawater with the exception of a portion of the smolts from Brood year 2011. The procedures for smolt-to-adult rearing and release were documented in detail for one particular brood year (Van Doornik et al. 2022), which is characteristic of rearing procedures and conditions in the other years. Table S2 provides the numbers of embryos collected and smolts and adult releases for every year of the study. Annually, the timing of adult releases was based on the earliest determination that females had begun to ovulate, which was determined by the ability to express eggs with pressure applied to the abdomen. The approach attempted to balance the risk of pre-spawning mortality (e.g., predation) from releasing fish too early with the risk of over-ripening of eggs, which can reduce viability beginning approximately one week post-ovulation (Springate et al. 1984). Most often adults were released in two or more groups (Supplement Table S4). The first group would include females that had ovulated and those whose bellies felt softer and were expected to ovulate in the next couple of weeks. Subsequent groups were released when the first of the remaining females had ovulated. Males were considered mature and ready for release when milt could be manually expressed. In each pulse the attempt was made to release females with a roughly equal number of sexually mature males. The study was not designed to determine the relative contributions of fish released as smolts and those released as adults.

## Statistical analyses

We used Bayesian regression models to estimate the change in mean abundance and spawn timing between each phase for the control and treatment streams (McElreath 2016). We fit separate models for abundance and spawn timing, but both models had the same structure. The response variable for the abundance model was log abundance ($\log_e$(abundance + 1)) and the response for the spawn timing model was median spawning day of the year. Both models included main effects for phase (before, during, after), treatment (control, supplemented), and their interaction, as well as random stream and year effects (non-nested). To account for serial dependence, we modeled the residuals of both models as a first order autocorrelated process.

Change in mean abundance and median spawning day across phases for the control and supplemented groups was quantified as the difference in the posterior means between phases for each treatment group, which is analogous in concept to effect size. Differences in the phase-wise change in abundance and spawn timing between the control and supplemented groups were quantified as the percent overlap between posterior distributions between the two treatment groups, which can be thought of as a measure of confidence that the distributions are different (Pastore and Calcagni 2019). Combined, these two methods allowed us to examine the degree that phase-wise changes in abundance or spawn timing are dependent on the treatment group.

We used weakly informative student-t prior distributions for all model parameters with 3 degrees of freedom and standard deviations of 2.5 (Lemoine 2019; Banner et al. 2020). The prior for the autocorrelation term was truncated to the domain -1, 1 and the priors for the random effect standard deviations and residual standard deviation were restricted to be positive.

Models were estimated using the “brms” R package and Stan (version 2.26.1) using four chains run for 2000 iterations each following a 500-iteration warm-up (6000 total posterior samples; Bürkner 2017) (Carpenter et al. 2017). Convergence and fit were assessed using effective sample size, R-hat, and visual methods (e.g., trace-plots and posterior predictive checks; Gabry et al. 2019). All estimated parameters had an effective sample size of at least 1000, R-hat values less than 1.05, and no divergent transitions were observed.

We assessed variance in spawn timing because variance can be reduced in hatchery populations and has been shown to be highly heritable (Abadía-Cardoso et al. 2013). We used a nonparametric bootstrap approach to evaluate whether spawn timing variance (variance in the day of year of spawning) changed across experimental stages (Efron and Tibshirani 1993). Specifically, we generated 1,000 bootstrap data sets by resampling the daily redd count data for each stream with replacement. We then calculated summary statistics for each bootstrap dataset, which provided a distribution of spawn timing variances by stream and stage. Our primary test statistic was the ratio of the spawn timing variance in the before period to the after period for each stream; ratio values greater than one indicate a reduction in spawn timing variance from the before to the after period.

## Results

### Abundance

Over the entire study period, redd abundance ranged from zero for Big Beef Creek in 2022 to 809 for the Skokomish River in 2015 (Figure 3; Figure S1). For all three supplemented populations, maximum abundance occurred during the supplementation phase, whereas only one of the four control populations had maximum abundance during the supplementation phase (Union River in 2019). Conversely, for three of the four control populations, minimum abundance occurred during the supplement phase (2017 for Little Quilcene River, Tahuya River, and Union River), whereas minimum abundance only occurred during the supplementation phase for one of the supplemental populations (Dewatto River in 2019).

Comparing changes in abundance between the supplemented and control population across the three phases provided a test of whether supplementation caused an increase or decrease in abundance and whether any changes during supplementation would persist in the generation after supplementation was terminated. Changes in abundance across the three phases were influenced more by supplementation than natural variability. For the supplemented populations, model results showed an increase in abundance from the before phase to the during phase with the entirety of the posterior distribution for the during-before contrast greater than 0. The effect waned in the generation after supplementation, but still 67% of the posterior distribution for the after-before contrast was greater than 0 (Table 1; Figure 4). In the control populations, abundance tended to decline over the course of the study period to the point where 91% of the posterior distribution for the after-before comparison was less than 0 (Table 1; Figure 4). For the during-before contrast, the posterior distributions of supplemented and control populations had little overlap (3.5%), indicating a substantial increase in spawner abundance caused by supplementation (Figure 4). For the after-before contrast, the decline in control populations and modest increase in the supplemented populations resulted in a 39.3% overlap in the posterior distributions (Figure 4). Taken together, the analysis demonstrates a strong positive effect of conservation hatcheries on abundance during supplementation that diminished to some degree after supplementation, but still indicates weakly positive effects from supplementation in a single generation after supplementation was terminated.

## Spawn timing

Across all years, spawning in Hood Canal steelhead populations spanned six months, occurring as early as mid-January and extending as late as mid-July. Spawn timing varied among the populations with the average median spawn day ranging from late February (day 59) for Big Beef Creek to the middle of May (day 138) for the Skokomish River (Figure 5). Among-population diversity in spawn timing persisted throughout the study period as there was no evidence for changes in spawn timing across the study period for either the control or supplemented populations (Figure 6). For both treatment groups, differences in median spawn day across phases were not discernable from zero at the 95% credibility level (Table 2). There was also considerable overlap in the posterior distributions of the phase-wise differences between the control and supplemented populations (> 45% for all comparisons; Figure 6), providing no support for an interaction between phase and treatment for spawn timing.

We found no evidence for consistent changes in spawn timing variance from the before stage to the after stage in either the supplemented or control populations (Figure 7). In particular, two of the supplemented streams showed an increase in spawn timing variance from the before to the after period (Duckabush and Dewatto) and one stream had a reduction in spawn timing variance (Skokomish). Similarly, for the control streams, two showed increases in variance and two showed declines in variance across the study period (Figure 7).

## Discussion

Determining whether conservation hatcheries have provided a benefit to natural populations depends on the objectives of the programs and the corresponding population response. The conservation hatchery programs clearly increased the number of redds constructed in the supplemented streams during supplementation, but the number of redds produced by natural-origin returning adults in the first generation after supplementation was only slightly greater than pre-supplementation levels. However, the abundance of redds in the control populations generally declined over the duration of the study. Ultimately, there was a 39% overlap in the posterior distributions of supplemented and control populations for the after-before contrast. Thus, the supplemented populations were in a modestly improved condition relative to control populations after supplementation than they were before. There was little evidence to suggest any shifts in median spawn timing in either the supplemented or control populations, as indicated by the considerable (68%) overlap in the after-before posterior distributions of supplemented and control populations. We also found evidence for stronger year effects on abundance than spawn timing, possibly suggesting that inter-annual variability in broad scale environmental conditions influenced abundance more strongly than spawn timing (Figure S2).

Anadromous salmonid supplementation programs increase the total number of spawning adults during the supplementation period (Waples et al. 2007; Paquet et al. 2011; Koch et al. 2022), but the effects on natural-origin spawner abundance and productivity are much more equivocal when considered across several species and a diversity of habitats (e.g., Buhle et al. 2009, Janowitz et al. 2017, Scheuerrel et al. 2015, Courter et al. 2019). Two previous studies, one of Chinook salmon (Venditti et al. 2018) and one of steelhead (Berejikian and Van Doornik 2018), included reference (natural) populations and both pre-supplementation and post-supplementation periods when only natural-origin adults were spawning. Both indicated the expected immediate increase in spawner abundance with the return of hatchery-produced fish. The addition of Chinook salmon spawners resulted in more juvenile offspring during the supplementation period while increases in adult abundance were less evident, and after supplementation abundance and productivity measured at all stages returned to roughly pre-supplementation levels (Venditti et al. 2018). A retrospective analysis of long-term data sets containing both hatchery and natural-origin fish throughout the time series, indicated little change in natural-origin Chinook salmon spawner density in supplemented populations (Scheuerell et al. 2015) relative to the same reference populations analyzed by Venditti et al. (2018). In a previous study, the Hamma Hamma River steelhead population in Hood Canal exhibited significantly greater redds post supplementation than pre-supplementation relative to four control populations and some measures of genetic diversity actually increased, apparently as an outcome of increased spawner abundance (Berejikian and Van Doornik 2018). Based on the two BACI-type analyses and Scheuerell et al. (2015), we would thus far conclude limited effects of supplementation programs on natural population abundance, and a slightly greater potential for positive demographic outcomes than negative.

Other studies lacking reference populations have typically modelled hatchery releases or adults on the spawning grounds as a covariate to potentially explain changes on abundance or productivity relative to other covariates. Hatcheries were associated with positive (Courter et al. 2022), negative (Buhle et al. 2009; Scheuerell et al. 2021) and no detectable changes in natural populations (Courter et al. 2019). A primary limitation of these observation studies is accounting for confounding factors and the challenges that creates with allocating variance in abundance or productivity in natural populations to specific factors, which may partly explain the inconsistent results among the studies (Courter 2022). For example, large-scale climate indicators were often included in top models explaining variation in the abundance and productivity metrics (Buhle et al. 2009; Scheuerrell et al. 2015; Courter et al. 2019; Scheuerrell et al. 2021; Courter et al. 2022), highlighting the importance of incorporating reference populations that experience similar early marine environments and interannual variability in Pacific Ocean conditions.

In the present study, redd abundance in the supplemented populations did not increase relative to control populations to the same extent as one similarly supplemented Hood Canal Stream (Hamma Hamma River, Berejikian and Van Doornik 2018). Ultimately, the Hamma Hamma River program resulted in a 2.6-fold increase in the number of redds after, compared to before, supplementation, and an increase in the effective population size and some measures of genetic variability.  The redd abundance has since averaged 23 redds per year through 2023; near the post-supplementation level (26 redds per year). Neither study was designed to investigate component effects of the supplementation program on population metrics, such as survival of released fish or the relative fitness of hatchery- and natural-origin spawners, but previous research provides information on the factors that may have limited the effectiveness of supplementation in the three populations included in this study. First generation hatchery-reared adult steelhead that were released as smolt (similar to the smolt release groups in this study) have been shown to exhibit variable, but lower fitness relative to natural-origin adults in the same environment (Araki et al. 2007; Berntson et al. 2011; Ford et al. 2016). The effectiveness of releasing adult females may have been compromised even further by their smaller body size (Table S4), and possibly other behavioral or physiological factors that appear to be common in captively reared salmon and steelhead (Venditti et al. 2013; Carr et al. 2004; Berejikian et al. 2008). For a single brood year in the Skokomish River, steelhead released at age-4 and age-5 represented 58% of adult steelhead sighted during snorkel surveys, and produced 31% of the juvenile offspring (Van Doornik et al. 2022), suggesting they were not as reproductively successful on a per individual basis. Even though the hatchery-produced adults released as smolts and adults were not as successful as natural-origin adults, they likely added to the juvenile offspring population in the Skokomish River (Van Doornik and Berejikian 2022) as well as the other two populations (Van Doornik et al. in prep). Understanding ecological conditions in both freshwater and marine environments, discussed below, may help to explain why increased production did not carry over to the post-supplementation phase.

The increased abundance during supplementation may not have sufficiently increased smolt production to support a more positive post-supplementation response. We speculate that density-dependent freshwater growth and survival may have played a role in limiting the long-term effectiveness of these conservation hatchery programs. Density-dependent processes appear to be limiting the recovery of anadromous salmonid populations in the Pacific Northwestern United States, even though adult abundance is a small fraction of historic levels. A basin-wide analysis in the Columbia and Snake Rivers indicated compensation was evident in the great majority of populations based on declining recruit-to-spawner ratios with increasing numbers of spawners (ISAB 2015). For Puget Sound steelhead, Scheuerrell et al. (2021) found evidence of compensatory density dependent regulation in a natural Steelhead population in the Skagit River (Puget Sound), at levels of spawner abundance an order of magnitude below its historic population size (Gayeski et al. 2011). This finding was coupled with evidence that juvenile survival was limited by low food consumption rates (Thompson and Beauchamp

2016; Thompson and Beauchamp 2014) similar to food limited growth in one of the supplemented rivers in the present study (Duckabush River; Marston et al. 2017). Steelhead respond to food limitations by increasing territory size, emigrating or reduced growth rates (Keeley 2000; Keeley 2000). In another more comprehensively monitored system, Keogh River (Vancouver Island BC), steelhead have most recently experienced a regime characterized by low freshwater productivity (despite low spawner abundance) and low marine survival, which appears to extend to other systems (Wilson et al. 2021)

The implementation of conservation hatchery programs evaluated in this study were partly motivated by the reasonable hypothesis that depensatory mechanisms (i.e, positive density dependence; Liermann and Hilborn 2001) were limiting the productivity of these relatively small populations and that providing a demographic boost would lessen depensatory predation on outmigrating smolts (Furey et al. 2021; Quinn et al. 2014). Steelhead smolts are the largest-bodied among anadromous salmonids in the region, and susceptible to considerable predation by avian and mammalian predators, particularly in Puget Sound and Hood Canal, where pinniped populations have been increasing for decades (NMFS 2019; Sobocinski et al. 2020). While the addition of hatchery smolts and adults appears to have contributed to the juvenile populations (Van Doornik et al. 2022), any increases in smolt production may have been insufficient to overcome high predation rates that can occur within hours to days after marine entry (see Moore et al. 2024).

Beyond the delta estuaries and Hood Canal, the end of the pre-supplementation phase and post-supplementation phase coincided with declines in steelhead abundance along the Washington Coast (McMillan et al. 2022). While this should have affected all study populations in a similar fashion, possible slight demographic increases in supplemented populations may have been muted by large-scale factors in the North Pacific Ocean. Climate change and the coastwide declines in steelhead marine survival have been evident since the 1980’s (Sobocinski et al. 2020), and abundance declines appear to have intensified during the latter half of this study; particularly following the marine heat wave in 2014-2016 (coast-wide abundance trends available at https://www.psmfc.org/steelhead/).

Spawn timing does not appear to have been altered by the supplementation programs, and there remains substantial spawn timing diversity among Hood Canal steelhead populations. Peak spawn timing ranged from early February (BBC) to late May (SF Skokomish River). In other larger river systems receiving hatchery inputs and over a longer period of time, there is evidence of shifts in spawn timing that relate to selecting early returning hatchery fish for spawning coupled with temporally-biased harvest strategies (McMillan et al. 2023). No artificial spawning was implemented in this conservation program, rather embryos were collected from naturally produced redds over substantial portions of the spawning seasons, and the programs spanned just two generations. Harvest was limited to small-scale subsistence fisheries on the SF Skokomish River. These factors likely limited the potential for reduced diversity or directional shifts in spawn timing, which is a highly heritable trait (Abadía-Cardoso et al. 2013; Manhard et al. 2018) and therefore susceptible to artificial selection (Tillotson et al. 2019). The considerable spawn timing diversity among Hood Canal steelhead populations appears to be associated with adaptations to temperature or possibly hydrologic differences among systems, which range from later spawning in colder, transitional (rain-snow) driven systems to earlier spawning in warmer, lowland, rain-driven systems (see Berejikian et al. 2013 for a characterization of the watersheds). The spawn timing diversity that still exists among populations may be important for the long-term viability of this population group. However, some of that diversity may now be imperiled because the earliest spawn timing occurred in one of the control populations (Big Beef Creek), which has declined to very low levels and had no redds observed in 2022. We did not detect consistent changes in spawn timing diversity within populations from before to after supplementation, suggesting that changes in diversity within populations reflected interannual variability in river conditions.

Reviews of the published literature have compiled substantial evidence that hatchery propagation of anadromous salmonid can affect genetic and phenotypic traits of hatchery population that may negatively impact natural populations (McMillan et al. 2023, Riddell et al. 2024). However, in situ studies conducted to date suggest that thoughtfully designed and carefully implemented conservation-oriented hatchery programs should be expected to have neutral to positive demographic effects on the natural populations they are designed to support. Genetic risks of hatcheries have been well documented (Naish et al. 2008) and may not be immediately evident or may extend beyond the timeframes of the BACI-type demographic-oriented studies discussed here. Genetic management of conservation programs aiming to minimize unintended changes has been considered for some time and continues to evolve (Faser et al. 2008, Waters et al. 2015). Science-based recommendations on best practices for supplementing salmon and other marine species (e.g., Lorenzen et al. 2012) have been developed over the past couple of decades. Improving the likelihood that conservation hatcheries will meet objectives will partly depend on understanding the ecological conditions of the target natural populations. Carefully planned evaluations of hatchery programs, ideally including monitored reference populations, will provide a basis for future efforts, which are sure to follow.

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## Competing interests

The authors declare no competing interests

## Author contribution statement

BAB: Conceptualization, Funding acquisition, Writing original draft, Writing - review and editing, Investigation, Methodology, Project Administration;

MJM: Data curation, Formal analysis, Visualization, Writing original draft, Writing - review and editing;

JL-W: Conceptualization, Data curation, Investigation, Project administration, Writing -review and editing;

MRD: Investigation, Data curation, Validation, Methodology, Writing original draft, Writing - review and editing;

KKS: Project administration, Investigation, Data curation, Validation, Writing - review and editing;

RE: Investigation, Data curation, Validation, Writing - review and editing;

AB: Investigation, Data curation, Validation, Writing - review and editing

**Data and code availability statement**: The data and code that support the findings of this study are openly available at ______________________________________

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Table 1. Posterior means and credibility intervals for the phase-wise abundance changes. All values are in units of number of redds (back transformations included bias correction).

| Comparison | Treatment | Mean | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|
| during - before | Control | -5.7 | -28.8 | 6.4 |
| after - during | Control | -2.9 | -17.4 | 7.5 |
| after - before | Control | -8.5 | -36.9 | 4.2 |
| during - before | Supplemented | 76.9 | 9.6 | 253.3 |
| after - during | Supplemented | -69.5 | -241.8 | -7.1 |
| after - before | Supplemented | 7.5 | -28.8 | 55.6 |

Table 2. Posterior means and credibility intervals for the phase-wise spawn timing changes. All values are in days.

| Comparison | Treatment | Mean | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|
| during - before | Control | 0.8 | -3.0 | 5.0 |
| after - during | Control | -2.3 | -7.4 | 2.6 |
| after - before | Control | -1.5 | -6.2 | 2.8 |
| during - before | Supplemented | -1.4 | -7.3 | 3.7 |
| after - during | Supplemented | 2.0 | -4.5 | 8.8 |
| after - before | Supplemented | 0.6 | -5.4 | 7.0 |

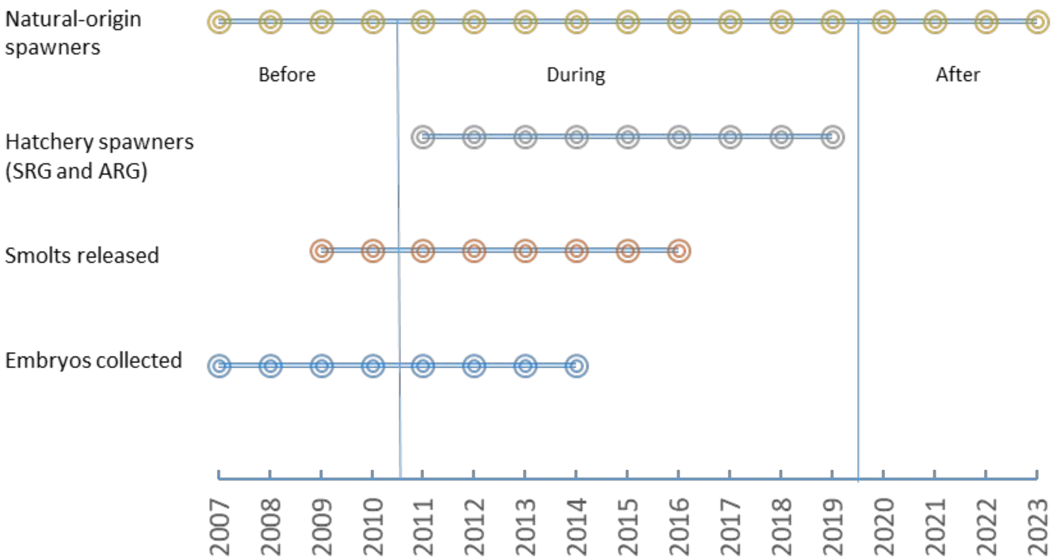

Figure 1. Timeline showing years in which embryos were collected to initiate captive rearing groups. Embryos were reared to age-2 and released as smolts and years when captively reared steelhead released as smolts (SRG) and as adults (ARG) were present on the spawning grounds.

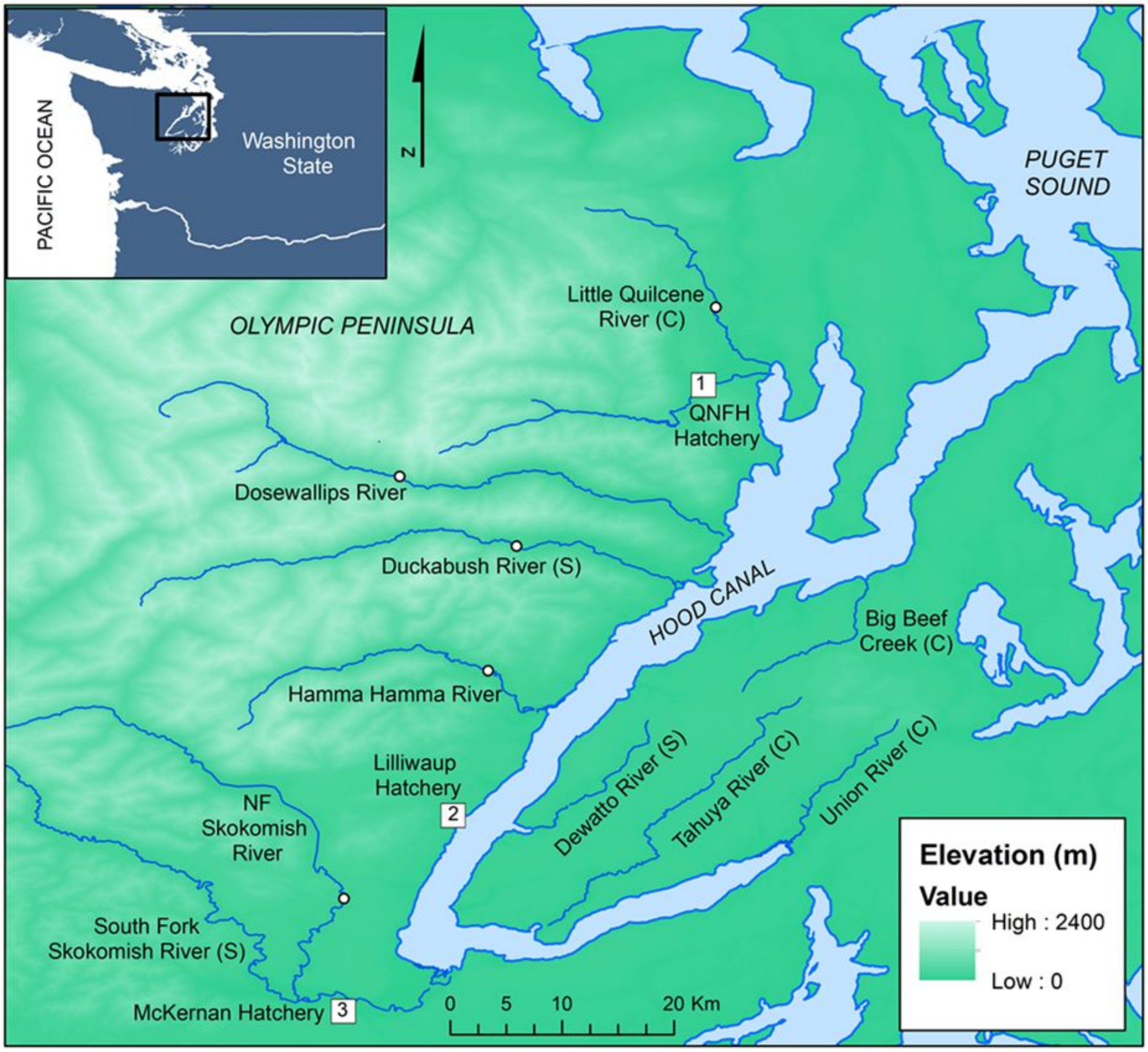

Figure 2. Map of the study area including streams that were supplemented (S) with smolts and adults and streams that were non-supplemented controls (C). Embryos for two populations (Dewatto and Duckabush) were incubated at the USFWS Quilcene National Fish Hatchery (1), transported to the Lilliwaup Hatchery (2) for rearing to the smolt and adult stages. South Fork Skokomish River steelhead were reared at the McKernan Hatchery (3). White circles indicate natural and human-made barriers to upstream migration (xy coordinate system: GCS_WGS_1984, datum: D_WGS_1984; Map created by M.E. Moore).

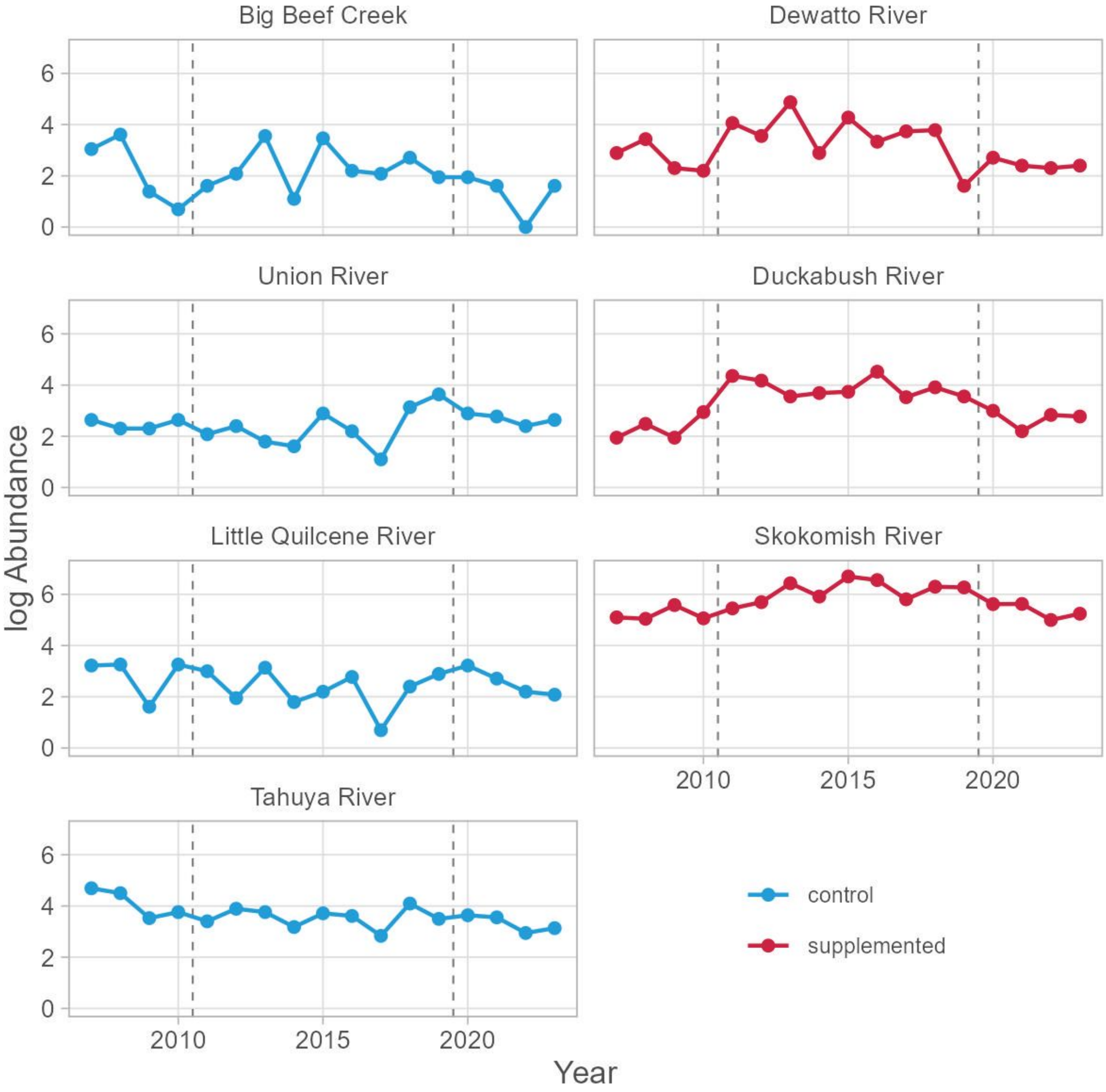

Figure 3. Steelhead abundance time series (log scale). Blue series show the control populations and red series show the supplemented populations. Dashed vertical lines indicate the breaks between the before, during, and after phases.

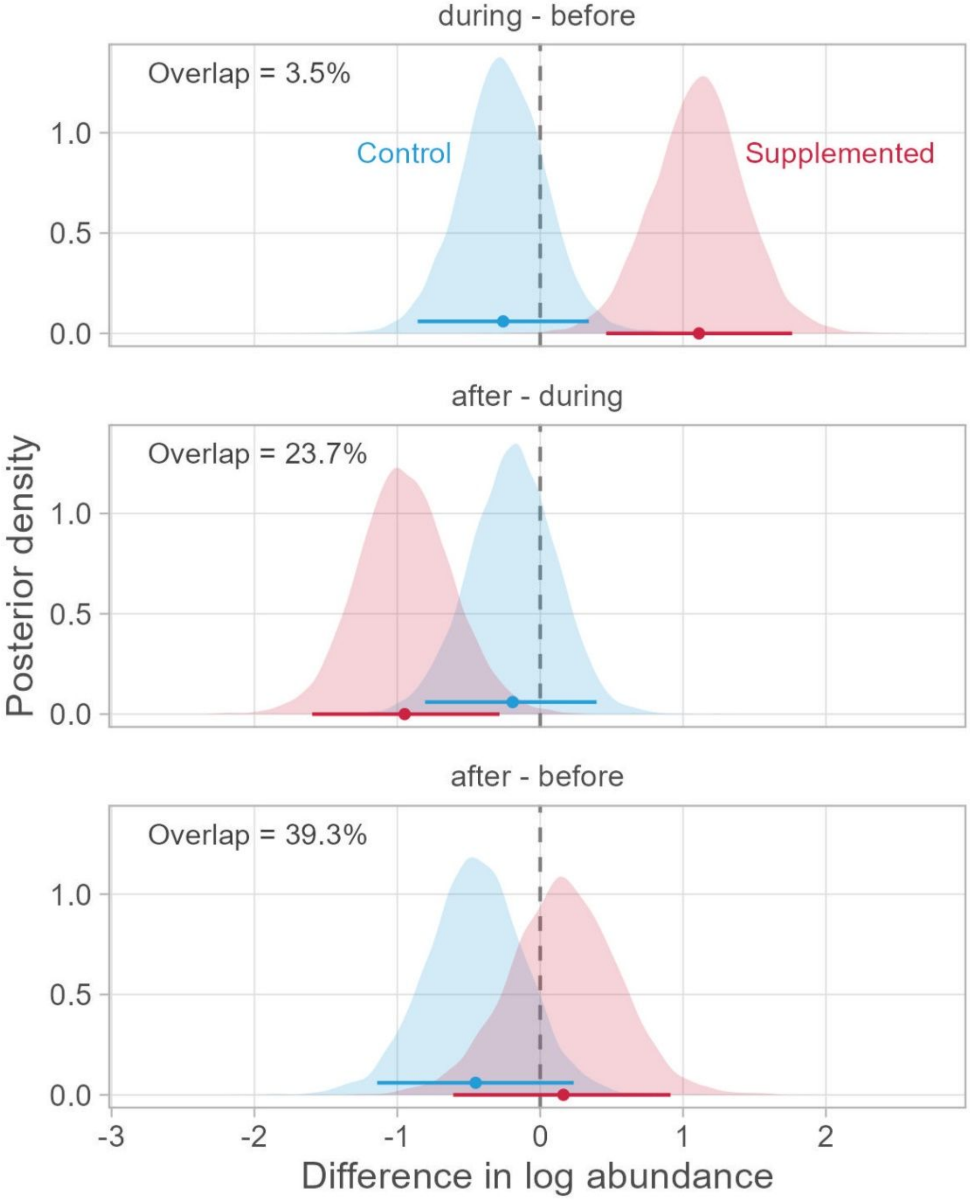

Figure 4. Posterior distributions of phase-wise differences in log abundance. Top panel shows the change in abundance between the before and during phases, middle panel shows the change between the during and after phases, and bottom panel shows the change between the before and after phases. Dots show the posterior mean and horizontal lines indicate the 95% credibility interval. Blue distributions are the control populations and red distributions are the supplemented populations. Overlap percentage is the percent of the treatment posterior distributions that overlap (lower number indicates less overlap in the distributions).

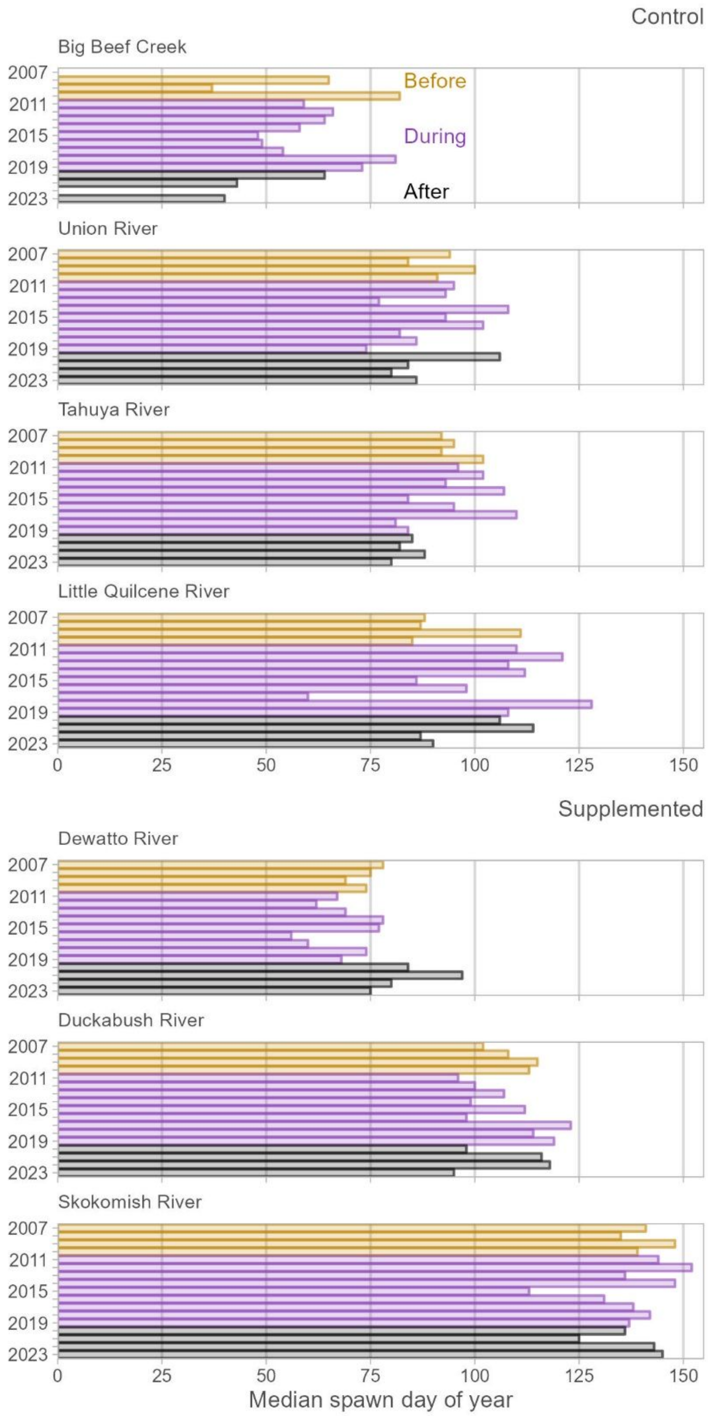

Figure 5. Time series of steelhead spawn timing. Blue series show the control populations and red series show the supplemented populations. Dashed vertical lines indicate the breaks between the before, during, and after phases.

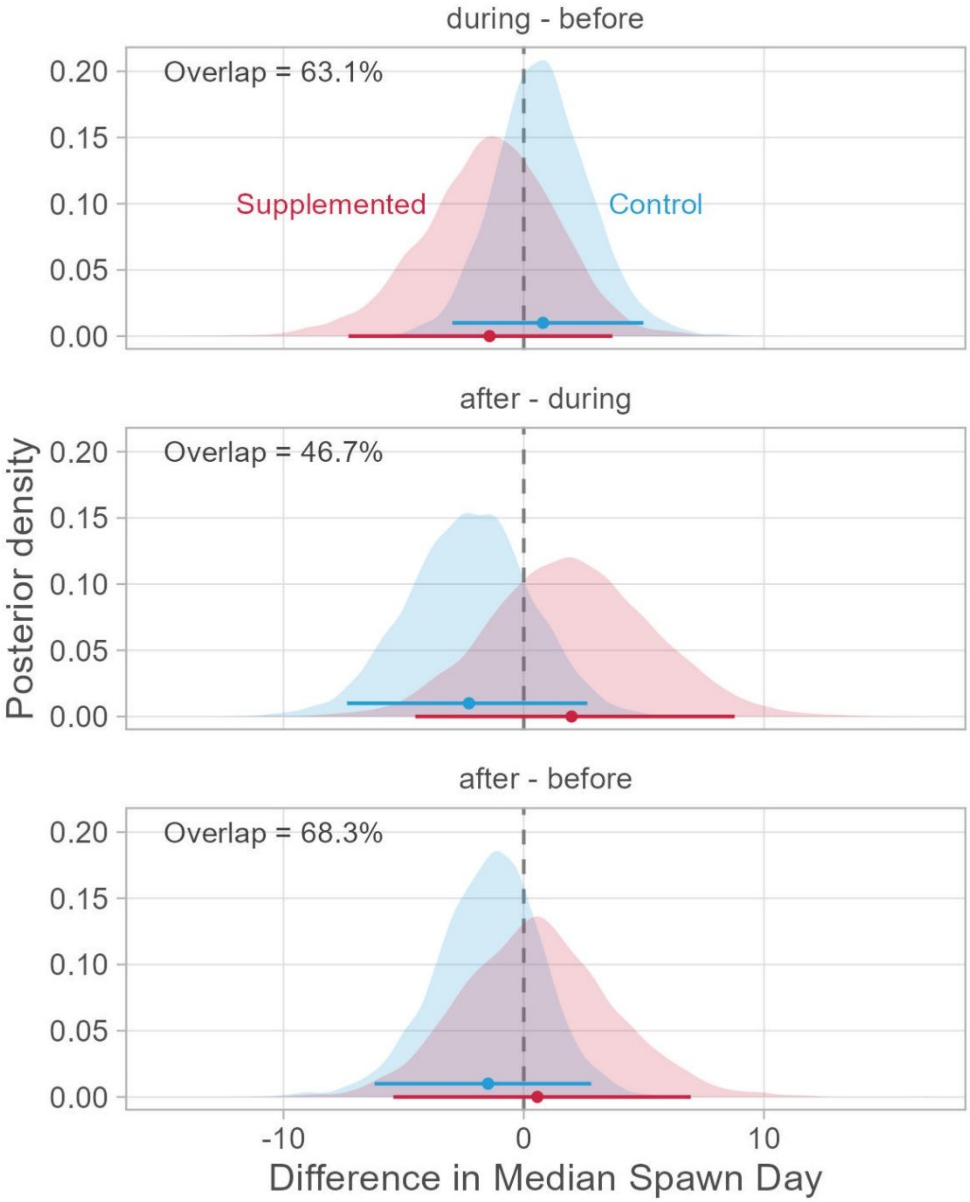

Figure 6. Posterior distributions of phase-wise differences in spawn timing. Top panel shows the change in abundance between the before and during phases, middle panel shows the change between the during and after phases, and bottom panel shows the change between the before and after phases. Dots show the posterior mean and horizontal lines indicate the 95% credibility interval. Blue distributions are the control populations and red distributions are the supplemented populations. Overlap percentage is the percent of the treatment posterior distributions that overlap (lower number indicates less overlap in the distributions).

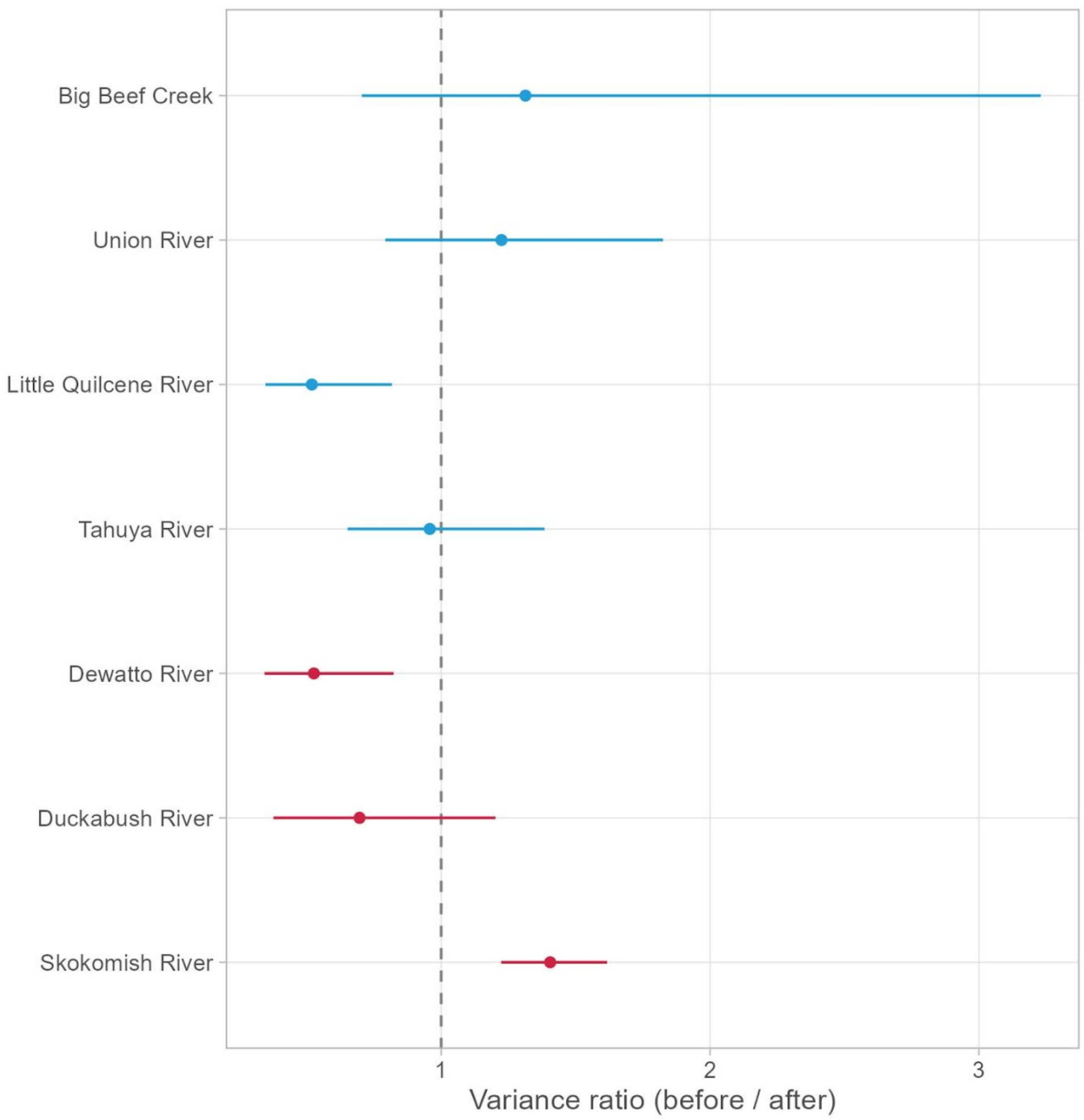

Figure 7. Spawn timing variance ratios for the before period compared to the after period for each stream. Dots show the median bootstrap ratio and horizontal lines show the 95% confidence interval.