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Life history responses to salmon habitat restoration

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Three similarly sized, yet naturally varying, watersheds in the Lower Columbia River Basin were the focus of a Before-After-Control-Impact (BACI) study from 2001-2024. The study was designed to evaluate the effectiveness of habitat restoration on salmon and steelhead (*Oncorhynchus* spp.) recovery. The intensity of restoration was planned to increase smolt abundance, but the consequences for life history diversity were not initially considered. However, the streams support diverse juvenile life histories of coho salmon (*O. kisutch*) and steelhead (*O. mykiss*), which may benefit resilience in ways that are underappreciated and potentially comparable to enhancing productivity. To further evaluate life history responses to restoration, we compared density, fork length (FL), age at outmigration, biomass, and growth (for coho only). We tested for effects of basin, restoration, and their interaction, while controlling for confounding factors such as yearly variation and density dependence. The best-supported models all included a main effect of basin, indicating that natural watershed processes produced juvenile fish populations that differed significantly from one another. Prior to any restoration, Mill Creek, the control (reference) stream, showed the highest coho density and the lowest steelhead density and biomass compared to the impact (treatment) streams. Mill Creek also produced the oldest but smallest steelhead, and smallest, slowest growing coho smolts. When the analysis identified effects of restoration (for coho density, growth, and biomass) or a restoration-by-basin interaction (for coho and steelhead FL), both treatment streams showed positive responses. While life history diversity can enhance the resilience of salmon populations, restoration projects rarely account for it. This study suggests that effective restoration can preserve life history diversity while targeting specific habitat factors and life stages that limit population recovery.

KEYWORDS
age at outmigration, biomass, density, fork length (FL), growth, life history

1 Introduction

For decades, restoration of freshwater habitat has been prioritized as a recovery strategy for endangered Pacific salmon (*Oncorhynchus* spp.) listed under the U.S. Endangered Species Act (ESA, Barnas et al., 2015). Despite concerns about high costs of restoration efforts and the challenges of tracking recovery benefits to endangered fish populations using

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abundance-based measures (e.g., adult fish returns), this strategy remains widely supported in the Pacific Northwest, including the Columbia River Basin (Jaeger and Scheuerell, 2023). The significant investment in habitat restoration assumes that improvements in freshwater habitat will lead to increased fish abundance. However, despite spending billions of dollars since 1990, evidence supporting habitat restoration as an effective strategy is limited. One reason for this is that habitat restoration only addresses limiting factors within freshwater habitats, and the positive effects of restoration may be masked by negative factors occurring out-of-basin. Various natural and anthropogenic factors contribute to the decline of salmon populations, including habitat loss, dams, overfishing, hatchery impacts, environmental changes, disease, pollution, and predation, many of which occur outside riverine environments. Another important reason is that the long-term monitoring needed to detect change is rarely supported. As a result, detecting increases in salmon and steelhead (*O. mykiss*) adult abundance, as outlined in recovery plans, becomes challenging (Bilby et al., 2024).

In the Pacific Northwest, a network of long-term intensively monitored watersheds (IMWs) was established to answer the question of whether habitat restoration resulted in higher abundances of Pacific salmon and steelhead populations at the watershed scale (Bennett et al., 2016), and if so, why? The Lower Columbia IMW, where monitoring began in 2001, is part of this effort. These studies are designed as ecosystem experiments, allowing researchers to measure the effects of large-scale restoration efforts conducted over multiple years on fish populations. Working hypotheses underpinning the IMW studies include the expectation that there is a direct relationship between habitat condition and adult returns, that the restoration efforts are large enough to address habitat concerns, that the restoration signal is sufficiently large to detect over natural environmental variability, and that the fish response can be measured within the monitoring timeframe (Bisson et al., 2024). Additionally, the studies assume that fish populations in neighboring watersheds will respond similarly to the same level of habitat restoration, even though this assumption has not been fully explored.

Pacific salmon and steelhead exhibit a wide range of life history traits, including variation in body size and the timing of juvenile freshwater emigration and adult immigration, that is linked to survival and reproduction (Hilborn et al., 2003). As juveniles, individuals often occupy distinct habitats at different times, leading to differences in demographic rates throughout their life cycle (Sorel et al., 2023). Life history diversity helps buffer species from environmental variability and provides stability in populations exposed to varying levels of disturbance (Brennan et al., 2019). Indeed, diversity is identified as a key attribute in viable salmonid population analysis (McElhany et al., 2000), which predicts extinction risk for threatened and endangered salmon and steelhead populations listed under the ESA. Diversity in life history traits across riverscapes also enables fish to adapt to different habitats (Beechie et al., 2006). Restoration may affect life history diversity, although this effect may not be recognized if abundance is the sole measure of restoration success.

This study aims to identify changes in juvenile demographic and life history traits in response to restoration at the watershed scale across the three spatially contiguous focal watersheds that make up the Lower Columbia IMW. These traits include juvenile coho salmon (*O. kisutch*) and steelhead linear density (i.e., abundance divided by stream length), size, age at outmigration, growth, and biomass, which integrates information about abundance and size over a particular area. The study follows over two decades of intensive life cycle monitoring, including the post-restoration era from 2015 to 2024. Coho salmon and steelhead were chosen for the study because they spend a longer period rearing in freshwater than other species present in the watersheds like Chinook (*O. tshawytscha*) and chum salmon (*O. keta*), making them more vulnerable to limiting factors in freshwater, including both density-dependent factors (e.g., competition) and density-independent factors (e.g., low stream flows and high stream temperatures). Since restoration activities in the Lower Columbia IMW complex targeted the improvement of overwinter habitats where coho and steelhead rear, the observed variation in demographic and life history traits (e.g., density, size, age, growth, and biomass) may be more informative than examining changes in abundance alone for evaluating the effectiveness of freshwater habitat restoration on salmon and steelhead recovery.

We evaluated changes in juvenile salmon demographic and life history traits using a Before-After-Control-Impact (BACI) study design. Our goal was to leverage decades of juvenile monitoring data to test whether restoration efforts aimed at increasing rearing capacity and promoting growth achieved their intended outcomes in treatment streams. We predicted that juvenile traits would (1) be similar across streams before restoration began. As restoration progressed, we expected that actions to enhance overwinter rearing capacity for juvenile coho and steelhead would (2) increase smolt abundance within each stream's anadromous habitat, leading to higher smolt density and biomass in the treatment streams. For each life history trait, we anticipated a stronger response in Abernathy Creek, where restoration efforts were more intensive than in Germany Creek. We further expected that habitat improvements would (3) enhance growth potential, producing larger body sizes and higher growth rates from the treatment streams, particularly in Abernathy Creek. Finally, we predicted that greater growth in treatment streams would (4) reduce the age at outmigration, as faster-growing fish are more likely to migrate earlier (Roni et al., 2012).

2 Materials and methods

2.1 Study area

The Lower Columbia IMW complex consists of Mill, Abernathy, and Germany creeks (Figure 1). These interconnected basins are located within the Grays-Elochoman watershed of southwest Washington State and flow into the Columbia River between river kilometers (km) 87 and 90. The basins range from 60

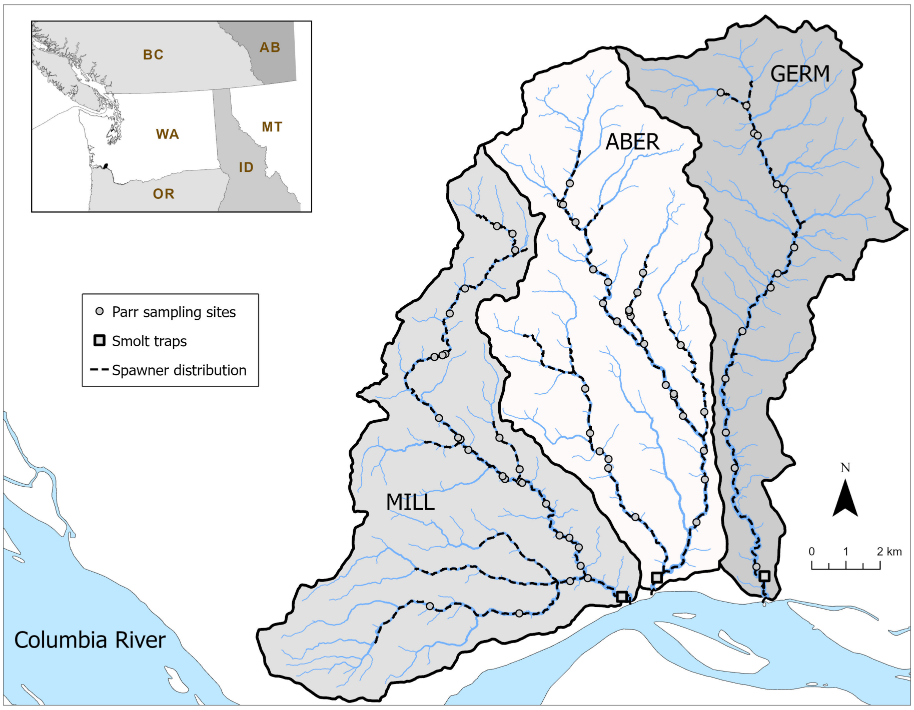

FIGURE 1
Map of Mill (MILL), Abernathy (ABER), and Germany (GERM) creeks that make up the Lower Columbia Intensively Monitored Watershed complex, showing parr sampling sites, smolt trap locations, and spawner distribution.

to 75 km^2 and are mostly composed of private and state-owned lands, with much of the upper portions being managed as a commercial forest for over a century. The lower sections of all three basins feature a mix of small forest landowners, agricultural areas, and rural residential developments. Agricultural valleys extend up the main stems of Abernathy and Germany creeks, but this is less pronounced in Mill Creek. The estimated extent of accessible anadromous habitat is 39.2 km in Mill Creek (the reference site), 36.5 km in Abernathy Creek, and 19.9 km in Germany Creek (Buehrens, 2024). Mill Creek has the lowest headwater elevation of 555 m, while Abernathy and Germany creeks drain steeper basins with headwater elevations reaching up to 806 m (Bilby et al., 2005). Median stream gradient within the anadromous zone is lowest in Germany Creek (1.06%), highest in Mill Creek (2.55%), and intermediate (1.93%) in Abernathy Creek. The hydrology of the region is rain-dominant, with annual precipitation ranging from 150 to 230 cm per year; peak flows occur between November and March and summer base flows occur between August and September. Median wintertime flows are approximately 5 cubic m per second (m^3 s^{-1}), while summer base flows are around 0.3 m^3 s^{-1}.

Geologically, the basins are composed of upper Tertiary volcanic and Columbia River Quaternary sedimentary rock. The area is covered by second-growth forest dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*), with red alder (*Alnus rubra*) being the dominate tree in riparian zones. Logging along the riparian margins over the last century has reduced the recruitment of large wood to the streams, disrupting sediment transport processes that sustain salmonid spawning and rearing habitats. The Lower Columbia IMW complex suffers from impaired habitat features, including channel scour, confinement, and riparian degradation (HDR Inc. and Cramer Fish Sciences, 2009; LCFRB, 2016). These issues negatively impact habitat, resulting in high stream temperatures, reduced floodplain function, and restricted fish passage which adversely affect juvenile coho salmon and steelhead during their summer parr and overwinter rearing periods. As such, rearing habitats have been the focus of restoration treatments and monitoring effort.

Coho salmon in these watersheds are part of the Lower Columbia Evolutionary Significant Unit (ESU) which is listed as threatened under the ESA; steelhead are part of the Southwest Washington Distinct Population Segment and are not listed under the ESA. Both species are distributed across the stream network in Mill and Abernathy creeks. Their distribution is mostly limited to main stem habitat in Germany Creek.

2.2 Restoration actions

The timeline for restoration was later in the Lower Columbia IMW than in other IMWs in the Pacific Northwest. Treatment plans were developed in 2009 and then updated in 2016 when it was determined that restoration efforts would focus on Abernathy Creek (HDR Inc. and Cramer Fish Sciences, 2009; LCFRB, 2016). Pre-restoration fish monitoring established that coho smolt production was strongly density-dependent and that overwinter survival (parr-to-smolt) was a survival bottleneck (Zimmerman et al., 2015). Treatments were focused on increasing the quality and quantity of rearing habitat as a strategy for salmon recovery. Projects were prioritized based on how well they addressed the overwinter survival bottleneck and began earlier and were more intensive in Abernathy Creek than Germany Creek. They targeted in-stream habitat complexity, off-channel and side-channel reconnection, floodplain reconnection, fish passage, riparian planting and management, and bank stabilization.

In all, thirteen restoration projects were completed between 2012 and 2021 in main stem and tributary habitat across Abernathy Creek and four projects in Germany Creek (Table 1). Projects primarily consisted of large woody debris (LWD) enhancements to increase in-stream habitat complexity and floodplain connectivity but sometimes included other treatments such as fish passage or riparian planting. A nutrient treatment project was also completed in Germany Creek (Fall 2010 to Fall 2013) and Abernathy Creek (Spring 2013 to Spring 2015) with the goal of increasing fish size and survival but was found to have had only short-term impacts (Sturza, 2017).

2.3 Field methods

Fish monitoring was conducted annually in each watershed beginning at the end of the summer rearing season (August and September) and during the smolt emigration season the following spring (March-June), using standard monitoring protocols of the American Fisheries Society (Crawford et al., 2007a; b; Volkhardt et al., 2007). In summer, we used beach seining and backpack electrofishing surveys at randomly selected stream reaches to sample age-0 coho parr. Coho ≥ 65 mm were measured for fork length (FL) to the nearest mm, weighed to the nearest 0.1 g, and implanted with a full duplex 12.5 mm passive integrated transponder (PIT) tag (106 mg, 134.2 kHz, www.biomark.com). During the spring emigration, we used a 1.5 m rotary screw trap positioned near the mouth of each watershed to capture coho and steelhead smolts. A subsample of the fish captured were measured, weighed, and sampled for scales for age analysis. All captured fish were manually scanned for the presence of a PIT tag.

Coho and steelhead smolt abundance in spring was estimated using a single partial capture trap, mark-recapture study design stratified by time (Carlson et al., 1998; Volkhardt et al., 2007). The study design consisted of counting fish captured in the trap and marking a known number of the captured fish for release at an upstream site. Marked fish that were subsequently recaptured were used to estimate trap capture probability and determine Lincoln-Peterson estimates of total fish emigrating past the traps. Unbiased smolt abundance estimates were generated using time-stratified Petersen estimators that accounted for missed trapping days and heterogeneity in capture probabilities throughout the emigration period. Maximum likelihood estimation was used from 2001-2016 (Carlson et al., 1998; Volkhardt et al., 2007; Seiler et al., 2002) whereas a Bayesian method, with hierarchical modeling of trap efficiency, was used for 2017–2024 using the R package BTPSAS (Bayesian Time-Stratified Population Analysis System; Bonner and Schwarz, 2011).

2.4 Data analysis

We compared juvenile demographic and life history variables among basins before and after restoration. Intensive restoration began in Abernathy Creek in 2015 (corresponding to outmigration year 2017 for age-1 coho and steelhead smolts) and in Germany Creek in 2020 (smolt year 2022). For Abernathy Creek, we defined 2001–2016 as the pre-restoration period and 2017–2024 the post-restoration period. For Germany Creek, the pre- and post-restoration periods were 2001–2021 and 2022-2024, respectively. We evaluated the effects of basin and restoration on the following juvenile metrics: annual linear density (smolts km^{-1}), size (FL, mm), age at outmigration (yr), parr-to-smolt growth rate (mm d^{-1}, coho only), and biomass (kg km^{-1}). Stream length (km) for annual linear density and biomass was the estimated extent of accessible anadromous habitat (Buehrens, 2024) and did not vary before and after restoration.

Our main objective was to evaluate the effects of basin and restoration on juvenile demographic and life history traits. To quantify these relationships, we used linear mixed models (LMMs) or generalized linear mixed models (GLMMs) to test whether juvenile metrics varied as a function of basin and restoration (Bolker, 2015). We then used likelihood ratio tests to identify the most parsimonious model structure (Burnham and Anderson, 2002). This was our primary analysis. The following four nested models were used in this analysis:

1. No basin or restoration effects
2. Basin effect
3. Basin and restoration effects
4. Basin and restoration effects and their interaction

To account for inter-annual variability and potential interannual trends, we included year as a random effect in all models. For some juvenile metrics, additional covariates were incorporated to account for relevant biological processes (e.g., day of recapture to represent seasonal effects on growth rates). These cases are described in detail for specific analyses below.

A second objective was to compare juvenile demographic and life history traits across basins prior to restoration (e.g., smolts outmigrating <2017) as we had *a priori* expectations that these attributes would be similar prior to restoration. To test this hypothesis, we refit model 2, which included a basin effect but no restoration effect, using data from before 2017. We then estimated basin effect sizes using marginal means and evaluated statistical differences among basins with Tukey *post-hoc* tests.

Our third objective was to quantify restoration effects on juvenile attributes in the treatment basins. When we detected a restoration effect, we used model 4, which allowed for different effects of restoration in each basin, to predict the expected value of

TABLE 1 Summary of restoration projects completed in Abernathy and Germany creeks between 2012 and 2021, including completion date, primary treatment, and instream length.

Basin	Project name	Date complete	Primary treatment	Length (km)
Abernathy	Abernathy Creek Bridge Removal Project	2012	FR	0.03
Abernathy	Abernathy Creek Two Bridges	2012	FR	0.46
Abernathy	Abernathy Creek Tidal Restoration[a]	2013	OC/SC	0.25
Abernathy	Abernathy 5A Side Channel Project	2015	OC/SC	0.18
Abernathy	Abernathy Sitka Spruce	2015	IHC	0.16
Abernathy	Abernathy Creek Davis Site	2017	OC/SC/IHC	0.55
Abernathy	Abernathy Creek Wisconsin Site Project	2016	IHC	0.92
Abernathy	Abernathy Creek Cameron Site	2016	IHC	1.95
Abernathy	Abernathy Creek Midway Project	2016	IHC	0.90
Abernathy	Abernathy Creek Headwaters Implementation	2020	IHC	2.09
Abernathy	Sarah Creek Habitat & Passage Enhancement	2019	FP & IHC	0.85
Abernathy	Erick Creek Instream Habitat Restoration	2020	IHC	1.29
Abernathy	Abernathy Creek Mainline Restoration IMW	2021	IHC	1.01
Germany	Germany Creek Restoration Smith Site	2020	IHC	0.85
Germany	Germany Creek Andrews Site	2020	IHC	1.37
Germany	IMW Godinho Restoration	2021	IHC	0.98
Germany	Germany Creek Stream Restoration Kosiba	2022	IHC	0.66

[a]Project occurred downstream of sampling locations, so fish response was likely not detectable.
Primary treatments are floodplain reconnection (FR), off-channel/s.ide-channel (OC/SC), instream habitat complexity (IHC), and fish passage (FP).

each juvenile attribute during the post-restoration period (2017–2024 for Abernathy Creek and 2022–2024 for Germany Creek). We then used the fitted model to predict what those values would be if restoration never occurred. Restoration effects from this *in silico* experiment are reported as the average annual percent improvement relative to a no-restoration scenario. This approach accounted for interannual trends and was a more complete comparison than simple before-after averages. It also enabled consistent comparisons among the various juvenile attributes by presenting them on the same scale. To estimate uncertainty, we simulated 1,000 sets of predictions from the fitted model, calculated average restoration effects for each basin, and determined the 0.025 and 0.975 quartiles of those values as the 95% bootstrap confidence interval (CI).

When providing P values throughout this paper, we use the "language of evidence" proposed in Muff et al. (2022), in which $P < 0.010$ corresponds to "strong evidence", $P < 0.050$ corresponds to "moderate evidence", $P < 0.100$ corresponds to "weak evidence", and $P \geq 0.100$ corresponds to "little or no evidence".

2.4.1 Coho and steelhead smolt density

Because basins differ substantially in total available habitat, comparisons of smolt abundance among basins can be misleading. To account for this, we standardized annual smolt abundance by dividing smolt abundance by unit stream length, yielding linear density (smolts km^{-1}). For density comparisons, we used rounded values (to the nearest whole fish) as the response variable in GLMMs assuming a negative binomial error distribution. For each species, density estimates were available for 24 years per basin.

2.4.2 Coho and steelhead smolt FL

For size comparisons, we included smolt density as a fixed effect to account for potential density dependence. A detailed analysis of density-dependent processes in these basins is provided in Anderson et al. (2025). Steelhead smolts ranged in age from 1 to 5 years, with FL increasing with age; therefore, age was included as a factor in all steelhead FL models, with the single age-5 observation excluded. Coho and steelhead FL was modeled using LMMs assuming a Gaussian error distribution. In total, we analyzed 50,285 coho and 7,409 steelhead FL observations, with corresponding age data for all steelhead. Although our primary focus was on comparing models 1-4, we additionally tested for density dependence using F-tests with Satterthwaite's approximation for degrees of freedom, as implemented in the R package lmerTest (Kuznetsova et al., 2017).

2.4.3 Coho and steelhead smolt age at outmigration

For age comparisons, we used the abundance-weighted mean age at outmigration as the response and fit LMMs assuming a Gaussian error distribution. Coho age data were only available from

2019-2024 (six years per basin), providing insufficient data to fit a model including the restoration × basin interaction (model 4). Accordingly, this model and the pre-restoration basin comparison were excluded from coho age analyses. Given the limited sample size, we evaluated individual coho data points for undue influence using Cook's distance and re-fit the model after excluding observations exceeding the standard threshold of 4/n (Cook's distance > 0.220). For steelhead, age estimates were available for 17 years per basin, allowing evaluation of the restoration × basin interaction.

2.4.4 Coho growth rate

For growth rate comparisons, the response variable was the daily change in FL between age-0 coho parr captured in summer and age-1 smolts recaptured the following spring. Smolt density was included as a fixed effect to account for potential density dependence, and growth was modeled using LMMs assuming a Gaussian error distribution. Because growth rates vary seasonally, we also evaluated the effects of initial capture and recapture day of year as fixed effects. Since we wanted to identify which variable(s) explained the seasonality, we used Akaike Information Criterion (AIC) to compare models, as it usually favors the one with the best predictive power. Growth rate data were available for 1,369 individuals. While our focus was on comparing models 1-4, we also tested for density dependence using F-tests with Satterthwaite's approximation for degrees of freedom.

2.4.5 Coho and steelhead smolt biomass

To contextualize overall differences among basins and assess the effect of restoration, we calculated annual coho and steelhead smolt biomass per unit stream length. Using paired length and weight data, we first estimated the logarithmic length-weight relationship and then used it to predict the weight of smolts with only length measurements (see Section 2.4.2). Average smolt weight was then calculated for each basin and year, multiplied by the corresponding abundance, and divided by the stream length (km) to yield biomass (kg km^{-1}). This resulted in 24 years of biomass estimates per basin for each species.

Log-transformed biomass values were used as the response variable in LMMs to test for basin and restoration effects (models 1–4 as described above), assuming a Gaussian error distribution. To distinguish these from subsequent bootstrapping analyses, we refer to these as results from the primary analysis. For steelhead, biomass depends in part on age at outmigration; thus, observed differences among years or basins may reflect variation in age composition, length-at-age, or abundance.

Because biomass is a derived life history variable, we used parametric bootstrapping to account for error propagation and validate model comparisons (see Supplementary Materials). We report:

i) The frequency with which the model with the highest likelihood ratio support in each bootstrap iteration (i.e., the model with significant evidence for included terms but not for more complex models at $P < 0.050$) matched the best model identified in the primary analyses.

ii) The frequency with which the bootstrapped restoration effect was positive.

2.4.6 Model validation

We evaluated model diagnostics using a simulation-based approach implemented in the R package DHARMa (https://figshare.com/s/ee17bda0cb1b85d38637) (Hartig, 2024). For the best-supported model of each juvenile demographic or life history attribute, we examined QQ plots, residual distributions, within-group uniformity, and dispersion. Because simulation-based tests for deviations from model assumptions (e.g., Kolmogorov-Smirnov tests, dispersion tests, and outlier tests) can be sensitive to sample size, and several analyses included large datasets, we focused on the magnitude of deviations from expectations rather than the significance of individual tests.

2.4.7 Pairwise basin comparisons

Comparing statistical support for models 1–4 using the primary analysis maximized our ability to detect overall restoration effects, but it was less effective for identifying cases in which only one basin exhibited a meaningful restoration effect. In the primary analysis, detecting differences in restoration between basins required sufficient data to provide statistical evidence of an interaction effect. Without enough data, we could observe an overall restoration effect that did not significantly differ between basins, even if only one treatment basin experienced an effect.

To address this limitation, we conducted a supplementary analysis in which, for each variable, we compared a single treatment basin (Germany Creek or Abernathy Creek) with the reference stream (Mill Creek) by refitting models 1–3 using the appropriate subset of the data. We then compared these models using likelihood ratio tests, where support for model 3 indicated evidence for a restoration effect in the treatment basin under consideration. While subsetting data in this way reduced statistical power and prevented direct comparisons between Germany Creek and Abernathy Creek, it ensured that evidence for restoration in each treatment basin was evaluated independently of the other basin.

2.4.8 Software

All analyses were performed in R 4.2.0 (R Core Team, 2021) using the following key packages: tidyverse (Wickham et al., 2019) to process data; BTSPAS (Bonner and Schwarz, 2014) to estimate abundances from mark-recapture data; lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), and emmeans (Lenth, 2024) to fit and interpret models; DHARMa (Hartig, 2024) for model diagnostics; ggplot2 (Wickham, 2016) and patchwork (Pedersen, 2024) to generate figures.

3 Results

Statistical models indicated that juvenile coho and steelhead demographic and life history traits varied by basin, restoration, and their interactions (Table 2, Supplementary Table S1). The assumption that juvenile attributes were similar prior to restoration (2001-2016) was not supported (Table 3). When statistical models found strong support for a restoration effect, the expectation that responses would always be positive and consistently higher in Abernathy Creek relative to Germany Creek was supported, except for coho biomass, which had a higher restoration response in Germany Creek (Table 4). Finally, hypotheses that restoration would increase coho growth rates and coho and steelhead FL were supported, but the expectation that these increases would result in lower median age of outmigration was not supported for either species.

3.1 Coho and steelhead smolt density

Before restoration activities began in the study area (i.e., baseline conditions), Abernathy Creek exhibited the lowest median coho density (228.95 smolt km^{-1}; Figure 2A). Coho densities were 11.6% higher in Germany Creek (255.60 smolt km^{-1}) and 33.6% higher in Mill Creek (305.95 smolt km^{-1}). Counter to the hypothesis of no basin differences prior to restoration, we found moderate evidence for differences between Mill and Abernathy creeks ($P = 0.036$; Supplementary Table S2), but little or no evidence for differences between Abernathy and Germany creeks or between Germany and Mill creeks ($P > 0.100$ in both comparisons). Despite having the highest coho density, steelhead density was lowest in Mill Creek (52.59 smolt km^{-1}; Figure 2B). Steelhead densities were 118.9% higher in Abernathy Creek (115.13 smolt km^{-1}) and 559.4% higher in Germany Creek (346.83 smolt km^{-1}). Contrary to expectations, we found strong evidence for pre-restoration differences among all basin pairs ($P < 0.001$ in all comparisons; Supplementary Table S2).

Using the full time series of coho density data, comparison of statistical models indicated moderate evidence for basin and restoration effects (Model 1 vs. Model 3: $\chi^2 = 7.93$, df = 3, $P = 0.048$; Table 2, Supplementary Table S1), but little or no evidence for their interaction (Model 3 vs. Model 4: $\chi^2 = 0.28$, df = 1, $P = 0.598$). As expected, restoration led to a simulated 33.5% (95% bootstrap CI = 9.1% to 98.1%; Figure 2C, Table 4) increase in coho density in Abernathy Creek relative to model expectations if restoration did not occur. However, for this isolated case, supplementary pairwise basin comparisons qualitatively differed from the primary analysis and did not support a restoration effect for coho density in Germany Creek.

For steelhead density, we found strong evidence for a basin effect (Model 1 vs. Model 2: $\chi^2 = 116.75$, df = 2, $P < 0.001$; Table 2, Supplementary Table S1), but contrary to expectations, little or no evidence for a restoration effect (Model 2 vs. Model 3: $\chi^2 = 2.10$, df = 1, $P = 0.152$).

3.2 Coho and steelhead smolt size

During the pre-restoration period, we observed similar patterns in smolt size for both coho and steelhead. Mill Creek had the smallest median coho FL (107.61 mm; Figure 3A). Coho FL was 4.6% higher in Abernathy Creek (112.52 mm) and 8.2% higher in Germany Creek (116.45 mm). Mill Creek also had the smallest median steelhead FL (156.94 mm; Figure 3B). Steelhead FL was 5.4% higher in Abernathy Creek (165.43 mm) and 12.6% higher in Germany Creek (176.65 mm). Contrary to expectations, we found strong evidence for pre-restoration differences among all basin pairs for both species ($P < 0.001$; Supplementary Table S2).

For coho, comparison of statistical models indicated strong evidence for both basin (Model 1 vs. Model 2: $\chi^2 = 6817.74$, df = 2, $P < 0.001$; Table 2, Supplementary Table S1) and restoration effects (Model 2 vs. Model 3: $\chi^2 = 131.46$, df = 1, $P < 0.001$), and moderate evidence for their interaction (Model 3 vs. Model 4: $\chi^2 = 4.84$, df = 1, $P = 0.028$). As expected, restoration led to a simulated 2.6% (95% bootstrap CI = -6.0% to 13.0%; Figure 3C, Table 4) increase in coho FL in Abernathy Creek and 2.0% (95% bootstrap CI = -10.9% to 17.7%) increase in Germany Creek relative to model expectations if restoration did not occur.

For steelhead, comparison of statistical models indicated strong evidence for basin effects (Model 1 vs. Model 2: $\chi^2 = 225.78$, df = 2, $P < 0.001$; Table 2, Supplementary Table S1), restoration effects (Model 2 vs. Model 3: $\chi^2 = 15.08$, df = 1, $P < 0.001$), and their interaction (Model 3 vs. Model 4: $\chi^2 = 12.02$, df = 1, $P = 0.001$). As expected, restoration led to a simulated 3.1% (95% bootstrap CI = -1.8% to 9.1%; Figure 3D, Table 4) increase in steelhead FL in Abernathy Creek and 0.5% (95% bootstrap CI = -7.8% to 10.1%) increase in Germany Creek relative to model expectations if restoration did not occur.

Although not the focus of this analysis, we found strong evidence for a density-dependent effect on coho FL ($\chi^2 = 115.7$, df = 1, $P < 0.001$). For every 100 additional smolts per km, expected coho FL was reduced by 1.07 mm. We found little or no evidence for a density-dependent effect on steelhead FL ($\chi^2 = 2.34$, df = 1, $P = 0.126$).

3.3 Coho and steelhead smolt age at outmigration

We did not have measurements for coho age at outmigration before 2017 (Figure 4A), so we were unable to compare basins before this time. During the pre-restoration period, steelhead in Abernathy Creek had the lowest median steelhead age at outmigration (2.00 yr; Figure 4B). Steelhead age was 5.7% higher in Germany Creek (2.11 yr) and 15.1% higher in Mill Creek (2.30 yr). Contrary to expectations, we found strong evidence for the pre-restoration difference between Mill and Abernathy creeks ($P < 0.001$; Supplementary Table S2), moderate evidence for the difference between Mill and Germany creeks ($P = 0.011$) but little or no evidence for the difference between Abernathy and Germany creeks ($P = 0.167$).

Using the full time series of coho age data, comparison of statistical models indicated strong evidence for a basin effect (Model 1 vs. Model 2; $\chi^2 = 10.52$, df = 2, $P = 0.005$; Table 2, Supplementary Table S1) but contrary to expectations, little or no evidence for a restoration effect (Model 2 vs. Model 3; $\chi^2 = 1.10$, df = 1, $P = 0.295$). As with coho,

TABLE 2 The best-fit model selected for each life history response variable from the candidate set.

Response	Model 1 Intercept-only	Model 2 Basin	Model 3 Basin + Restoration	Model 4 Basin × Restoration
Coho density (smolts km^{-1})			×	
Coho size (FL, mm)				×
Coho age at outmigration		×		NA
Coho growth rate (mm FL day^{-1})			×	
Coho biomass (kg km^{-1})			×	
Steelhead density (smolts km^{-1})		×		
Steelhead size (FL, mm)				×
Steelhead age at outmigration		×		
Steelhead biomass (kg km^{-1})		×		

NA = model was not included in the candidate set.

steelhead model comparison indicated strong evidence for a basin effect (Model 1 vs. Model 2; χ^2 = 27.65, df = 2, P < 0.002; Table 2, Supplementary Table S1) but little or no evidence for a restoration effect (Model 2 vs. Model 3; χ^2 = 0.03, df = 1, P = 0.865).

3.4 Coho growth rate

When comparing methods to account for seasonality in parr-to-smolt growth rate, we found, based on AIC scores, that models 1-4 improved most when the day of recapture was included, but not the day of capture (Supplementary Table S3). For this reason, day of recapture was incorporated into each model for the comparison.

During the pre-restoration period, Mill Creek had the lowest median coho growth rate (0.13 mm day^{-1}; Figure 5A). Coho growth rate was 5.1% higher in Abernathy Creek (0.14 mm day^{-1}) and 15.7% higher in Germany Creek (0.15 mm day^{-1}). Contrary to expectations, we found strong evidence for differences between Mill and Germany creeks (P < 0.001; Supplementary Table S2) and between Germany and Abernathy creeks (P = 0.002), but little or no evidence for a difference between Mill and Abernathy creeks (P = 0.286).

Using the full time series of coho growth rate data, comparison of statistical models indicated strong evidence for a basin effect (Model 1 vs. Model 2; χ^2 = 141.36, df = 2, P < 0.001; Table 2, Supplementary Table S1), moderate evidence for a restoration effect (Model 2 vs. Model 3; χ^2 = 6.17, df = 1, P = 0.013), but little or no evidence for their interaction (Model 3 vs. Model 4; χ^2 = 0.07, df = 1, P = 0.796). As expected, restoration led to a simulated 7.5% (95% bootstrap CI = 2.2% to 14.2%; Figure 5B, Table 4) increase in growth rate in Abernathy Creek and 5.7% (95% bootstrap CI = -2.3% to 14.7%) increase in Germany Creek relative to model expectations if restoration did not occur. We found little or no evidence for a density-dependent effect on growth rate (χ^2 = 0.009, df = 1, P = 0.924).

TABLE 3 Basin comparisons among each smolt life history response variable prior to any restoration (<2017) in the Lower Columbia Intensively Monitored Watersheds complex.

Response	Basin comparisons
Coho density (smolts km^{-1})	Mill > Abernathy
Coho size (FL, mm)	Germany > Abernathy > Mill
Coho age at outmigration	NA
Coho growth rate (mm FL day^{-1})	Germany > Abernathy; Germany > Mill
Coho biomass (kg km^{-1})	NS
Steelhead density (smolts km^{-1})	Germany > Abernathy > Mill
Steelhead size (FL, mm)	Germany > Abernathy > Mill
Steelhead age at outmigration	Mill > Germany; Mill > Abernathy
Steelhead biomass (kg km^{-1})	Germany > Abernathy > Mill

NA = too few years for pre-restoration basin comparisons. NS = no pairwise comparisons significant at the P < 0.100 level.

3.5 Coho and steelhead smolt biomass

During the pre-restoration period, median coho biomass was lowest in Abernathy Creek (3.49 kg km^{-1}; Figure 6A). Coho biomass was 15.4% higher in Mill Creek (4.03 kg km^{-1}) and 18.0% higher in Germany Creek (4.12 kg km^{-1}). Steelhead followed a markedly different pattern. Median steelhead biomass was lowest in Mill Creek (2.07 kg km^{-1}; Figure 6B). Biomass was 133.6% higher in Abernathy Creek (4.83 kg km^{-1}) and 692.9% higher in Germany Creek (16.38 kg km^{-1}). As expected, we found little or no evidence for differences in coho biomass among basins (P > 0.100 for all pairwise comparisons; Supplementary Table S2), but strong evidence for differences in steelhead biomass (P < 0.001 for all comparisons; Supplementary Table S2).

Comparison of statistical models for biomass differed between species. For coho, we found weak evidence for a basin effect (Model 1 vs. Model 2; χ^2 = 5.44, df = 2, P = 0.066; Table 2, Supplementary Table S1), strong evidence for a restoration effect (Model 2 vs.

TABLE 4 Percent increase in each response variable in the treatment basins after restoration, with 95% bootstrapped confidence intervals.

Response	Percent increase after restoration	
	Abernathy creek	Germany creek
Coho density (smolts km^{-1})	33.5% (9.1% - 98.1%)	NS
Coho size (FL, mm)	2.6% (-6.0% - 13.0%)	2.0% (-10.9% - 17.7%)
Coho age at outmigration	NA	NS
Coho growth rate (mm FL day^{-1})	7.5% (2.2% - 14.2%)	5.7% (-2.3% - 14.7%)
Coho biomass (kg km^{-1})	32.7% (4.8% - 89.2%)	54.0% (1.0% - 158.5%)
Steelhead density (smolts km^{-1})	NS	NS
Steelhead size (FL, mm)	3.1% (-1.8% - 9.1%)	0.5% (-7.8% - 10.1%)
Steelhead age at outmigration	NS	NS
Steelhead biomass (kg km^{-1})	NS	NS

NA = too few years for pre-restoration basin comparisons. NS = change not significant at the $P < 0.100$ level based on pairwise comparison with reference basin.

Model 3; $\chi^2 = 6.91$, df = 1, P = 0.009), but little or no evidence for their interaction (Model 3 vs. Model 4; $\chi^2 = 0.43$, df = 1, P = 0.514). As expected, restoration led to a simulated 32.7% (95% bootstrap CI = 4.8% to 89.2%; Figure 6C, Table 4) increase in coho biomass in Abernathy Creek and 54.0% (95% bootstrap CI = 1.0% to 158.5%) increase in Germany Creek relative to model expectations if restoration did not occur.

For steelhead, we found strong evidence for a basin effect (Model 1 vs. Model 2; $\chi^2 = 120.17$, df = 2, P < 0.001; Table 2, Supplementary Table S1), moderate evidence for a restoration effect (Model 2 vs. Model 3; $\chi^2 = 4.18$, df = 1, P = 0.041), but little or no evidence for their interaction (Model 3 vs. Model 4; $\chi^2 = 0.52$, df = 1, P = 0.470).

Parametric bootstrapping supported the primary analysis for coho biomass but not steelhead. The best model for coho biomass identified using the primary analysis (Model 3, basin and restoration effects) was identified as the best model in 70.8% of simulations using likelihood ratio tests. The restoration effect in this model had positive values in 100% of bootstraps, consistent with our finding of a significant and positive effect of restoration. In contrast, the best model for steelhead biomass in the primary analysis (Model 3) was only identified as the best model in 5.2% of simulations using likelihood ratio tests. Instead, bootstrapping favored Model 2 (basin effect only), which was identified as the best model using likelihood ratio tests in 94.7% of simulations. The estimated restoration effects were positive in only 86.9% of simulations, further suggesting there was not a restoration effect. Based on these results, we accept the primary analysis for coho biomass but choose to treat Model 2 (basin effect only) as the best model for steelhead biomass.

3.6 Pairwise basin comparisons

Separately comparing the reference basin (Mill Creek) with each of the treatment basins (Abernathy Creek and Germany Creek) generally produced qualitatively similar results to the primary analyses (Supplementary Table S4), with at least weak evidence for a restoration effect in each treatment stream for the juvenile attributes for which the primary analyses identified a restoration effect. The one exception was coho smolt density; we initially found moderate evidence for a restoration effect in Germany Creek, but when we used pairwise basin comparisons, we found little or no evidence for this effect (Model 2 vs. Model 1: $\chi^2 = 0.02$, df = 1, P = 0.900; Model 3 vs. Model 1: $\chi^2 = 3.26$, df = 2, P = 0.196) Using pairwise comparisons, we did find weak evidence for a restoration effect in Abernathy Creek (Model 2 vs. Model 1: $\chi^2 = 0.02$, df = 1, P = 0.9; Model 3 vs. Model 1: $\chi^2 = 3.26$, df = 2, P = 0.196; Model 3 vs. Model 2: $\chi^2 = 3.24$, df = 1, P = 0.072). Consistent with reduced statistical power associated from fitting models to the data from only two basins at a time, evidence for restoration effects for other juvenile metrics was often reduced (e.g., moderate instead of strong, or weak instead of moderate).

4 Discussion

Mill, Abernathy, and Germany creeks within the Lower Columbia IMW complex play a vital role in salmon conservation and recovery. Natural differences across these watersheds create variable conditions that support distinct juvenile life history traits, such as size, age at outmigration, and growth rate, which influence demographic patterns such as density and biomass. Our finding of basin differences in coho and steelhead smolt juvenile attributes before restoration began was counter to the expectation that traits would be similar across Lower Columbia IMW streams prior to restoration. This variation is something that conservation planners often overlook, but provides insight into diversity at the watershed scale, which is exceedingly rare, and could help identify limiting factors to help with recovery planning and prioritization across suites of actions that may include habitat restoration (Polivka et al., 2020). For example, using a diverse suite of restoration techniques (e.g., barrier removal, LWD additions, riparian planting, floodplain connection), could help support naturally occurring variations in life history expression. Enhancing life history diversity through

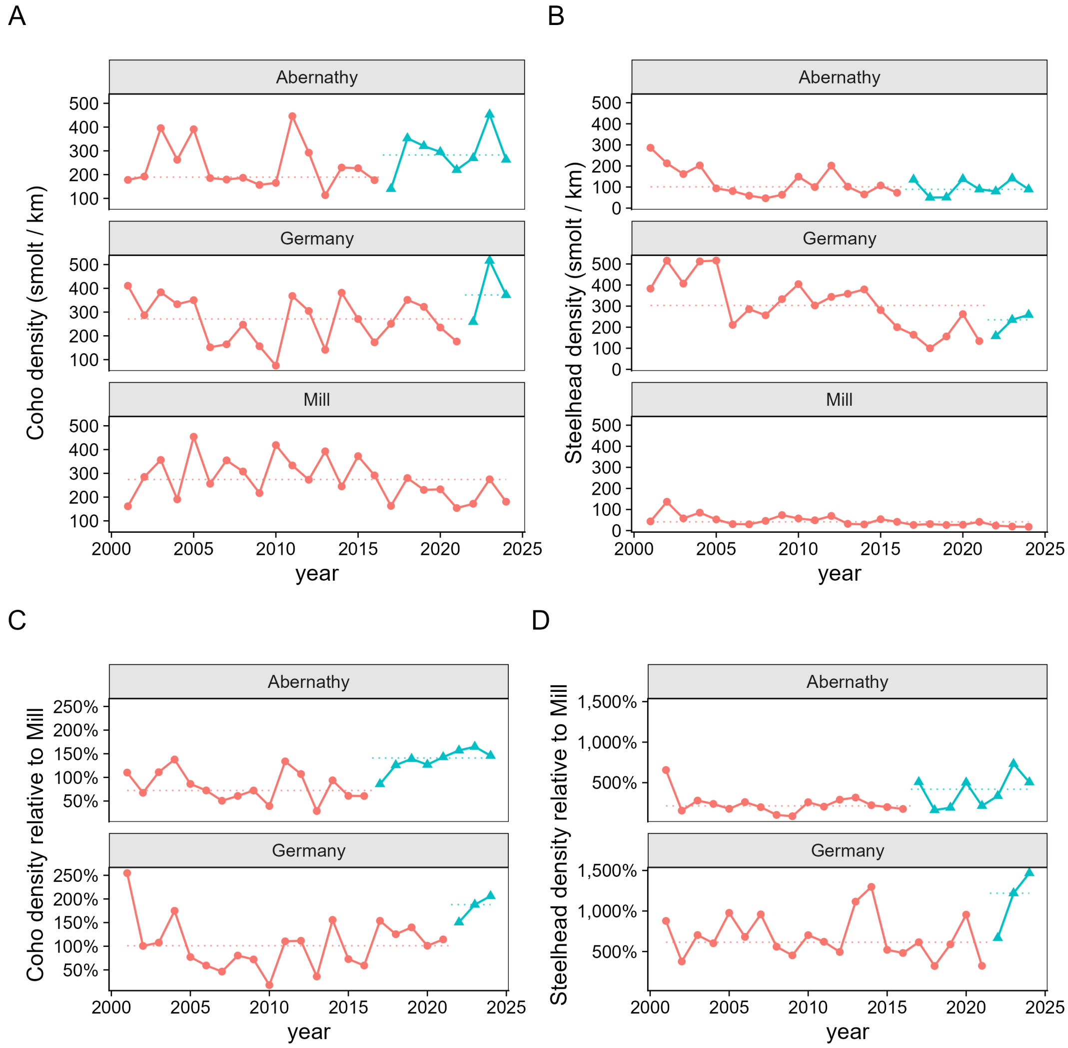

FIGURE 2
Average **(A)** coho and **(B)** steelhead density (smolts km^{-1}) by basin and year; coral circles represent pre-restoration, blue triangles represent post-restoration, and dotted lines show median values across years. **(C, D)** Graphical representations of restoration effect showing yearling density in Abernathy and Germany creeks (treatment basins) relative to Mill Creek (reference basin). Differences in median values between pre- and post-restoration years **(A, B)** reflect both effects of restoration and background temporal trends; to isolate the effects of restoration, it is necessary to compare treatment streams directly to Mill Creek **(C, D)**.

restoration may improve viability and lead to greater population stability but finding evidence for this was not a goal of our study.

We expected the largest restoration effects to occur in Abernathy Creek, given the longer restoration duration and greater intensity of effort in that watershed. This expectation was generally supported; however, we were surprised to observe the largest increase in coho biomass was in Germany Creek. This result is particularly noteworthy as only 3 years of post-restoration data were available. In both restored streams, treatments targeted habitat critical for limiting life stages during the overwinter rearing period. Consequently, the large, positive response in juvenile coho biomass represents one of the most substantial restoration effects ever documented across the IMWs of the Pacific Northwest. These results also emphasize the importance of restoration intensity, and the extent of treatments needed to produce and detect changes in smolt abundance at the watershed scale. One modeling study concluded that, on average, restoration of 20% of floodplain and in-channel habitat in a watershed is needed to increase coho and steelhead smolt production (Roni et al., 2010). That value was exceeded in Abernathy Creek (29%) and almost met in Germany Creek (19%), suggesting that it is important to treat as much instream habitat as possible, at least within small coastal streams.

Biomass is an indicator of the overall health of an ecosystem. Our finding that the highest coho and steelhead biomass occurred in Germany Creek, even before restoration began, suggests that it is the most productive system in the Lower Columbia IMW complex. Notably, steelhead biomass was three to ten times higher in Germany Creek than the other two basins. Biomass is the direct result of food web dynamics controlled by environmental conditions within the stream, including channel morphology, water temperature, light availability, nutrient concentration, and

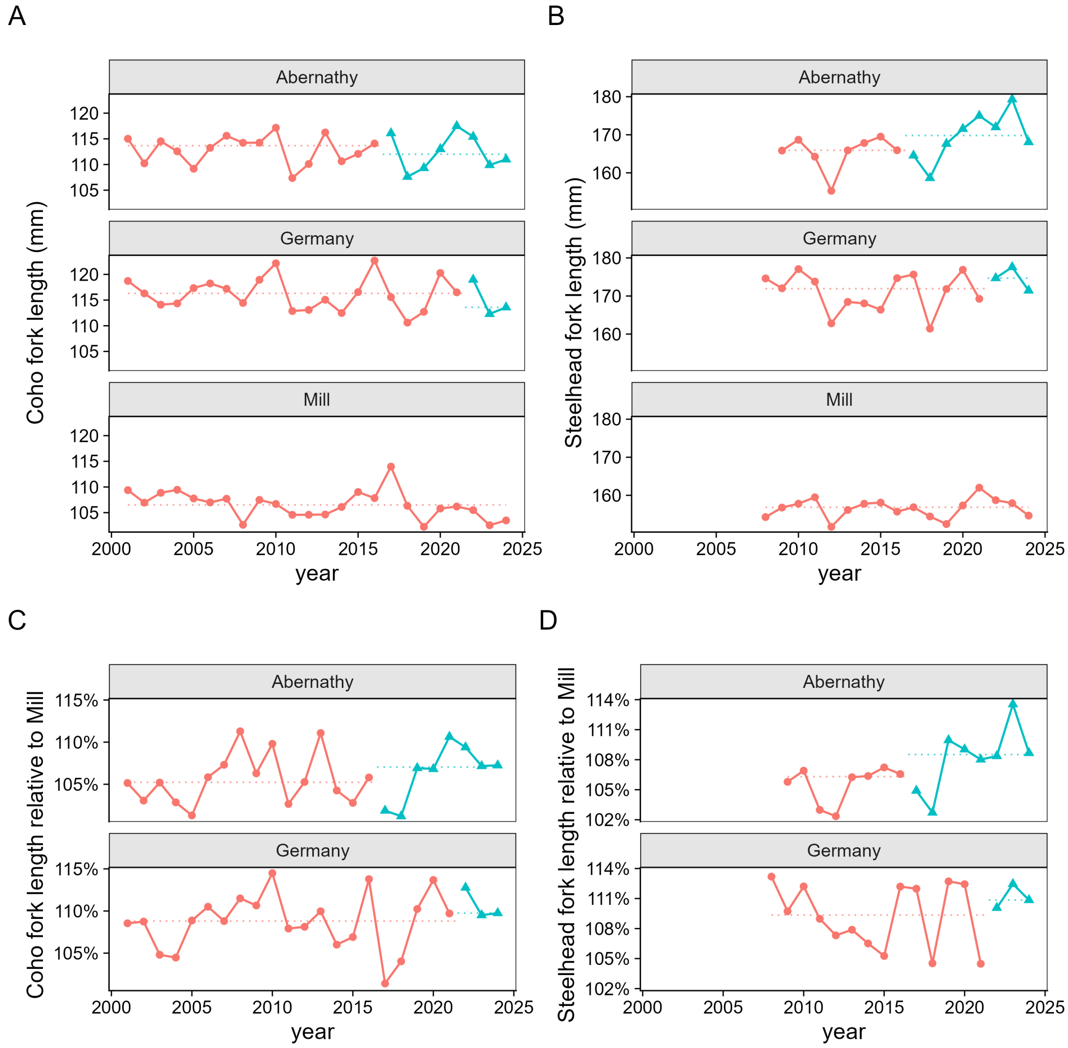

FIGURE 3
Average fork length (FL, mm) of **(A)** coho age-1 smolts and **(B)** steelhead age-2 smolts by basin and year; coral circles represent pre-restoration, blue triangles represent post-restoration, and dotted lines show median values across years. **(C, D)** Graphical representations of restoration effect showing yearling average lengths in Abernathy and Germany creeks (treatment basins) relative to Mill Creek (reference basin). Differences in median values between pre- and post-restoration years **(A, B)** reflect both effects of restoration and background temporal trends; to isolate the effects of restoration, it is necessary to compare treatment streams directly to Mill Creek **(C, D)**. Steelhead lengths depended in part on age; we present the most common age (age-2). For all ages, see Supplemental Figure S1.

riparian habitat (Benjamin et al., 2022). Within the anadromous zone, Germany Creek has the lowest stream gradient but second highest elevation among the study basins. The low stream gradient may increase habitat suitability for coho via increases in low velocity areas (Sandercock, 1991). Conversely, steelhead generally prefer high velocity habitats (Bisson et al., 1988), indicating that habitat complexity in the high elevation anadromous zone of Germany Creek provides favorable growing conditions for steelhead. The combination of high velocity habitat in the upper anadromous zone and low velocity downstream seems to benefit both species, but in different ways, which is important to recognize when designing restoration treatments to support these species.

Our study was the first to describe and compare juvenile attributes across the Lower Columbia IMW. Several investigations could follow-up from this work to inform how habitat restoration management actions might impact life history variation at the project scale, or how treatments targeting prey availability and prey quality might influence growth and survival. For example, while spawner density is an important factor explaining growth and size patterns in juvenile salmon (Rinella et al., 2012), prey biomass has been shown to be an even more important determinant of growth rate in Atlantic salmon (*Salmo salar*) juveniles (Ward et al., 2009). The drivers of coho growth in this system could be better understood with more detailed analyses. For instance, because we know where parr were tagged, we could compare coho growth rates of fish tagged across the watershed (headwaters, tributaries, lower main stem, etc.) to better understand which natal habitat produced the fastest growing parr. Based on the hypothesis that faster growing coho smolts are larger and survive better than their slower-growing conspecifics (Quinn and Peterson, 1996; Ebersole et al., 2006), these results could be used to

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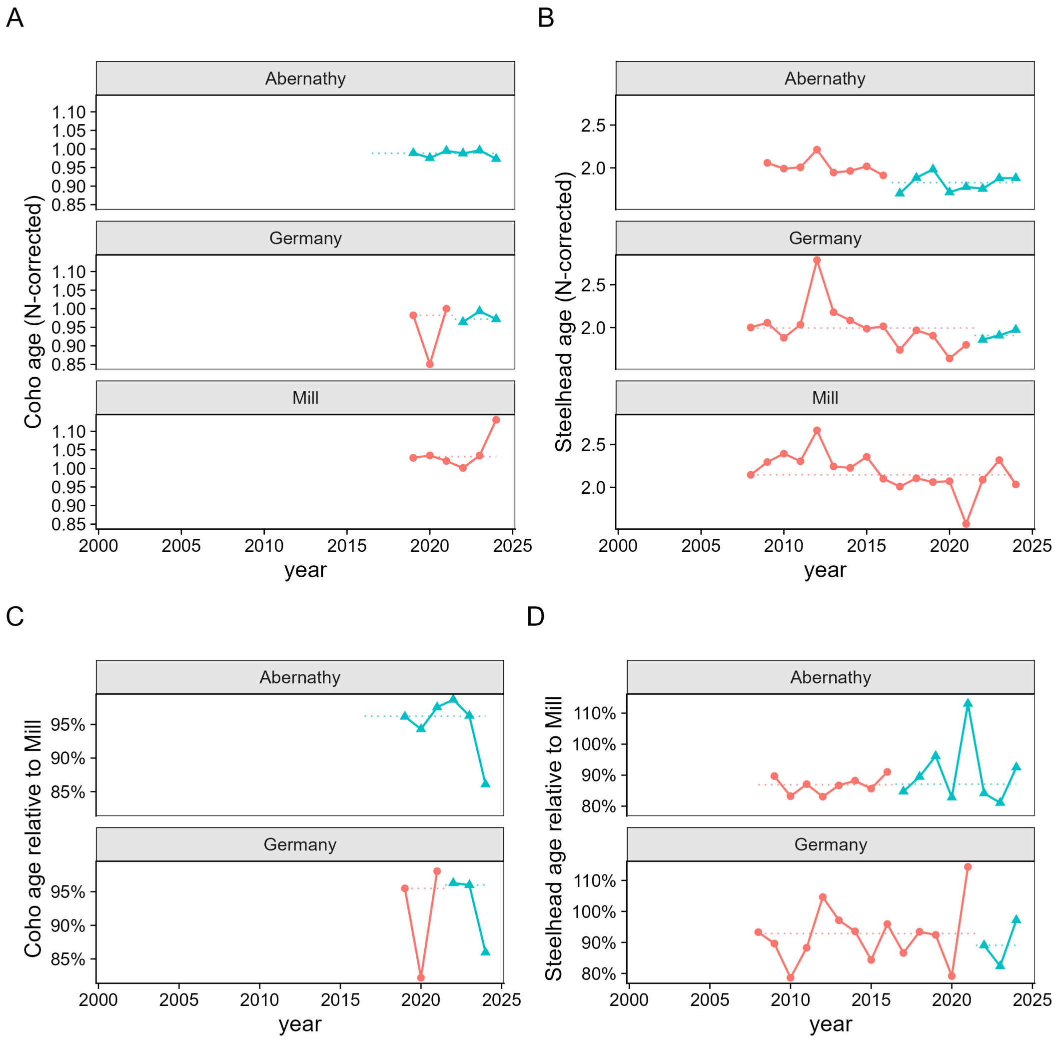

FIGURE 4
Abundance-corrected average age at outmigration of **(A)** coho and **(B)** steelhead by basin and year; coral circles represent pre-restoration, blue triangles represent post-restoration, and dotted lines show median values across years. **(C, D)** Graphical representations of restoration effect showing age at outmigration in Abernathy and Germany creeks (treatment basins) relative to Mill Creek (reference basin). Differences in median values between pre- and post-restoration years **(A, B)** reflect both effects of restoration and background temporal trends; to isolate the effects of restoration, it is necessary to compare treatment streams directly to Mill Creek **(C, D)**.

promote the recovery of natural processes in less productive areas, for instance, by enhancing natural riparian vegetation or moderating stream temperatures to provide optimal foraging opportunities for rearing juveniles during the overwinter period.

The substantial variation in juvenile attributes we observed among basins is known to enhance resilience in salmon and steelhead populations (Hilborn et al., 2003; Moore et al., 2014) and implies that the life history diversity can come from complex interactions within and among species and their habitat (Munsch et al., 2023). Restoration efforts that maintain natural variability in freshwater may be more effective at supporting multiple life histories (Bisson et al., 2009). In the Lower Columbia IMW, this might be accomplished by focusing on restoring a range of habitats and natural processes to encourage various life history strategies to allow them to spread out risk over time and space (i.e., the portfolio concept, Schindler et al., 2015).

The Lower Columbia IMW study followed a BACI experimental design, assuming fish populations in Mill Creek (reference) and Abernathy and Germany creeks (treatments) would respond similarly in the absence of restoration. Although researchers have criticized this design (Underwood, 1994; Smokorowski and Randall, 2017), few have explored whether BACI designs can effectively evaluate fish responses to restoration treatments (Conner et al., 2016). Fish communities that exhibit a wide range of traits, such as size and age at outmigration, or growth rate, may better adapt to environmental changes, potentially dampening the apparent impact of habitat degradation. In effect, life history diversity can buffer reference streams from disturbance, allowing fish to reproduce and survive under altered conditions, and thereby support a more resilient ecosystem. Monitoring studies that focus solely on abundance or productivity as a measure of restoration success risk missing benefits linked to life history diversity.

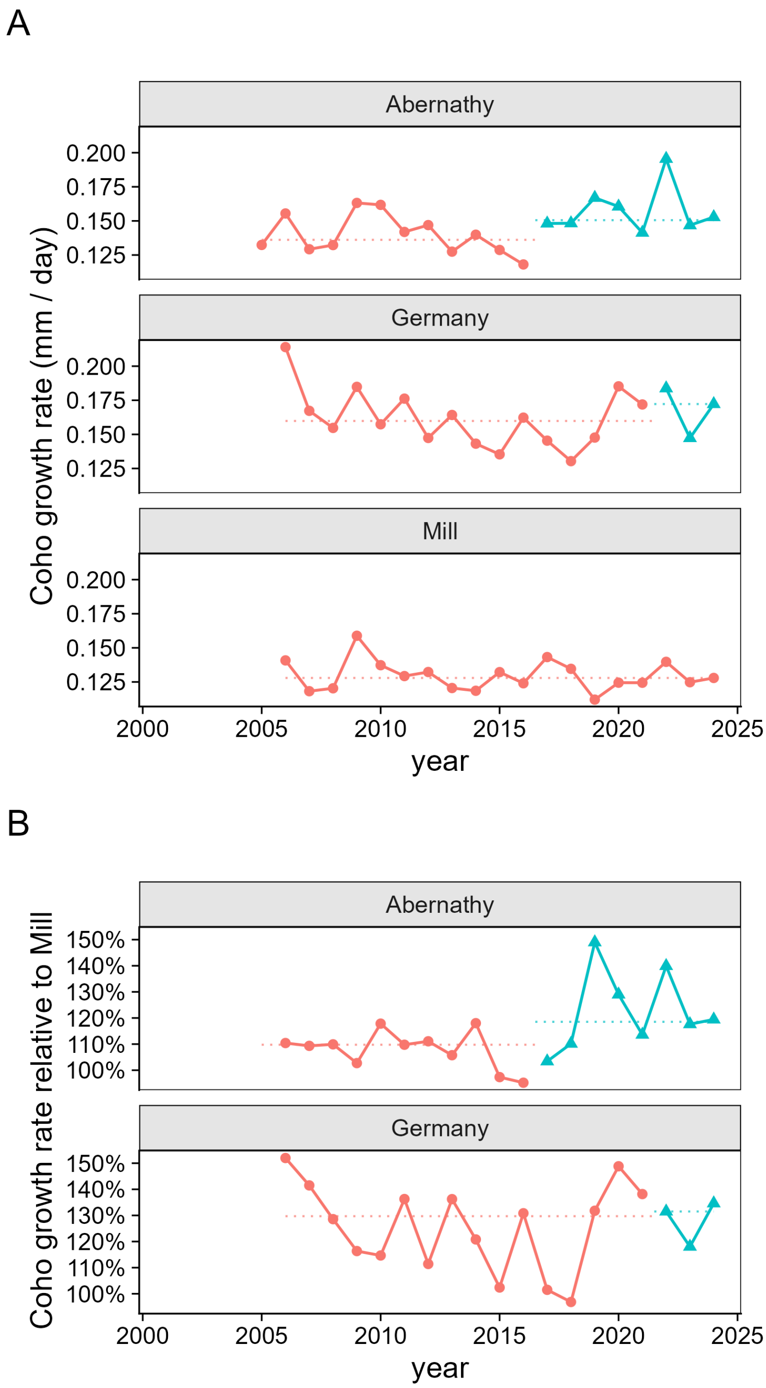

FIGURE 5
(A) Average coho growth rate (mm d^{-1}) by basin and year; coral circles represent pre-restoration, blue triangles represent post-restoration, and dotted lines show median values across years. **(B)** Graphical representations of restoration effect showing growth rate in Abernathy and Germany creeks (treatment basins) relative to Mill Creek (reference basin). Differences in median values between pre- and post-restoration years **(A)** reflect both effects of restoration and background temporal trends; to isolate the effects of restoration, it is necessary to compare treatment streams directly to Mill Creek **(B)**.

Our study did not include adult abundance as a population response variable. After freshwater emigration, salmon and steelhead encounter numerous external pressures, including ocean conditions (Peterson et al., 2014), warming waters (Mantua et al., 1997), hatchery interactions (Cunningham et al., 2018), interspecies competition (Ruggerone et al., 2023; Connors et al., 2025), shifting distributions (Shelton et al., 2021), declining productivity (Oke et al., 2020), predation (Nelson et al., 2024), fishery impacts (Mundy, 1997), and climate change (Crozier and Siegel, 2023). These factors can obscure freshwater restoration benefits and make it challenging to draw associations between changes in habitat with changes in returning adult numbers. Because freshwater restoration

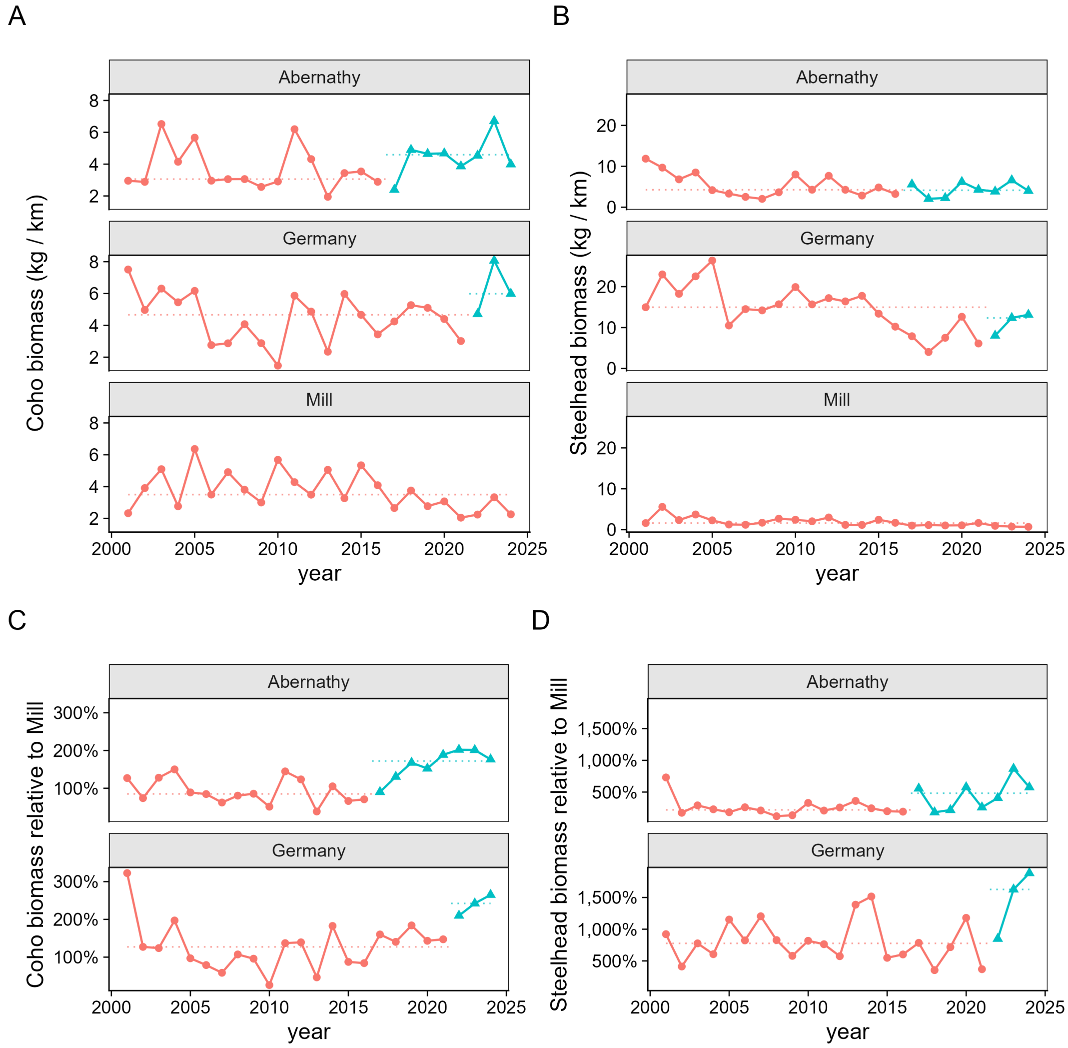

FIGURE 6
Estimated **(A)** coho and **(B)** steelhead biomass (kg km^{-1}) by basin and year; coral circles represent pre-restoration, blue triangles represent post-restoration, and dotted lines show median values across years. **(C, D)** Graphical representations of restoration effect showing yearly biomass in Abernathy and Germany creeks (treatment basins) relative to Mill Creek (reference basin). Biomass was calculated from observed length-mass relationship and abundance estimates (see Methods for details). Differences in median values between pre- and post-restoration years **(A, B)** reflect both effects of restoration and background temporal trends; to isolate the effects of restoration, it is necessary to compare treatment streams directly to Mill Creek **(C, D)**.

more directly impacts juvenile life stages, changes to these life history stages in response to restoration are often easier to account for, but thorough understanding of threats to recovery across the entire life cycle, including variability in marine ecosystem productivity, harvest rates, and climate, can lead to more holistic, scientifically based recovery strategies. Because treatment streams in the Lower Columbia IMW received some of the most intensive restoration treatments of any of the IMWs, this complex has some of the greatest potential to boost juvenile productivity through restoration, which may translate to increased adult abundance, although this may require at least ten years of post-restoration monitoring to fully establish (Bilby et al., 2022).

Restoration in Abernathy and Germany creeks began later than in other Pacific Northwest IMWs, resulting in a longer pre-restoration monitoring period. This allowed us to document interannual differences in juvenile attributes that would have gone unnoticed without intensive monitoring. The pre-restoration differences identified in this study and subsequent increases in things like density and biomass after only 3–8 years following restoration are notable, as previous studies suggested that detecting restoration effects would require many years (Roni et al., 2010; Bilby et al., 2024). In fact, a power analysis conducted for the Lower Columbia IMW found that detecting a 42-47% increase in coho smolt abundance and a 30-52% increase in steelhead would require ten years of post-treatment monitoring (Zimmerman et al., 2015). Our ability to detect significant restoration effects was even more surprising given that that our analysis defined the post-restoration period based on when treatments began, not when they concluded. However, continued monitoring may find that restoration impacts are short lived and ongoing treatments may be required to keep pace with the rate of habitat degradation (Bilby et al., 2024). In general, coho and steelhead are sensitive to warming stream temperatures and low summer flows, both of which are predicted to intensify in the following decades (Rupp et al., 2017; Wainwright and Weitkamp, 2013), so the need for ongoing habitat treatments may emerge as time goes by.

In the Lower Columbia IMW, limiting factors identified for coho and steelhead included high sediment loads and unstable channels (which affect egg incubation), poor riparian and instream complexity (which limit fry colonization), and insufficient quantity and diversity of juvenile rearing habitat (HDR Inc. and Cramer Fish Sciences, 2009; LCFRB, 2016). Key constraints on juvenile stages included the lack of large woody debris (LWD) and pools, poor riparian conditions, altered flows and temperatures, and deficient side-channel connectivity. Restoration actions varied by treatment type, scale, and intensity; however, additions of LWD were prioritized to enhance habitat diversity, promote pool formation, and sort sediment to improve spawning and rearing conditions. Because restoration did not occur outside of the defined anadromous habitat, unit stream length used to calculate juvenile density and biomass did not vary for the pre-and post-restoration periods. Moreover, when evaluating juvenile attributes at the watershed scale, we did not consider any changes to the quality of juvenile overwinter habitat, which has been identified as a bottleneck where coho and steelhead experience the greatest density dependence (Beechie et al., 2023; Rosenfeld and Hatfield, 2006). A logical next step to help guide restoration would be to examine associations between juvenile traits and watershed-scale measures of habitat quality, such as LWD abundance, pool frequency, the level of floodplain or side-channel connectivity, or production of invertebrate prey, which may help identify which restoration actions were most successful at improving the performance of individuals measured in this study (e.g., growth, biomass).

5 Conclusions

Our study evaluated juvenile coho and steelhead demographic and life history traits across 24 years of intensive monitoring in three streams that make up the Lower Columbia IMW complex. We identified basin and restoration effects associated with fish density, FL, age at outmigration, growth rate, and biomass. In all cases, we found significant effects of basin, despite the proximity of these watersheds to one another. Baseline conditions in the reference stream (Mill Creek) produced smolts that were different from the treatment streams, likely related to natural variability in habitat. Restoration contributed to increases in density, size, growth rate, and biomass, but the expectation that restoration would lead to younger age at outmigration on account of faster growth rates was not supported. Restoration activities occurred earlier and were more extensive and intensive in Abernathy Creek than Germany Creek, and as expected the magnitude of responses reflected this varying level of treatment, except for coho biomass, where the positive response was higher in Germany Creek than Abernathy Creek. However, we caution against overinterpretation of the restoration effects in Germany Creek as only 3 out of the last 24 years can be considered post-restoration monitoring years, and it may be too early to be certain about a restoration response. Nevertheless, this study highlights the importance of intensive monitoring for identifying variation in juvenile demographic and life history traits that provide complementary metrics to juvenile abundance. Restoration plans are rarely developed to support and promote life history diversity despite the importance it may have to population resilience. Our work demonstrates the nuances amongst spatially contiguous watersheds that support metapopulations of salmon and steelhead. Management of the habitat that lacks awareness of this natural variability may miss opportunities to support the life history diversity that currently exists, focusing instead on status quo restoration techniques that are expected to modify the habitat in similar ways.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: FigShare, https://figshare.com/s/ee17bda0cb1b85d38637.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this study was completed under a NOAA 4(d) permit of the U.S. Endangered Species Act. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JL: Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. ML: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. CE: Conceptualization, Formal Analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1695522/full#supplementary-material

SUPPLEMENTARY TABLE 1
Summary of model comparisons for each life history variable. "Additional fixed effects" identifies cases in which additional terms were added to address competitive processes (e.g. coho density to account for potential density dependence of fork lengths). Each model also included a random intercept for year. Highlights in the "Method" section identify the best supported model overall. Highlights in "P value" identify likelihood ratio tests that were significant at the P < 0.050 level.

SUPPLEMENTARY TABLE 2
Results of *post-hoc* analyses identifying differences between basins prior to any restoration. Model 2 was fit to data before 2017, and Tukey Honest Difference method was used to compare the effects of basin. There was no coho age at outmigration data before 2017, so that life history trait was omitted. The test statistic varied depending on the life history variable—either the T or Z ratio—and is identified in "ratio type" column.

SUPPLEMENTARY TABLE 3
Model comparisons of seasonality terms for coho growth models. For each of our model formulations (models 1-4), we fit alternative models that included either capture day, recapture day, both, or neither. Each of these alternative models are sorted by ΔAIC score, with the best model (ΔAIC = 0) at the top.

SUPPLEMENTARY TABLE 4
Pairwise basin comparisons (treatment vs. reference stream). For each of our life history variables, we fit models 1-3 (null, basin-only, and basin + restoration effects) to the data subset to only Germany and Mill creeks and then to only Abernathy and Mill creeks and used likelihood ratio tests to identify support for restoration effects. There was no pre-restoration coho age data in Abernathy Creek, so we did not fit model 3 in that case.

SUPPLEMENTARY FIGURE 1
Expansion of Figures 3B, D to show age-1 through age-4. **(A)** Steelhead fork length (FL, mm) averaged by basin, year, and age; dashed lines show mean across years for pre- and post-restoration periods. **(B)** As in **(A)**, but values from treatment basins Abernathy and Germany are scaled by values from control basin Mill.

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