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Life history diversity of *Oncorhynchus mykiss* in the Elwha River during and following dam removal

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Intensively monitored watersheds provide long-term data sets for evaluating land management activities and can also identify causal mechanisms for population-level changes in aquatic species including life history diversity in salmonids. The influence of dam removal (ecosystem restoration), conservation hatchery practices, and an in-river fishing moratorium (i.e., management actions) on life history diversity in salmonids has not been fully evaluated. We used scale and genetic samples collected during intensive monitoring following these management actions in the Elwha River to determine their influence on the expression of life history traits in *Oncorhynchus mykiss*. We evaluated adult migratory patterns, age at migration, and degree of repeat spawning to determine if they changed through time, in both hatchery- and natural-origin individuals. We also assessed if genetic diversity shifted through time, reflecting demographic changes after these management actions. Using age data from scales, together with run timing data, we identified 39 different *O. mykiss* life history (hatchery- and natural-origin) strategies in the Elwha River from 2013 to 2024 based on age at migratory events. The number of life history strategies identified increased from 18 strategies during dam removal impacts to 38 strategies after dam removal impacts; however, this difference was largely due to differences in temporal and spatial sampling effort through time. Life history diversity and the increase from during- to post-dam removal impacts were much greater for natural-origin than for hatchery-origin *O. mykiss*. Although life history diversity appeared to increase over time, overall genetic structure decreased, and diversity was largely unchanged. Resident and anadromous individuals were observed, with anadromous individuals displaying winter and summer migration timing. Winter steelhead smolt age, time spent at sea, total age, and repeat

spawning life histories varied by period and origin. Intensive monitoring allowed us to document the combined positive influence of large-scale dam removal, conservation hatchery supplementation, and a fishing moratorium on life history diversification in *O. mykiss* in the Elwha River.

KEYWORDS

dam removal, diversity, life history, *O. mykiss*, restoration, fishing moratorium, conservation hatchery

1 Introduction

Intensively monitored watersheds (IMWs) can provide long-term data sets for evaluating land use and habitat restoration activities as well as identifying causal mechanisms that result in demographic or population-level changes in aquatic species (Bisson et al., 2023). IMWs can also provide information regarding biological and/or evolutionary changes through time (Bennett et al., 2016). The most notable IMWs on the west coast of North America, Carnation Creek (Hartman et al., 1996; Tschaplinski et al., 2025; Tschaplinski and Pike, 2017) and the Alsea watershed (Bisson et al., 2008; Hatten et al., 2018), have been cornerstones for understanding the impacts of logging on stream habitat and have also provided important information regarding salmonid habitat requirements (Bustard and Narver, 1975; Tschaplinski and Hartman, 1983), migratory patterns (Hartman et al., 1982), and life history strategies (Holtby and Healey, 1990). Additional life history information has been provided by more recent examples of IMWs for assessing the effectiveness of habitat restoration (Bennett et al., 2016; Bilby et al., 2023). The abundance of life history strategies in a river basin for any given salmonid species is influenced by both biotic (Archer et al., 2019; Birnie-Gauvin et al., 2021) and abiotic factors (Bailey et al., 2018; Beechie et al., 2006). Thus, life history strategies may influence watershed recolonization through their “re-establishment” following barrier removal, providing more diverse biotic and abiotic conditions (Duda et al., 2021; Pess et al., 2024, 2014).

The study of life history is important because life history traits influence fitness and are therefore subject to selection pressure (Carlson and Seamons, 2008; Gotthard, 2001; Hutchings, 2003). Life history diversity allows populations to utilize as much of the available habitat as possible, thereby reducing the risk of extirpation by spreading the risk across multiple life history strategies and locations (Bradford et al., 2001; Hodge et al., 2016; Kendall et al., 2015; Stearns, 1992). Life history diversity can thus mediate potential declines in abundance due to variation in survival of asynchronous life histories in relation to environmental variability (Atlas et al., 2023; Moore et al., 2014). Both biological and physical factors influence life history expression in salmon and steelhead, including genetic makeup and maternal effects, physiological effects including metabolism, and environmental conditions, particularly at a young age, which have an impact on growth and development (Archer et al., 2019; Bailey et al., 2018; Birnie-Gauvin et al., 2021; Kendall et al., 2015). Complexity in habitat and environmental, genetic, and phenotypic conditions are thus expected to generate

the conditions from which diverse life histories can evolve and be expressed.

Oncorhynchus mykiss display numerous life history strategies through variation in traits, including migratory and residency, and are an example of life history diversity in Pacific Northwest watersheds (Kendall et al., 2015). For example, *O. mykiss* display up to 55 life history strategies based on migratory tendencies and age at different life events (i.e., smolt and adult return) (Zimmerman et al., 2022), with 30 or more life history strategies reported for several populations (Hodge et al., 2016; Moore et al., 2014; Shapovalov and Taft, 1954; Thorpe, 1994). *O. mykiss* display four general migratory patterns through partial or facultative migratory strategy (Archer et al., 2019; Chapman et al., 2011), namely, nonmigratory resident (Hodge et al., 2016), lacustrine (migrate to and from lakes), partial anadromy (i.e., estuarine use and short-duration marine use) (Peterson et al., 2017), and anadromous individuals that migrate to sea and rear for more than a year before returning as mature adults (Peterson et al., 2017). Resident individuals may live up to 12 years (Moore et al., 2014). Migrating individuals may migrate to sea at the age of 1 to 7 years (Peven, et al., 1994) and remain at sea for 2 months to 6 years (Moore et al., 2014; Peterson et al., 2017). *O. mykiss* are iteroparous, spawning up to five times in their lifetime (Busby et al., 1996); however, greater levels of repeat spawning have been observed for introduced populations (Dedual, 2023; Riva-Rossi et al., 2007). These different migratory and spawning patterns provide numerous possible life history strategies.

While all these life histories and the factors influencing their expression are not typically documented for salmon or steelhead populations, elements of each general factor (i.e., genetic, physiology, demographic, and physical environment) can be attained in IMWs. These data provide the opportunity to evaluate not only the effects of large-scale restoration actions, such as dam removal, but also the biological conditions necessary for life history re-expression to occur. For example, natural selection and/or genetic drift diminishing genetic variation underlying distinct forms may result in staggered life history expression. Barrier removal and restored connectivity, for example, resulted in the rapid recovery of early return timing life histories of steelhead, but not Chinook salmon, in the Elwha River (Elwha Klallam Language: kʷitʃən), likely due to the genetics of the remnant population (Ledger et al., 2023; Pess et al., 2024). Restored connectivity also allows for the possibility of gene flow or admixture, providing novel genetic variation from which life history diversity could be expressed. IMWs provide the opportunity to assess not only the

ecological but also the demographic mechanisms underlying rapid re-expression of life history diversity (Ledger et al., 2023; Pess et al., 2024).

The removal of two dams in the Elwha River, changes in hatchery practices, and an in-river fishing moratorium (no directed harvest through 2011–2023) enacted to protect salmonids during dam removal (Pess et al., 2024; Peters et al., 2024a) (i.e., management actions) were expected to increase life history diversity in the Elwha River *O. mykiss* population. This expectation is due to the dramatic increase in variable habitats becoming available after dam removal, the reduced influence of hatchery fish in the system, and reduced mortality, all of which have been shown to influence life history diversity (Archer et al., 2019; Bailey et al., 2018; Birnie-Gauvin et al., 2021; Kendall et al., 2015). Prior to dam removal, *O. mykiss* consisted of resident fish upstream of the two dams, out-of-basin hatchery *O. mykiss* populations (Chambers Creek winter stock, program terminated in 2013; and Skamania summer steelhead stock, program terminated in 2000), and a small number (hundreds) of naturally spawning steelhead downstream of the two dams (Pess et al., 2008). Adult resident *O. mykiss* (Corbett and Brenkman, 2012) and juvenile downstream migrants would periodically pass over both dams, with juveniles greater than 160 mm being adaptable to seawater (Hiss and Wunderlich, 1994). Whether these downstream migrants went to sea and successfully returned as adults is unknown. However, these individuals were expected to contribute to *O. mykiss* recovery following dam removal (Brenkman et al., 2008; Ward et al., 2008; Winans et al., 2017).

In this paper, we describe how intensive monitoring of the Elwha River *O. mykiss* demographics during and after dam removal impacts was used to quantify changes in life history in *O. mykiss*. It was hypothesized that removing the two dams (Pess et al., 2008), terminating the non-native hatchery program, initiating the native steelhead hatchery program, and implementing the in-river fishing moratorium (Pess et al., 2024) would increase life history diversity of *O. mykiss* in the Elwha River, which was dominated by out-of-basin hatchery production. This study focuses on during- and post-management action impacts and assumes that life history diversity during dam removal is similar to that observed prior to dam removal. The objectives of this study were to assess the hypotheses that (1) *O. mykiss* life history diversity would increase through time and (2) these increases would be due to (a) altered adult migratory patterns/timing (i.e., summer, winter, resident, and partial anadromy), (b) age at smolt and adult migration, and (c) degree of repeat spawning; and lastly (3) to determine if the hypothesized changes in life history diversity were associated with gene flow from within and outside of the Elwha River, including natural- or hatchery-origin individuals. The genetics hypothesis includes samples from pre-dam removal in addition to the during- and post-dam removal impact periods, while the others do not include pre-dam removal information. We test these hypotheses using scale and genetic samples collected during seasonal capture data for *O. mykiss* to determine the life history and genetic diversity of *O. mykiss* in the Elwha River during (2013–2018) and after dam (2019–2024) removal impacts (hereafter termed period, see section 2.2.2 Statistical analysis for date selection reasoning). We report

how several life history metrics vary by period (during and after impact) and origin, as well as their relationship to gene flow, and emphasize the utility of data collected using the IMW approach to identify these shifts.

2 Methods

2.1 Study area

The 833-km² Elwha River basin drains the north slopes of the Olympic Mountains (Figure 1). The river flows 72 km from an elevation of 1,372 m to sea level where it enters the Strait of Juan de Fuca. The morphology of the basin is a series of alternating canyons and floodplain reaches. The furthest canyon downstream (Elwha) starts at approximately river kilometer (rkm) 7.9 and the furthest upstream canyon (Carlson) starts at approximately rkm 51. The length of the canyon reaches varies from 0.8 to 6.5 km, while the length of the floodplain reaches varies from approximately 2 to 12 km. The Elwha basin is subject to a maritime climate characterized by dry summers and cool, wet winters (Acker et al., 2008) with variable precipitation from the headwaters (550 cm) to the river mouth (100 cm). The river has a bimodal hydrograph associated with winter freshets and spring snowmelt, resulting in an average annual discharge of 43 m³/s (Duda et al., 2011).

Most (83%) of the Elwha basin is a roadless wilderness area within the Olympic National Park. The remaining watershed is public, private, and tribal lands. Land management activities with the greatest impact on the river ecosystem were the construction and subsequent removal of two mainstem dams. The Elwha Dam was constructed at rkm 7.9 in 1912, and the Glines Canyon Dam was constructed at rkm 21.4 in 1927. Both structures lacked fish passage, effectively blocking the upstream migration of anadromous salmonids at rkm 7.9, a 95% reduction in available habitat (Brenkman et al., 2019). This also limited the migration of resident salmonids to sections between the dams, except for a few individuals that migrated or fell downstream over the dams (Corbett and Brenkman, 2012). These migratory barriers significantly reduced salmonid population size and species composition (Pess et al., 2008). The removal of both dams was initiated in 2011, with the Elwha Dam fully removed in April 2012 and the Glines Canyon Dam fully removed in 2014 (Brenkman et al., 2019). A rockfall within Glines Canyon occurred shortly after the complete removal of the Glines Canyon Dam, creating a significant barrier. The rockfall was partially removed in 2015 and completely removed in September 2016 (Brenkman et al., 2019; Ertle et al., 2019).

The Elwha River was historically very productive with all five species of Pacific salmon (*Oncorhynchus* sp.), two runs of steelhead (summer and winter) (*O. mykiss*), coastal cutthroat (*O. clarkii*), bull trout (*Salvelinus confluentus*), eulachon (*Thaleichthys pacificus*), and Pacific lamprey (*Entosphenus tridentatus*) (Brenkman et al., 2008; Pess et al., 2008; Wunderlich et al., 1994). Brook trout (*S. fontinalis*) are the only non-native species present and have generally been isolated to the section of river between Elwha and

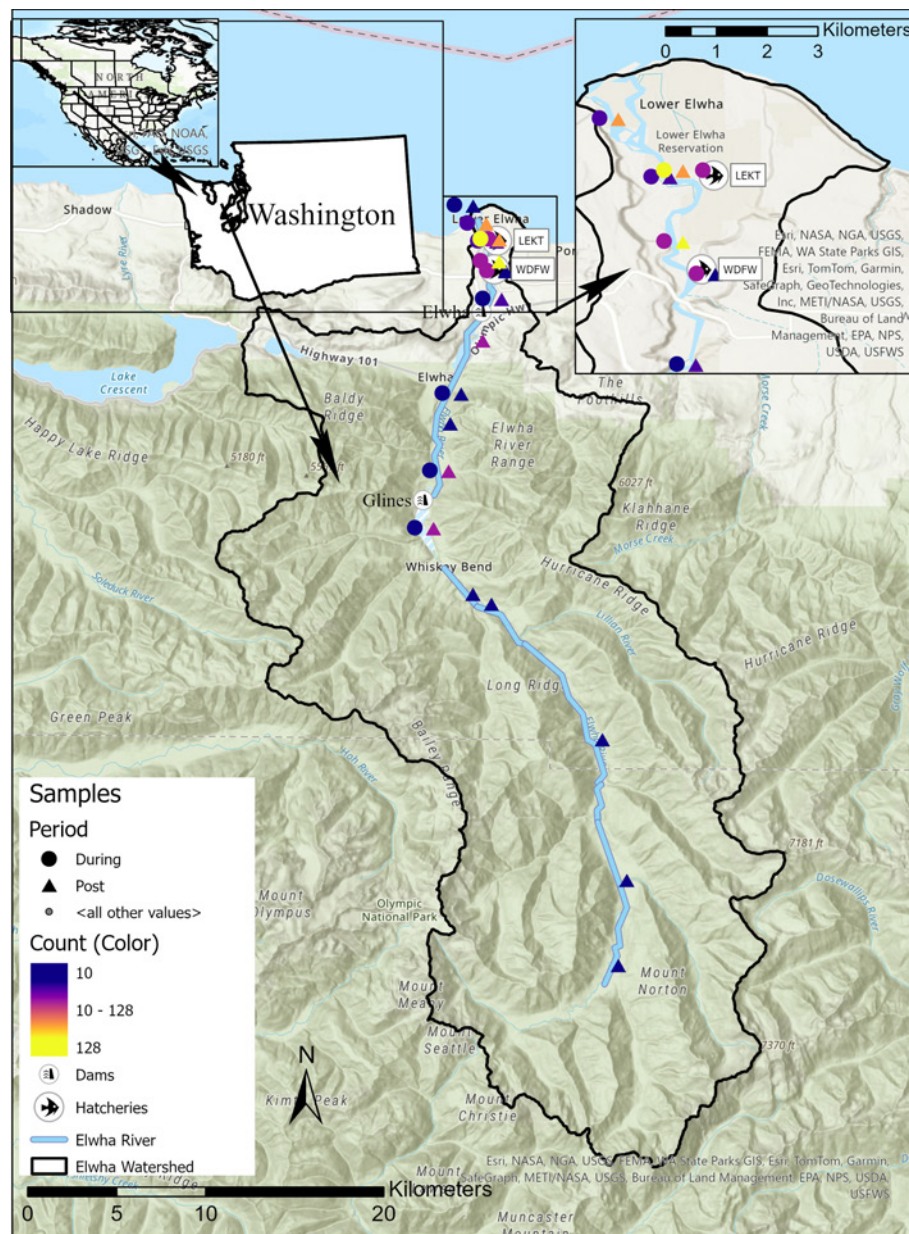


FIGURE 1

Study area and locations where scale and genetic samples were collected (centered roughly by sample reaches) from April 2013 to August 2024. The marker type represents period, and the color represents different sample sizes. The two former dam and operating hatcheries in the system are also noted.

Glines Canyons (Brenkman et al., 2008). Dam removal resulted in fish passage, allowing anadromous fish to access historic habitat (Brenkman et al., 2019; Duda et al., 2021), increased population and productivity metrics (Pess et al., 2024; Peters et al., 2024a), and increased anadromy of bull trout (Brenkman et al., 2019; Quinn et al., 2017).

Contemporary genetic and life history diversity of *O. mykiss* in the Elwha River is a product of the evolutionary history in the system prior to dam construction, the construction and removal of the dams, and historic and current hatchery stocking/production. Hatchery releases from non-native stocks have been common in the Elwha River since 1914 (Brenkman et al., 2008). Resident *O. mykiss* from these releases have reproduced successfully, and their gene

pool has likely mixed with native Elwha *O. mykiss*. However, their alleles represent a limited proportion (0%–20%, generally <5%) of those observed in the 1990s (Phelps et al., 2001) and more recently represent approximately 1% of all non-hatchery *O. mykiss* alleles (Winans et al., 2017). In addition, millions of winter (4.3 million), summer (0.5 million), and unspecified (0.4 million) steelhead were stocked in the Elwha River from 1916 to 2014 (Duda et al., 2018; Winans et al., 2017). These steelhead releases included at least three out-of-basin populations, including Chambers Creek early timed winter steelhead from the Lower Elwha Klallam Tribe (LEKT) hatchery in the lower river, which was initiated in 1976.

After these early introductions, the LEKT hatchery program was maintained using broodstock collected from the Elwha River

(largely Chambers Creek stock) and operated purely as a supplementation facility (LEKT, 2011a). Because of low numbers of returning adults (i.e., 45–246) prior to dam removal and the potential impacts of sediments released during dam removal, a conservation hatchery program for native Elwha River winter steelhead was initiated in 2005. This started with the development of captive brood derived from eyed eggs or emergent fry collected from the Elwha River downstream of the former Elwha Dam and transitioned to the use of returning adults when the returns were sufficient to support the hatchery program (LEKT, 2011b). In addition, adult natural-origin (NOR) and hatchery-origin (HOR) winter steelhead were relocated from downstream of the former Elwha Dam to the Indian Creek and Little River in 2012–2014 and 2016 to help jumpstart reintroduction into the middle reaches of the river and to protect them from elevated turbidity levels associated with dam removal (Pess et al., 2024).

This stocking history has likely influenced the genetic composition of *O. mykiss* in the Elwha River. Prior to dam removal, there were multiple genetic groups identified, generally explained by the dams or natural barriers (Fraik et al., 2021; Winans et al., 2017), with decreased genetic structure and increased admixture following dam removal (Fraik et al., 2021). In addition, the dams did not appear to reduce genetic diversity associated with life history strategies of *O. mykiss* in the Elwha River (Fraik et al., 2021). However, these early studies were limited in their geographic and temporal scope.

2.2 Measuring life history diversity

Life history diversity was examined using several metrics including general run timing (i.e., winter and summer) and age at different life history events (from scales). We used scales to assess life history diversity of *O. mykiss* by assessing age at different life history events (i.e., smolt, age at sea, and total age). Scale samples were collected opportunistically during surveys conducted for other purposes associated with the intensive monitoring associated with dam removal (Pess et al., 2024; Peters et al., 2024a) including species composition for estimating abundance using SONAR (Pess et al., 2024), telemetry studies (Brenkman et al., 2019), tagging during riverscape surveys (Duda et al., 2021), and distribution sampling to assess the proportion of HOR spawners in the population (Peters et al., 2024b). These projects captured fish using either a tangle net, gillnet, or angling. Fish were measured for fork length using a tape, scales were removed from just above the lateral line between the posterior end of the dorsal fin and origin of the anal fin, and genetic samples were collected by clipping a portion of the upper lobe of the caudal fin prior to releasing the fish back into the river. Scales were stored on wax paper in individually marked envelopes and genetic samples were collected on chromatographic blotting paper, quickly air dried, and stored in individually marked envelopes. This sampling strategy resulted in sample sizes that were unbalanced and varied by origin during the two periods, in part due to increases in abundance of natural-origin steelhead over time (Pess et al., 2024; Peters et al., 2024a).

2.2.1 Age analysis using scales

Scales were analyzed to determine age, anadromy, origin, and repeat spawning for *O. mykiss* (Copeland et al., 2018; Seamons et al., 2009; Shapovalov and Taft, 1954). The scale analysis was completed by the Washington Department of Fish and Wildlife (WDFW) Fish Ageing Lab. Scales were mounted on gummed scale cards in the laboratory. Acetate impressions of each card were made using a heated hydraulic press and viewed using a digital microscope camera (e.g., Leica S9i[®]). We identified alternating zones of tightly and widely spaced circuli, termed annuli, to describe the number of winters or years a fish has lived. We used variation in circulus spacing and distance between annuli to identify if a fish had left freshwater or remained in freshwater until it was captured (Supplementary Figures 1A–C). Iteroparity was identified based on scars present when a scale resorbs during a previous spawning migration then regrows, leaving an identifiable scar (Supplementary Figure 1A). The run timing for summer and winter run steelhead was based on capture date, and their age was designated using the European age notation described in Koo (1962) and adapted for winter and summer steelhead (Washington Department of Game, 1978; Scott and Gill, 2008). For steelhead, numbers to the left of the decimal point represent years spent in freshwater (i.e., outmigration age) and “.” indicates the initial seaward migration. Numbers to the right of the decimal point indicate years at sea and the “+” was used for winter run steelhead to represent the annulus that occur(s) as the fish migrate back to freshwater and an additional year at sea (i.e., 1.1+ represents 1 year freshwater, 2 years at sea). This is not used for fish designated as summer run. An “S” denotes a spawn scar. If an age reader determined that the *O. mykiss* did not go to sea based on circulus and annulus spacing, then the number of winters was recorded, and any spawn scars were noted. Supplementary Figure 1 shows an example of a winter (A) and summer (B) run steelhead life history and resident *O. mykiss* life history (C).

Fish origin (natural or hatchery) was determined based on freshwater growth patterns and the presence/absence of an adipose fin clip and/or Coded-Wire-Tag. Hatchery steelhead have been marked using different strategies through time. From the 2011 and 2012 brood years, they were Coded-Wire-Tagged, while those after 2012 had their adipose fin clipped to indicate hatchery origin. The adipose clip efficiency ranged from 93.3% to 97.4%. Origin determined by freshwater growth patterns on scales of steelhead has been shown to be accurate to identify unmarked hatchery fish (Bernard and Myers, 1996; Seamons et al., 2009). Given this and the different mark strategies used, we used scale analysis to identify origin.

2.2.2 Statistical analysis

Life history diversity from scale analysis was based on outmigration age, years at sea, total age, and repeat spawning. We compared diversity within these metrics during- (2013–2018) and post-dam removal (2019–2024) impacts and by origin (HOR or NOR). The during-dam removal impact period covers the period

during dam removal (2012–2014), rockfall removal (2015–2016) (Ertle et al., 2019), and the associated impacts of excessive sediment transport in the system (Pess et al., 2024).

For winter steelhead, we used the Cochran–Mantel–Haenszel (CMH) test (Cochran, 1954; Mantel and Haenszel, 1959) to determine if there was an association between origin and the specific life history metrics examined (i.e., outmigration age, years at sea, total age, and repeat spawning), while controlling for period (i.e., during-/post-dam removal impacts). We also completed a Woolf test (Woolf, 1955) to assess the homogeneity of the three factors (i.e., period, origin, and metric). We used the groupwise CMH function in the R stats package (R Core Team, 2025) to analyze the components of the resulting contingency tables using Fisher's exact test if the CMH test results were significant. Sample sizes were too small to complete these tests for summer steelhead and resident *O. mykiss* (<50 each); thus, only general summaries are provided for these groups.

2.2.3 Genetic population structure and diversity analyses

We employed genetic analyses to understand if gene flow or admixture may have resulted in shifts in the genetic composition following dam removal. We used fin clips sampled from 2,979 putative *O. mykiss* between 2004 and 2024 from 30 general study reaches. We generated restriction site-associated DNA sequencing (RADseq) data using the bestRAD protocol (Ali et al., 2016) and called genetically variable markers [single-nucleotide polymorphisms (SNPs)]. In short, following quality checks using fastQC, deconvoluted and demultiplexed sequences were aligned to the *O. mykiss* Arlee genome (Gao et al., 2021) and then genotyped as a single population using the STACKS pipeline (Catchen et al., 2011). Filtering was conducted thereafter to remove fish with high missing data, likely erroneous genotypes, and fish with *O. clarkii* ancestry (Supplementary Materials and Methods). Additional details regarding sample collection, DNA library preparation, genotyping, identification, and removal of fish with *O. clarkii* ancestry and subsequent filtering are available in the Supplementary Materials (Supplementary Materials and Methods).

Using these genetic data, we subsequently tested if (1) gene flow from outside the Elwha River, (2) gene flow from within the Elwha River, or (3) admixture within the Elwha River changed significantly following dam removal. To do this, we tested whether there were significant changes in the number of genetic clusters (K), the frequency of each genetic cluster's ancestry (Q), the sum total ancestry, and the proportion of ancestry mixture (Mix_Q) over time using ADMIXTURE (Alexander et al., 2009). Changes in genetic structure were quantified by comparing changes in these values across cohorts of fish sampled in distinct temporal (during- and post-dam removal impacts) and yearly (annual) cohorts. We determined if genetic ancestry (Q) or ancestry mixture (Mix_Q) proportions changed after dam removal using a chi-square test for each temporal cohort. To determine if changes in migration or gene flow impacted standing genetic variation, we calculated observed heterozygosity for each individual and quantified changes across each temporal and annual cohort. Observed heterozygosity was calculated using the R package "snpr" (Hemstrom and Jones, 2023) and differences in heterozygosity across temporal cohorts were compared using the Kruskal–Wallis test.

Pearson's correlation coefficients were then calculated to assess whether temporal changes in observed heterozygosity were more strongly correlated with the changes in the predominant ancestry (Q) or admixture (Mix_Q). All statistical tests were conducted in R using functions in the R package "stats", and statistical significance was determined if p -values adjusted for multiple tests were < 0.01. More details on the specific models, statistical tests, and hypothesis testing can be found in the Supplementary Materials and Methods.

3 Results

3.1 Life history diversity

Scale samples originated from 13 general sampling locations from 2013 to 2024. The number of samples varied by location (3–229) (Table 1; Figures 1, 2), year (0–95), migratory type, run timing, and origin (Supplementary Table 1). The lower river sites had the greatest number of samples, which represented most of the samples collected (Table 1; Figures 1, 2). Most of the samples collected were from winter run steelhead ($n = 747$). Fewer but similar numbers of samples were collected from summer run steelhead and resident rainbow trout (<50 each). Sample sizes for winter steelhead, summer steelhead, and resident fish varied by period (Table 1; Figure 2). Both HOR and NOR *O. mykiss* were present in the samples (Table 1). NOR steelhead made up 29.5% of the samples during-dam removal but 75.5% of the samples post-dam removal impact (Table 1). Significantly more samples were collected in the middle (between the former dams) and upper reach (upstream of the former Glines Canyon Dam) for the post-impact period (Figure 2). The differences in sample origin during- and post-impact influenced life history observed during the periods (Figure 2); thus, only general comparisons are completed to describe the number of life histories displayed by *O. mykiss* for the different impact periods.

We identified 39 different *O. mykiss* (HOR and NOR combined) life history strategies in the Elwha River based on age at major life history events (i.e., migrations and repeat spawning) using scale analysis (Figure 3). The during-impact period consisted of 18 life history strategies while the post-impact period consisted of 38. However, this difference is largely accounted for by the increased sampling in the middle and upper river post-impact (Figure 2). Life history diversity was greater in the upper basin in general (Figure 2A) and increased from the lower river to the upper river for resident *O. mykiss* and summer steelhead (Figures 2A, B). NOR *O. mykiss* had greater life history diversity than HOR *O. mykiss* during-dam removal impact (HOR: 5; NOR: 17) and post-dam removal impact (HOR: 9; NOR: 36). We identified two migratory strategies (resident and anadromous) and two run timings for migratory *O. mykiss* (winter and summer) based on scale analyses and capture timing/condition.

3.1.1 Winter steelhead

We identified 20 different winter steelhead (HOR and NOR combined) life history strategies in the Elwha River based on age at major life history events (i.e., migrations and repeat spawning)

TABLE 1 Sample size of readable *O. mykiss* scales and unique life histories observed during (2013–2018) and post dam removal impacts (2019–2024) by reach, life history, run timing, and origin (NOR: natural origin; HOR: hatchery origin) in the Elwha River.

Reach	Life history	Run	Samples		Unique life histories	
			During	Post	During	Post
HOR—Resident						
Lower	Resident	Summer	0	1	0	1
Lower	Resident	NA	0	4	0	2
Middle	Resident	Summer	0	1	0	1
Middle	Resident	NA	0	1	0	1
Unknown	Resident	Summer	1	0	1	0
HOR—Winter Steelhead						
Lower	Steelhead	Winter	170	129	1	0
Middle	Steelhead	Winter	4	2	0	2
Upper	Steelhead	Winter	0	1	0	1
Unknown	Steelhead	Winter	6	0	0	0
NOR—Resident						
Lower	Resident	Summer	1	1	1	1
Lower	Resident	NA	0	1	0	1
Middle	Resident	Summer	1	7	1	4
Middle	Resident	NA	0	2	0	2
Upper	Resident	Summer	0	24	0	3
Upper	Resident	NA	0	3	0	0
Unknown	Resident	Summer	1	0	1	0
NOR—Summer Steelhead						
Lower	Steelhead	Summer	2	4	2	0
Middle	Steelhead	Summer	1	1	1	1
Upper	Steelhead	Summer	1	20	1	4
NOR—Winter Steelhead						
Lower	Steelhead	Winter	60	232	4	7
Middle	Steelhead	Winter	7	88	4	4
Upper	Steelhead	Winter	2	42	2	5
Unknown	Steelhead	Winter	0	4	0	0
Summary for all reaches, life history, and run						
All	All	Hatchery	181	139	2	8
All	All	Natural	76	429	17	32

Reach designations are lower: mouth to Elwha Canyon; middle: Elwha Canyon to Glines Canyon; upper: upstream of Glines Canyon. Unknown represents samples lacking a sampling location ($n = 12$).

using scale analysis (Figure 4). We observed 11 from during-impact and 20 from the post-impact samples. Similar to overall *O. mykiss* life history diversity, this was largely driven by increased sampling effort in the middle and upper river (Figure 2D). As with overall *O. mykiss*, life history diversity of winter steelhead was greater for NOR during (HOR: 4; NOR: 11) and post impact (HOR: 4; NOR 19). Winter steelhead outmigration age varied during and after impact removal and by origin (Figures 5A, B). Winter steelhead out-migrated at primarily 2 years old; however, both 1-year-old and 3-year-old outmigrants were observed in NORs (Figure 5A). There were significant differences in outmigration age during and after impact and by origin (CHM test: $p = 0.0039$) with no statistically

significant interaction among period (during impact and post impact) and origin (Woolf test: $p = 0.5256$). Outmigration age varied during and after impact removal for NOR winter steelhead (Fisher’s exact test: $p = 0.0216$), but not for HOR winter steelhead (CMH test: $p = 1.0$), which were all released as 2-year-old smolts. Outmigration age of winter steelhead varied by origin during (Fisher’s exact test: $p < 0.0001$) and after impact (Fisher’s exact test: $p < 0.0001$), with 1-year-, 3-year-, and 4-year-old outmigrants observed for NORs (Figure 5A). Most winter steelhead, regardless of origin, returned to spawn after 2 years at sea; however, years at sea varied during and following impact and by origin (CMH test: $p < 0.0001$; Figures 5C, D).

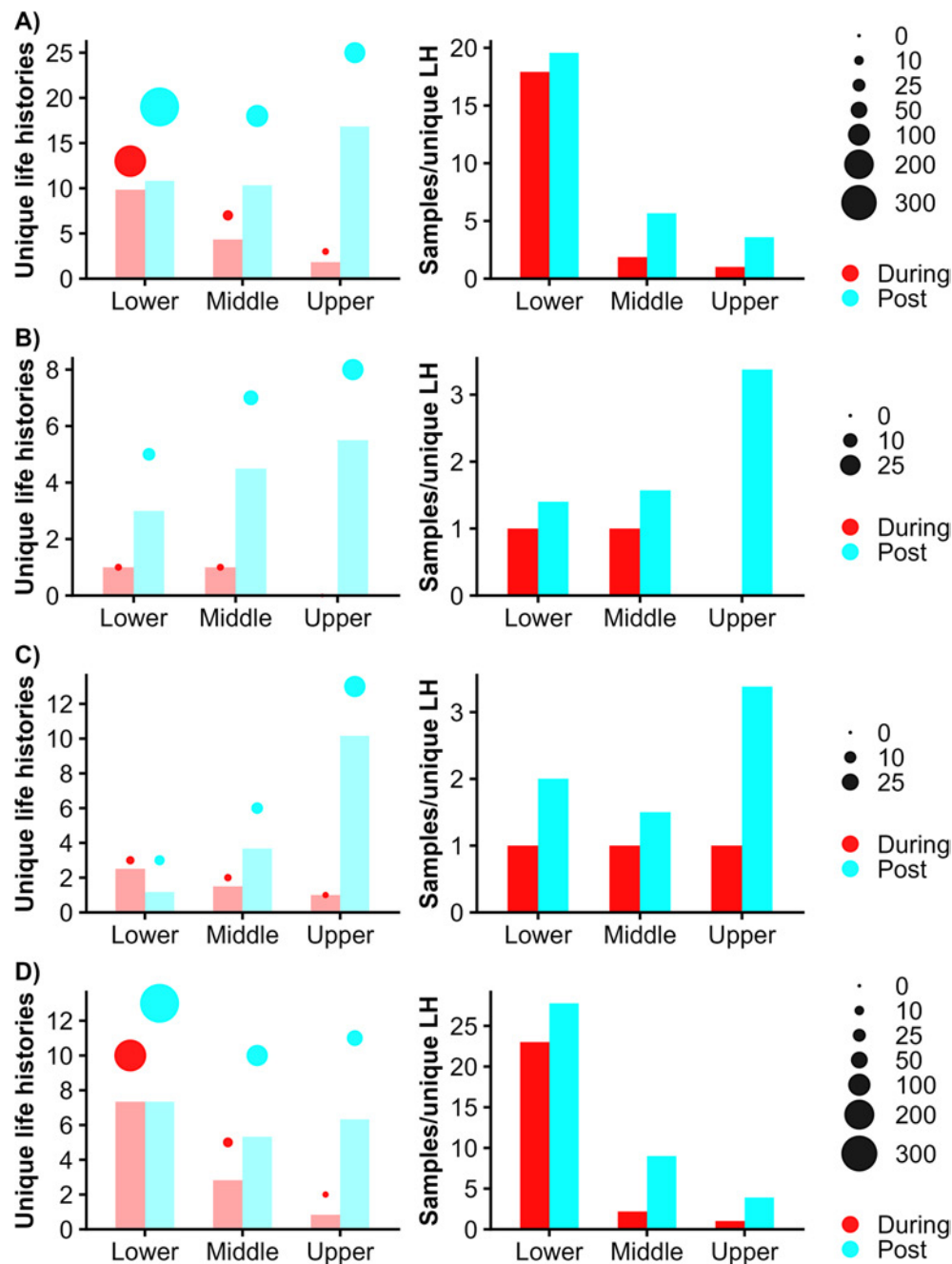


FIGURE 2

Unique life histories for (A) all *O. mykiss*, (B) resident *O. mykiss*, (C) summer steelhead, and (D) winter steelhead by reach. The circles in the left panel show the total number of samples based on size and the total number of life histories observed. The bars in the left panel show the unique life histories observed by reach. The right panel shows the number of samples per unique life history (LH) by reach.

There was no statistically significant interaction among period (during impact, post impact) and origin (Woolf test: $p = 0.7612$). The number of years at sea varied during and after impact for NOR winter steelhead (Fisher's exact test: $p = 0.0004$) but not for HOR winter steelhead (Fisher's exact test: $p = 0.1500$). The proportion of NORs returning after 2 years at sea increased, while the proportion returning after 1 and 3 years at sea decreased after impact. In addition, the years at sea varied among NOR and HOR winter steelhead during (Fisher's exact test: $p = 0.0019$), but not after impact (Fisher's exact test: $p = 0.1710$). NOR winter steelhead had greater proportions of 1 and 3 years at sea and reduced proportion of

2 years at sea than HOR winter steelhead for the during-impact period (Figures 5C, D).

The total age of winter steelhead was predominantly 4 years old, with total age ranging from 3 to 7 years old. Total age varied by period and origin (CMH test: $p = 0.0003$; Figures 5E, F). There was no interaction among these variables (Woolf test: $p = 0.7294$). Total age varied during and after impact for NOR winter steelhead (Fisher's exact test: $p = 0.0006$) but not HOR winter steelhead (Fisher's exact test: $p = 0.411$). There were proportionally fewer 3-year-old and proportionally more 4-year- to 7-year-old NORs after impact. Total age also varied among NOR and HOR winter

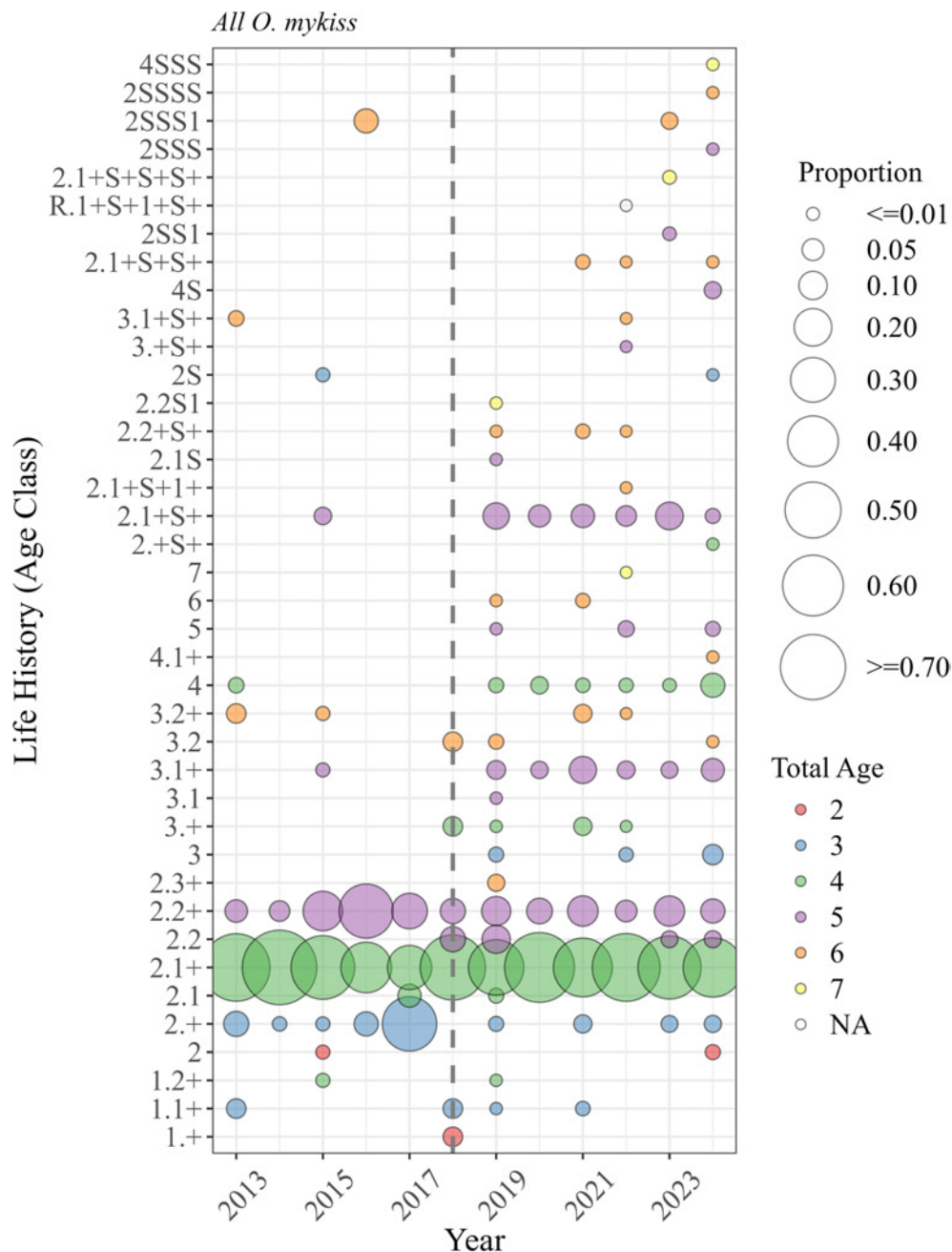


FIGURE 3

Proportion of all Elwha River *O. mykiss* by life history strategy and year based on scales from 2013 to 2024. The circle colors represent total age, while the size of the circle represents the proportion of fish each year displaying that life history pattern. Resident fish are represented by a number with no ".". Summer steelhead are represented by a number representing years of freshwater rearing, a ".", and a number representing years of seawater rearing. Winter steelhead are the same as summer steelhead, except they include "+" in the aging system. An "S" represents previous spawning event, with each "S" representing a specific spawning event. The vertical dashed line represents 2018, the cutoff between the during- (includes 2018) and post-dam removal impact periods.

steelhead during and after impact (Fisher's exact test: Both - $p < 0.0001$). NOR winter steelhead included fish that are 6 and 7 years old (post impact only), while HOR winter steelhead were only 3 to 5 years old.

Repeat spawning increased after impact relative to the during-impact period for both HOR and NOR winter steelhead. Because of small sample sizes associated with the different repeat life history spawners, we combined them and analyzed the data as repeat spawners vs. non-repeat spawners rather than by the different repeat spawning

strategies observed. Repeat spawning for HOR winter steelhead was 0.6% (1 of 180) during impact and 3.8% (5 of 132) after impact. In contrast, repeat spawning for NOR winter steelhead was 2.9% (2 of 69) during impact and 10.2% (37 of 364) after impact. These differences were significantly different for origin (CMH test: $p = 0.0107$). There was no interaction between period (during impact and after impact) and origin (Woolf test: $p = 0.6686$). No significant differences were observed for NOR or HOR winter steelhead by period (Fisher's exact test: HOR $p = 0.0866$; NOR $p = 0.0862$). HOR and NOR winter steelhead did not

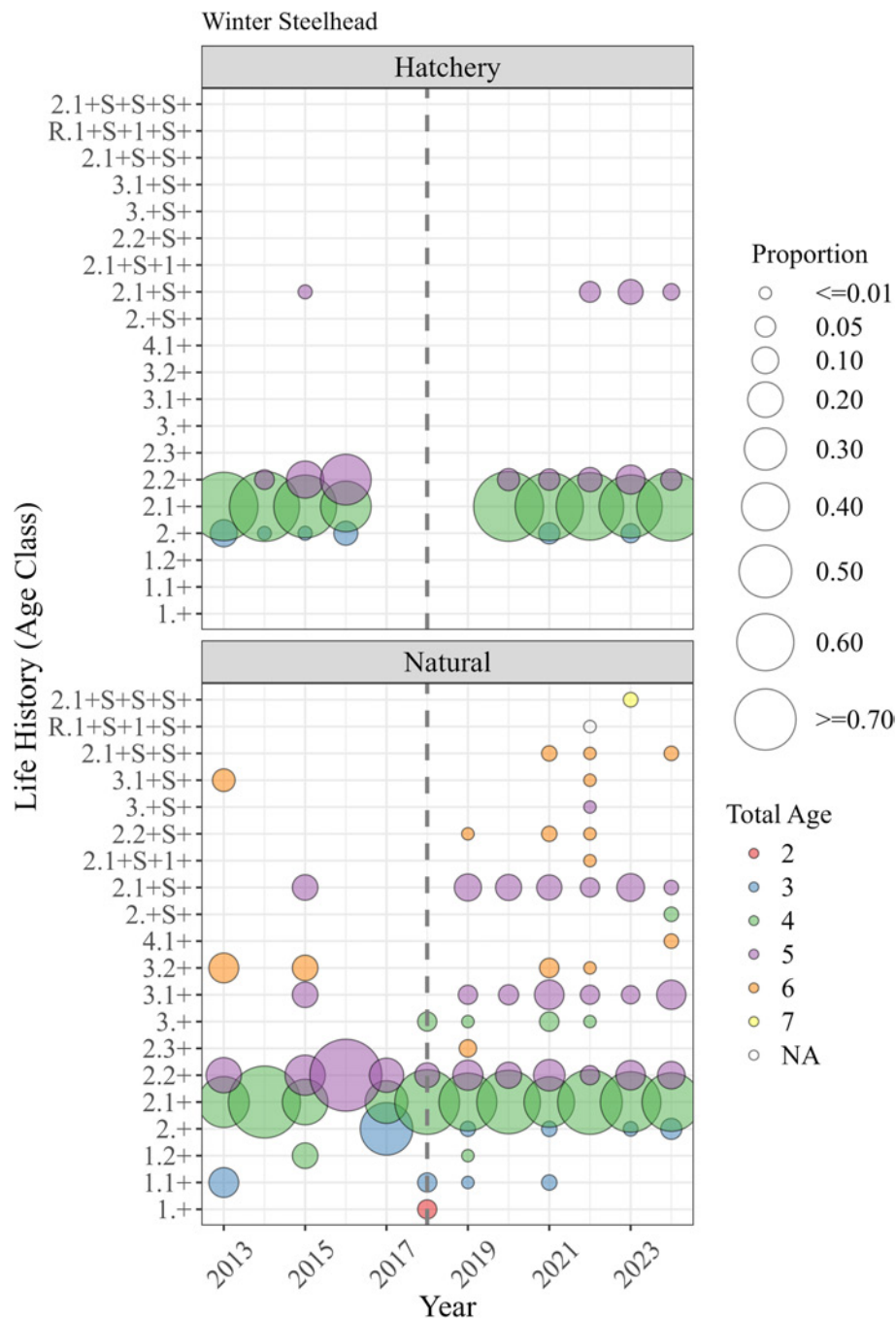


FIGURE 4

Proportion of Elwha River winter steelhead by life history strategy and year based on scales from 2013 to 2024. The circle colors represent total age, while the size of the circle represents the proportion of fish each year displaying that life history pattern. Life history (Age Class) represents years of freshwater rearing followed by a "." then years of seawater rearing, with the "+" distinguishing them as winter steelhead. An "S" represents previous spawning event, with each "S" representing a specific spawning event. The vertical dashed line represents 2018, the cutoff between the during- (includes 2018) and post-dam removal impact periods.

differ during dam removal impact (Fisher's exact test: $p = 0.1870$) but did after dam removal impact (Fisher's exact test: $p = 0.0378$) with greater repeat spawning by NORs than HORs for the post-impact period. NOR winter steelhead displayed five different repeat spawning strategies, while HOR winter steelhead displayed only one (Figures 5G, H). HOR winter steelhead always repeat spawned the next year, while NOR winter steelhead spawned the next year and skipped a year between repeat spawning activity.

3.1.2 Summer steelhead

General summaries of summer steelhead are provided since only 29 summer steelhead samples, all from NORs, were obtained over the years, preventing more in-depth analyses. Summer steelhead predominantly migrated to sea at 2 years old, but a portion also migrated at 3 years old (Figure 6A). Most spent 2 years at sea, but a portion also returned after a single year at sea. Summer steelhead

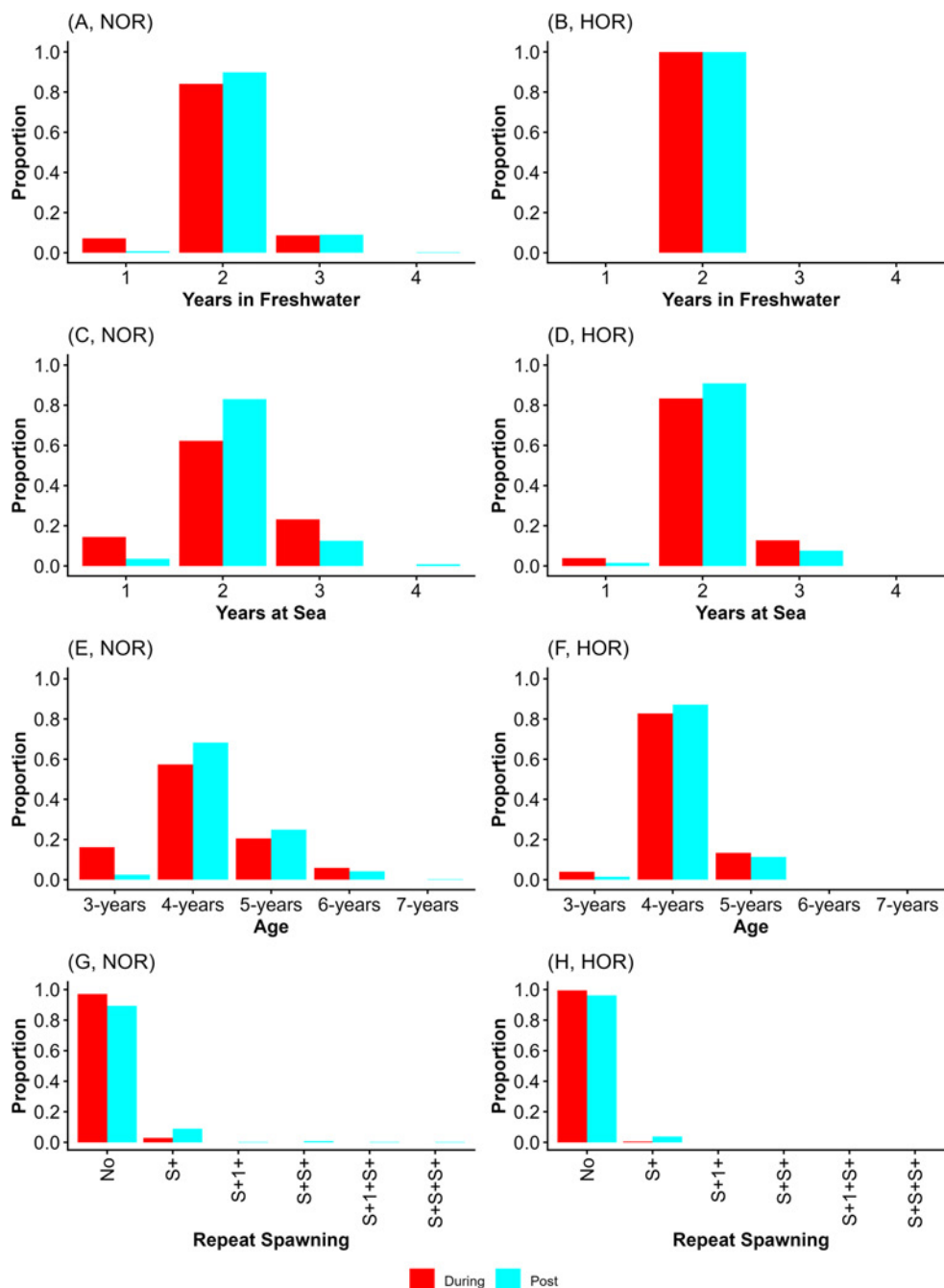


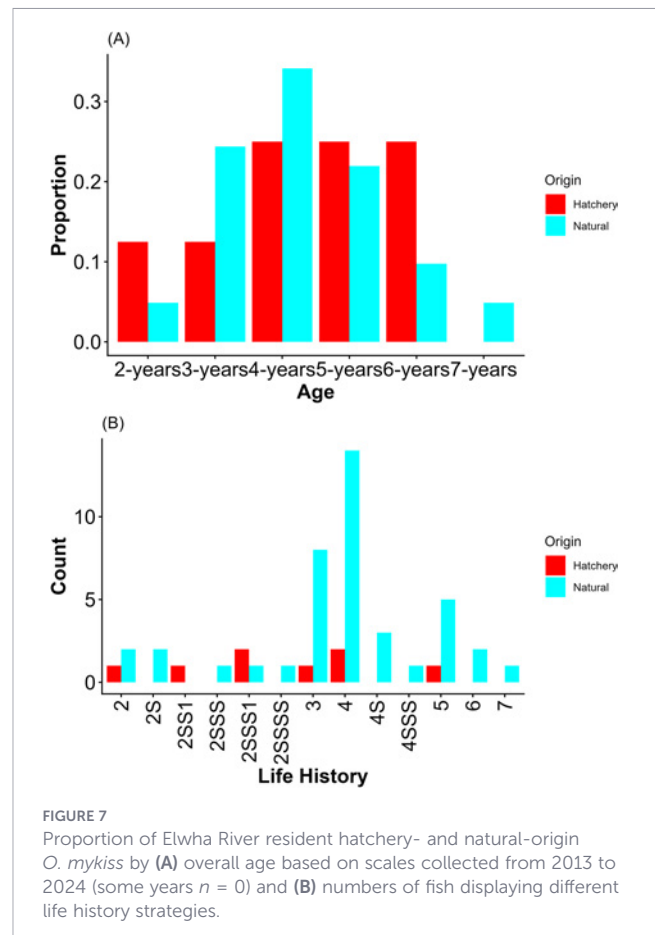
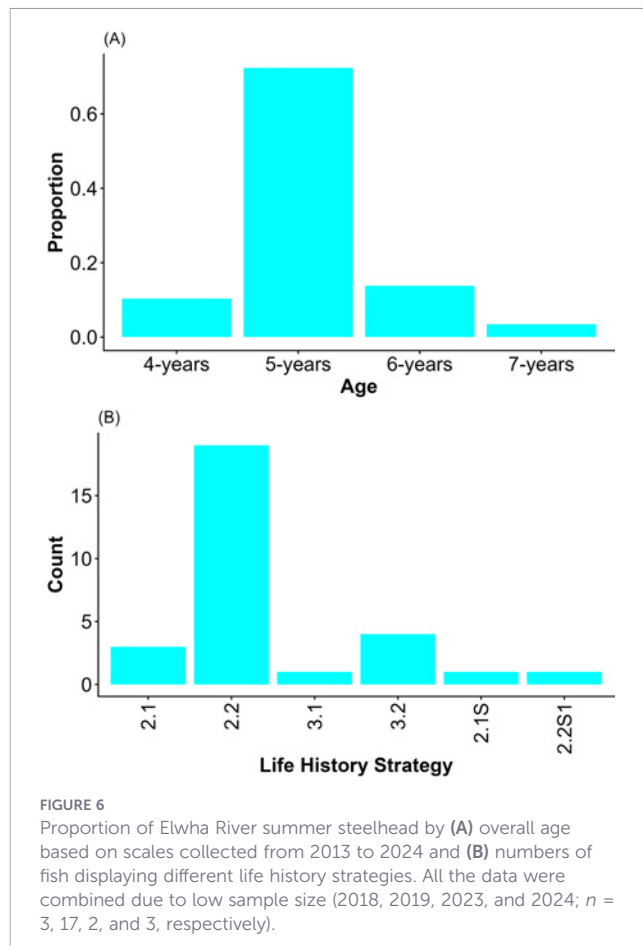
FIGURE 5

Proportion of natural- (NOR) and hatchery-origin (HOR) winter steelhead during and after dam removal impacts by outmigration age (A, B), years at sea (C, D), total age (E, F), and displaying different levels of repeat spawning (G, H). There was one age 2 NOR winter steelhead that is not shown on the chart.

were generally older than winter steelhead in the Elwha River, ranging from 4 to 7 years old, with 5 years old being the dominant age class (Figure 6B). Summer steelhead displayed six life history strategies (Figure 6). Two of the 29 summer steelhead sampled were on repeat spawning migrations (6.9%). One returned the year following its initial spawning run, while the other had spent an additional year at sea before returning to spawn again (Figure 6A).

3.1.3 Resident *O. mykiss*

Only general summaries could be provided for resident *O. mykiss* due to the small sample size ($n = 51$) and large differences in spatial distribution of samples by period (Table 1 and Figure 2B). Resident HOR ($n = 8$) and NOR ($n = 43$) *O. mykiss* ranged from 2 to 7 years old, with 4 years old being the dominant age class



(Figure 7A). HOR resident *O. mykiss* ranged from 2 to 6 years old, while NOR resident *O. mykiss* ranged from 3 to 7 years old. HOR and NOR resident *O. mykiss* displayed 6 and 12 life histories, respectively (Figure 7B). Repeat spawning increased for resident *O. mykiss* from two for the during-impact period to seven for the post-impact period; however, sample size increased substantially after impact (Figure 2B). Resident HOR *O. mykiss* spawned two and three times, while NOR resident *O. mykiss* spawned one, three, and four times. Overall, resident *O. mykiss* displayed greater repeat spawning (~20%) than either winter or summer steelhead.

3.2 Genetic structure and diversity analyses

After filtering out individuals with *O. clarkii* genetic ancestry ($N = 672$) and SNPs with low coverage and thinning our data set to retain one locus per 100,000 base pairs, we retained 2,297 individuals and 12,426 SNPs (Supplementary Table 2). We identified four genetic clusters (hereafter described relative to geographic barriers; Supplementary Figure 2) that reflected the structure generated by natural and anthropogenic barriers prior to dam removal. No novel genetic clusters appeared in the during- or post-impact periods, suggesting that gene flow was primarily occurring among Elwha River origin fish (Supplementary Figures 2C, D).

The frequency of the predominant genetic ancestry changed significantly over time, reflecting changes in the demographics of which populations rapidly responded to dam removal (Figure 8).

Before dams were removed, fish primarily were derived from the area downstream of Elwha Canyon (lower river) genetic cluster (mean χ^2 test = 37, $n = 197/200$), but the proportion of admixed fish significantly increased ($Mix_Q = 0.278$, mean χ^2 test = 45.3, $n = 169/200$). In the generations after dam removal, the predominant genetic ancestry switched to upstream of the Rica Canyon (upper river) (mean χ^2 test = 22.5, $n = 169/200$) and genetic admixture continued but did not significantly increase ($Mix_Q = 0.275$, mean χ^2 test = 80.8, $n = 200/200$). Taken together, these results supported high gene flow throughout the Elwha River, but not from outside of the basin.

We observed marginal increases in heterozygosity during impact (mean $H_o = 0.182 \pm 0.004$) but noticed decreases after impact (mean $H_o = 0.152 \pm 0.004$) relative to before dam removal (mean $H_o = 0.171 \pm 0.006$) (Figure 8A). Differences in heterozygosity were statistically significant (Kruskal $\chi^2 = 86.713$, $p < 0.01$) and were correlated to changes in individual's proportions of upper river ancestry (Pearson's correlation coefficient = -0.32 , $p < 0.01$) (Figure 8). Upper river genetic ancestry increased significantly in natural origin fish over time (Kruskal $\chi^2 = 73.676$, $p < 0.01$), but the predominant ancestry remained lower river and relatively unchanged in HOR over time (Kruskal $\chi^2 = 5.815$, $p = 0.056$) (Figures 8B, C). Changes in the frequency of admixture events (Mix_Q) following dam removal were positively correlated with heterozygosity in NOR (Pearson's correlation coefficient = 0.376 , $p < 0.01$) but not HOR (Pearson's correlation coefficient = -0.32 , $p = 0.14$).

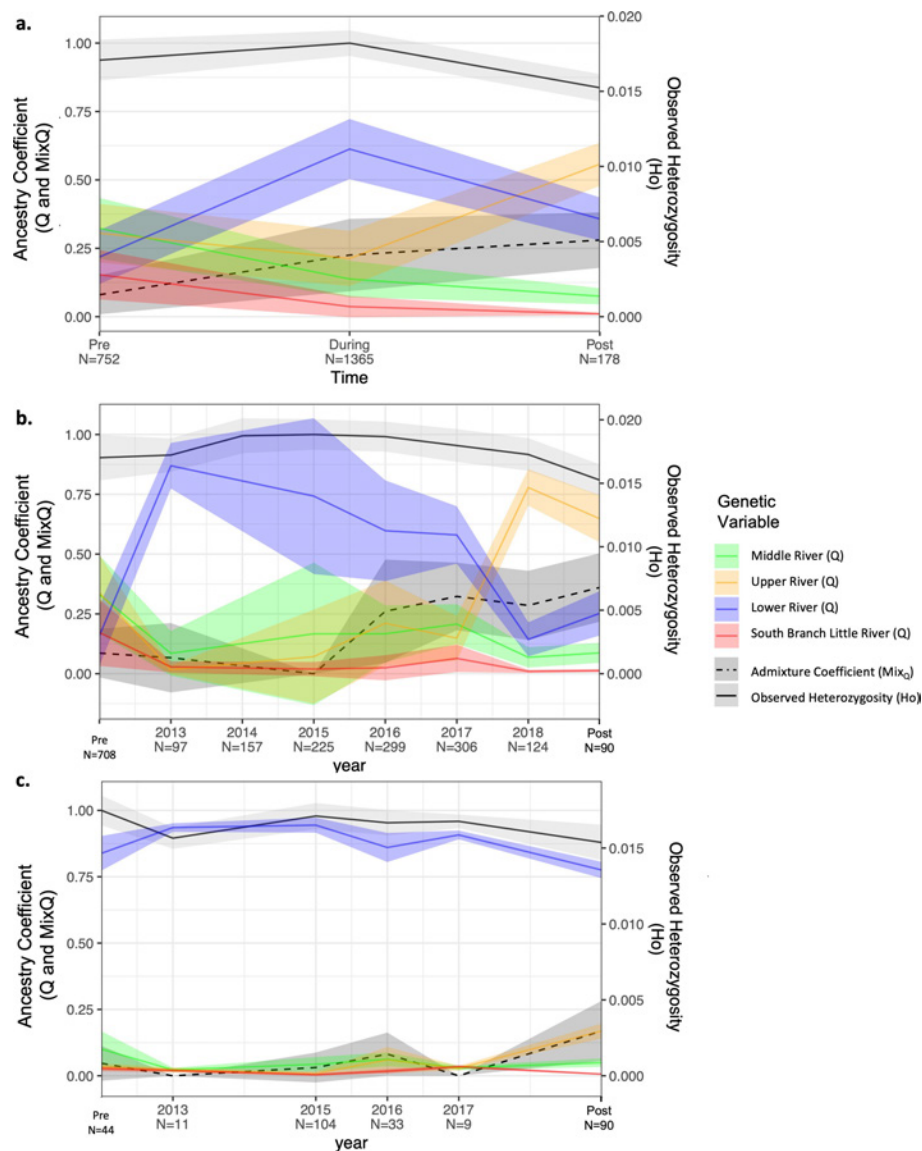


FIGURE 8

(A) Observed heterozygosity (H_o , black line), the proportions of genetic ancestry (q) from each genetic cluster (colored lines), and the admixture coefficient (Mix_Q , gray dashed line) varied significantly by temporal period (before, during, and after dam removal impacts) across all fish. (B) Natural-origin (NOR) *O. mykiss* and (C) hatchery-origin (HOR) *O. mykiss* had variable contributions from different genetic clusters (colored lines). While the genetic ancestry of HOR remained primarily lower river, the frequency of upper river NOR ancestry increased significantly following dam removal as did heterozygosity (black) and the admixture coefficient (gray dashed).

4 Discussion

IMWs provide valuable long-term data sets for evaluating management activities including habitat restoration. They can also provide valuable information for monitoring underrepresented metrics such as life history diversity (Bilby et al., 2023). The removal of two dams, implementation of a conservation hatchery, and in-river fishing moratorium on the Elwha River, Washington State, USA, has resulted in improved population status based on distribution, abundance, and productivity for winter steelhead (Pess et al., 2024; Peters et al., 2024a). Here, we show that long-term, consistent, and opportunistic monitoring has been useful in identifying changes in life history strategies in *O. mykiss* following the implementation of these three management actions. Elwha River *O. mykiss* displayed life history diversity like other larger basins, including two migratory strategies,

two adult run timing strategies, and multiple combinations of age at different life events (i.e., smolt and adult return). Differences in age at major life events varied by period and generally by origin. Repeat spawning increased for *O. mykiss* in general; however, the differences were not statistically significant by period and repeat spawning appeared to vary by migratory strategy, run timing, and origin. Genetic data revealed that restored connectivity increased intra-Elwha River gene flow and admixture but did not increase genetic diversity over time. We observed only a weak relationship between genetic diversity and genetic ancestry, suggesting that it is unlikely to have played a large role in rapid life history expansion.

O. mykiss display significant life history diversity throughout their range (Busby et al., 1996). From 2013 to 2024, approximately three generations after dam removal, the implementation of a conservation hatchery, and an in-river fishing moratorium, we

documented 39 different life history strategies for HOR and NOR Elwha River *O. mykiss* based on migration strategy, adult migration timing (i.e., summer and winter), age at different life events, and repeat spawning. The total number of life histories observed was like that observed in other larger river systems, with reports ranging from 36 to 55 (Hodge et al., 2016; Moore et al., 2014; Zimmerman et al., 2022). The number of life history strategies observed increased from 18 during impact to 38 after impact and was greater for NOR than for HOR Elwha River *O. mykiss*. This increase appears to be largely due to differences in temporal and spatial sample collection between the two periods (Figure 2). This resulted in a sample dominated by HOR steelhead for the during-impact period and a sample dominated by NOR *O. mykiss* including more resident and summer steelhead from the middle and upper river for the post-impact period (Table 1 and Figure 2). The increases in NOR samples for the post-impact period are partially due to the increased abundance of NOR winter and summer steelhead in the system. However, it is also due to increased sampling effort in the middle and upper watershed during that period. Life history diversity was generally greater in the upper river for overall *O. mykiss* (Figure 2A) and increased from the lower river to the upper river for resident *O. mykiss* and summer steelhead (Figures 2B, C). Thus, we cannot definitively say that life history diversity for all *O. mykiss* combined increased through time due to the implementation of the three management actions involved.

Life history expression in salmonids is influenced by both biological and physical factors, including genetics, physiology, and environmental conditions that influence their physiology and ultimately survival (Archer et al., 2019; Bailey et al., 2018; Birnie-Gauvin et al., 2021; Kendall et al., 2015). Thus, management actions that influence habitat conditions and availability such as habitat restoration (Bottom et al., 2005) and barrier removal (Bisson et al., 2008) or that influence survival can influence the expression of life history diversity. The combined influence of increased habitat availability, excessive sediment transport that decreased over time after dam removal, modified hatchery practices, and the lack of harvest during this study has influenced age at life history events for winter steelhead. These alterations include outmigration age, years at sea, total age, and repeat spawning. These changes were generally associated with fish origin, suggesting that the conservation hatchery program may influence life history diversity of HOR fish like traditional hatcheries (Peterson et al., 2017). We believe that each of these factors influenced the expression of life history traits, but dam removal likely had the greatest impact.

The potential influence of the three management actions implemented on the expression of life history traits in *O. mykiss* in the Elwha River varies substantially and appears to be quite complex due to interacting influences through time. Dam removal provided access to approximately 187 km of mainstem, floodplain channel, and tributary habitats with variable physical habitat, thermal, and hydraulic regimes (Brenkman et al., 2008; Munsch et al., 2023). These variable conditions can affect factors known to influence the expression of life history traits including food availability (Bailey et al., 2018; Jonsson et al., 2013), growth (Bailey et al., 2018; Nevoux et al., 2019), and seasonal fish size (Larsen et al., 2017). For example, life history variation has been

reported to vary among sub-basins within the Klamath basin (Hopelain, 1998). These benefits may have been mediated for several years following dam removal due to the release of approximately 20 MT of sediment (Warrick et al., 2015). This large-scale sediment release reduced invertebrate populations through at least 2014; however, juvenile salmonids adjusted by preying on different taxa, resulting in a similar energy uptake (Morley et al., 2020). In later years, the increases in adult abundance upstream of the former dams (Pess et al., 2024; Peters et al., 2024a) likely increased marine-derived nutrients that can benefit river productivity (Bilby et al., 1996; Wipfli et al., 1999) and subsequent growth in juvenile salmonids (Bilby et al., 1996; Scheuerell et al., 2007). However, these increases in adults also altered fish communities and increased juvenile densities and subsequent competition through time with potential impacts to juvenile *O. mykiss* growth (Duda et al., 2021; Munsch et al., 2023).

All three management actions implemented in the Elwha River can influence survival, which can result in increased life history diversity. Dam removal was expected to reduce salmonid survival initially, but those impacts were not as dire as expected and were largely absent by 2019 (Pess et al., 2024). The in-river fishing moratorium obviously increased survival by eliminating fishing-related mortality, with unknown fishing mortality in the marine environment. Reduced harvest has been shown to benefit species diversity, fish biomass, and body condition (Xiong et al., 2026), all of which could influence life history diversity. The hatchery program increases survival through the juvenile stage; however, it may also truncate potential life history diversity by releasing all the smolts as 2-year-olds, which appeared to impact future life history diversification, resulting in variation among HOR and NOR steelhead.

The increases in habitat availability with varying environmental conditions and variable productivity through time and hatchery practices likely influenced the differences observed for outmigration age. Outmigration age varied by period, with NOR outmigrants tending to be older for the post-impact period, due to fewer age 1 migrants (7% to 0.8%) and the appearance of age 4 outmigrants. Numerous factors associated with dam removal and ecosystem recovery may be responsible for the observed changes, including food availability (Bailey et al., 2018; Jonsson et al., 2013), growth (Bailey et al., 2018; Nevoux et al., 2019), size (Larsen et al., 2017), and competition (Nevoux et al., 2019). In addition, these factors will interact with one another and will be influenced by temperature (Birnie-Gauvin et al., 2021; Kendall et al., 2015). Hatchery practices resulting in all smolts being released at 2 years old resulted in the differences observed in outmigration age among the two groups. This also likely influenced the differences observed for subsequent life history stages.

The changes observed in outmigration age may have influenced the changes observed in the number of years at sea and total age. Outmigration age and size have been shown to influence years at sea (Catterson et al., 2020; Chapman, 1958; Peterson et al., 2017; Ward and Slaney, 1988). For example, younger and smaller *O. mykiss* smolts are more likely to express the half-pounder life history strategy in the Trinity River, California, USA (Peterson et al., 2017). Thus, the increased outmigration age in smolts is

consistent with the observed decrease in 1-year-old migrants observed in our study. Time at sea is generally inversely related to smolt size in steelhead (Chapman, 1958; Ward and Slaney, 1988). This contrasts with our results, where both smolt age (and assumed larger) and years at sea increased. The increase in both years in freshwater and years at sea obviously results in increased total age. Although the changes observed in years at sea could be due to varying marine conditions during these periods, this seems unlikely, since a similar change was not observed for HOR winter steelhead, which are all released as age 2 smolts. The consistent age and size of HOR smolt releases likely results in the reduced expression of life history strategies in these phases since, as stated above, these factors influence time at sea and subsequently total age.

Repeat spawning is an important trait in iteroparous species that is seen as a bet hedging approach (Birnie-Gauvin et al., 2021) and experienced spawners have greater lifetime reproductive success than single spawning individuals (Christie et al., 2018; Stubberud et al., 2022), making them potentially more important for population growth (Stubberud et al., 2022). For all *O. mykiss* combined, we observed more than a four-fold increase in repeat spawning life history strategies after impact compared to during impact. The percentage of HOR and NOR winter steelhead repeat spawners increased nearly seven- and four-fold, respectively. Although these increases for winter steelhead repeat spawning were not statistically significant by period, this is likely due to how few repeat spawners were observed for the during-impact period (HOR: 1; NOR: 2). Importantly, the increases in repeat spawning in the Elwha River occurred during a period when repeat spawning has decreased along the coast of Washington State, USA (Claiborne et al., 2026; Ohlberger et al., 2025). This variation may be due to the in-river fishing moratorium in the Elwha River, which would reduce the stress on adults during their spawning migration and post-spawning recovery, both of which are important for successful repeat spawning (Birnie-Gauvin et al., 2021). The level of repeat spawning observed in winter steelhead from the Elwha River after impact (i.e., 3.8% and 10.2% for HOR and NOR, respectively) meets expectations given its location. Repeat spawning generally ranges from 2.78% for Columbia River wild steelhead (Keefer and Caudill, 2014) to 36% in sub-basins in the Klamath system (Hodge et al., 2016). However, 63% of the life histories of winter Steelhead on the Olympic Peninsula, Washington State, USA, from 1994 to 2023 were repeat spawning life histories (Claiborne et al., 2026). Repeat spawning is generally reported to be reduced in northern rivers (Busby et al., 1996); however, repeat spawning rates contrasting this general observation have been reported for Southeast Alaska (Harding, 2008). Repeat spawning rates of 7.6% and 10% have been reported in the Skeena and Nass Rivers (Moore et al., 2014) and the Keogh River, British Columbia, Canada (Ward and Slaney, 1988). These are like those observed after impact in the Elwha River. Since the Elwha River is further south than these three systems, historically greater rates have been observed in the nearby Hoh River (Claiborne et al., 2026), and greater rates have been reported in Southeast Alaska, one might expect that further increases will occur over time. The significantly greater repeat spawning by NOR winter steelhead relative to HOR winter steelhead in the current study is consistent with the

observation that repeat spawning is generally greater in NOR steelhead than in HOR steelhead (Keefer and Caudill, 2014). HORs repeat spawned only once, while NORs repeat spawned up to three times in the Elwha River, which is within the range of repeat spawning reported in the literature (Busby et al., 1996; Moore et al., 2014). Repeat spawning also appeared to vary with migration strategy and run timing, generally being greater for resident *O. mykiss* and least for winter steelhead, with summer steelhead being intermediate.

In addition to the diversity in age at life history events, two migratory strategies were observed: non-migratory resident fish and anadromous migrants. Resident and anadromous life histories are common in *O. mykiss* populations (Kendall et al., 2015; Quinn, 2018), and their proportions vary among basins (Hodge et al., 2016; Kendall et al., 2015). Some anadromous *O. mykiss* in the Elwha River had spent 1 year (or less) at sea and were generally small (i.e., generally 450–550 mm). Although larger, this is like the “half-pounder” (generally <400 mm) strategy reported in Oregon and California, USA (Hodge et al., 2016; Peterson et al., 2017) and in the western Pacific Ocean (Pavlov et al., 2001). These smaller anadromous Elwha River *O. mykiss* do not appear to represent a half-pounder life history strategy. Half-pounders are generally immature (Hodge et al., 2016; Peterson et al., 2017). Although we did not kill the partial migrants during our study to assess maturity, they were classified broadly as new entries, holding, or spawning based on coloration and/or obvious signs of spawning (milt, spawned female). Several of these fish had spawned, suggesting that this strategy is not strictly a half-pounder life history strategy. Based on scale structure, 48% of the *O. mykiss* between 450 and 500 mm were anadromous.

O. mykiss life history characteristics appeared to vary with run timing and migratory strategy (i.e., anadromous and resident). Summer steelhead were generally older than winter steelhead (age 5 vs. age 4), with a greater proportion spending 2 years at sea. This is consistent with observations of summer and winter steelhead from the Kalama River, Washington, USA (Leider et al., 1986). Winter and summer steelhead appear to differ in their spatial use of the Elwha River, with summer alleles more common in samples from the upper Elwha River (Fraik et al., 2021; Ledger et al., 2023). In addition, we found that upper river ancestry was more common for the post-impact period than for the during-impact period. This ancestry shift may be due to greater time spent at sea and may generate a “lag” in genetic response, explaining why we did not observe any changes over time. However, it also may be due to differences in sampling through time (see below). We also observed differences between resident and anadromous *O. mykiss*. A greater proportion of resident *O. mykiss* in the Elwha River spawned multiple times relative to their anadromous counterparts. This is also consistent with other reports (Kuzishchin et al., 2007) and may be due to reduced energy expenditures for spawning relative to their anadromous counterparts, resulting in better nutritional state after spawning (Birnie-Gauvin et al., 2021; Willis et al., 2023).

Assessments of genetic structure and diversity can provide important context regarding the sources of biological variation contributing to life history diversity. Dispersal can provide one mechanism through which rapid evolution could occur. For

example, following restored connectivity immigrants can introduce novel genetic variation required for diverse life histories to be expressed. If this were the case, we would anticipate genetic ancestry and admixture to be correlated with increases in genetic diversity over time. We did not identify significant increases in genetic structure or immigration from outside of the Elwha River in the 12 years after dam removal (Fraik et al., 2021; Ledger et al., 2023). Genetic admixture among Elwha River genetic clusters increased for the during-impact period but did not appear correlated with heterozygosity. We observed weak, temporally inconsistent relationships between genetic diversity and genetic ancestry (Q), likely correlated with demographic rather than life history trends. One possible explanation for the decoupling of genetic and life history variation was the way we measured changes to diversity. Our study was limited to using opportunistically collected samples of both adult and juvenile *O. mykiss* in which population of origin or life history traits were rarely known. Gene flow could increase population-specific life history diversity by influencing local populations' genetics; this would be missed by our approach looking at riverscape level changes to heterozygosity over time. This seems unlikely, however, as we would expect a temporal lag in life history diversification associated with gene flow. The rapid expression of anadromous life history diversity in populations formerly isolated above dams suggests that these fish retained their ability to express these forms.

Diminished genetic diversity observed after dam removal impact may reflect dam removal dynamics and the expansion of the upper Elwha River genetic cluster. The Glines Canyon Dam was removed later than the lower river dam, delaying ocean-migrating fish for approximately one generation. Furthermore, summer steelhead (Pess et al., 2024) and the genetic variation associated with this life history (Fraik et al., 2021) are more frequent in the upper watershed. Taken together, this may explain a contracted demographic effect of the expansion of the upper watershed, which can result in a lag in genetic diversity. Additional genomic sampling of fish from specific populations in this IMW, such as the upper river, paired with life history information, can allow us to test hypotheses of the roles of different evolutionary mechanisms on the recovery of specific life histories.

Our ability to assess overall *O. mykiss* life history diversity was influenced by our sampling strategy and resulting sample availability. The scale samples used during this study were collected opportunistically during monitoring activities with different objectives such as assessing abundance and distribution, among others (Pess et al., 2024; Peters et al., 2024a). Thus, the sample collection varied spatially and temporally throughout the basin, with the number of samples collected by location, migratory type, run timing, and origin varying substantially by period (Table 1), which resulted in changes in life history observed for all *O. mykiss* combined, resident *O. mykiss*, and summer steelhead for the different periods (Figure 2). Our sampling strategy also resulted in proportionally fewer HOR fish for the post- than for the during-impact period (Table 1), potentially reducing our ability to detect rare or underrepresented life histories for HORs. Although sample availability for HOR and NOR *O. mykiss* varied among periods, the proportion of samples representing HOR and NOR *O.*

mykiss were likely similar to their proportion in the river during the two time periods. The sample proportions of 71.5% and 24.5% HOR for the during- and post-impact periods compares favorably with the approximate mean proportion of HOR and NOR winter steelhead (during ~ 70%, after ~50). Thus, reported differences in life history diversity among HOR and NOR *O. mykiss* for this study were not overly impacted by sample availability.

Despite the limitations imposed by the opportunistic nature of the sampling, significant observations related to *O. mykiss* life history were observed during this study. Because of the lack of samples, it is unclear how the current life history diversity compares to before dam removal. However, in three generations following the implementation of three management actions including dam removal, conservation hatchery, and fishing moratorium, life history diversity is similar to that reported for other larger basins and is trending better than a nearby system (Claiborne et al., 2026). Age at major outmigration, years at sea, total age, and repeat spawning changed during the two impact periods. These changes likely would have gone unnoticed if not for the intensive monitoring associated with dam removal in the Elwha River.

Given the changes in life history strategies displayed by *O. mykiss* during this study, we recommend continued monitoring to assess how life history diversity will continue to change over time. This strategy should ensure sampling is spatially and temporally consistent through time to avoid the issues observed during this study. This study reports data collected over a 12-year period, representing only three full generations for winter steelhead. While we observed significant shifts in the predominant genetic ancestry and admixture coefficients over time, we observed little change to genetic diversity. While this may be explained by lags associated with life history specific shifts in traits like generation time, this may also reflect stochasticity associated with sampling and demography. Thus, it seems unlikely that the system has reached “equilibrium”; thus, further changes should be expected as have been seen in long-term IMWs (Tschaplinski et al., 2025). In addition, future fisheries may influence life history diversity once implemented in the Elwha River. A fisheries moratorium enacted at the onset of dam removal restricted all in-river harvest through 2023 and *O. mykiss* harvest through the time of publication (Pess et al., 2024). Thus, the Elwha River provides a unique opportunity to explore how fisheries impact life history diversity. We recommend a dedicated study design be developed to address this question with better spatial representation matching the temporal availability of the different migratory strategies (i.e., timing, anadromy). This design should also consider potential differences resulting from different methods (i.e., angling and tangle net) since our limited data suggest that these different methods may differentially capture fish of different sizes.

5 Conclusions

IMWs provide long-term data sets for evaluating management activities on population metrics such as abundance, productivity, and distribution. We show here that IMWs can also provide valuable information regarding how life history diversity changes in populations following the combined influence of large-scale

restoration, implementation of a conservation hatchery, and an in-river fishing moratorium. Life history diversity is important because these traits influence fitness and are subject to selection pressure (Carlson and Seamons, 2008; Gotthard, 2001; Hutchings, 2003), ultimately buffering populations through portfolio effects (Moore et al., 2014; Schindler et al., 2010). The changes observed during the current study occurred over a relatively short period (i.e., 12 years or three generations). Continued monitoring of this system is important for several reasons. First, it seems unlikely that the system has reached equilibrium given the short period between the end of dam removal impacts and just having three generations of adult steelhead returns. Second, fisheries will eventually be reinstated, and it is likely that there will be a termination of the winter steelhead hatchery program; thus, future management actions will provide a unique opportunity to examine their impact on population metrics.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: NCBI BioProject PRJNA690579; and <https://catalog.data.gov/dataset?q=Life+history+diversity+of+Oncorhynchus+mykiss+in+the+Elwha+River+during+and+following+dam+removal>.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because we followed authorization of Federal and State sanctioned permits.

Author contributions

RP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. GP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. KD: Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. AC: Data curation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. JM: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. AF: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Supervision, Writing – original

draft, Writing – review & editing. ML: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. JJ: Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. MM: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. KN: Conceptualization, Data curation, Funding acquisition, Writing – original draft, Writing – review & editing. DP: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. TB: Data curation, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

Author KD owns and operates K. Denton and Associates, LLC and worked under contract with the Lower Elwha Tribe to collect data used in this study species composition sampling associated with SONAR.

The remaining 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.

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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.2026.1772015/full#supplementary-material>

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