Research Topics

Large-scale dam removal and ecosystem restoration

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Large-scale dam removal and ecosystem restoration

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Table of contents

Ecosystem Ecology and Water Quality

Diadromous and migratory fish populations

Terrestrial ecology

The human connection: social science, political ecology, and economics

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Editorial: Large-scale dam removal and ecosystem restoration

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Editorial on the Research Topic
Large-scale dam removal and ecosystem restoration

1 Introduction

Rivers underpin vital ecosystems that support aquatic and terrestrial biodiversity and many ecosystem services, including food, water, culture, and recreation (Dudgeon et al. 2006). After centuries of building dams on rivers across the world, river restoration via dam removal is receiving increased public attention, financial investment, and scientific study because of various issues of regarding dam infrastructure, such as obsolescence, sedimentation, and ecosystem degradation (Duda and Bellmore, 2022; East and Grant, 2023). Most dam removal projects to date have focused on smaller structures, but larger structures > 10 m tall have also started to be removed in increasing numbers. Recent estimates suggest that only a small fraction of all dam removals have been scientifically studied, with most focused on small dams and short time scales (Bellmore et al., 2016). Understanding the outcomes of large dam removal, where case studies are much more limited, depends on sustained research and monitoring efforts aimed at understanding restoration processes over large spatial and temporal scales (Figure 1). The ecological and socio-ecological study of large dam removal represents a new frontier in dam removal research: projects are larger, more recent, and provide an opportunity to understand the complex ecological changes and impacts to humans that occur with these transformative restoration projects.

This Research Topic contains a diverse array of large dam removal research studies to synthesize the issues, outcomes, tools, and study designs used to document river and ecosystem responses across physical, biological, and ecological domains. Papers address ecosystem ecology and water quality, diadromous and migratory fish populations, terrestrial ecology, and human systems, exploring dam removal effects and impacts in the first ten years since large dam removal in unique river systems found in North America

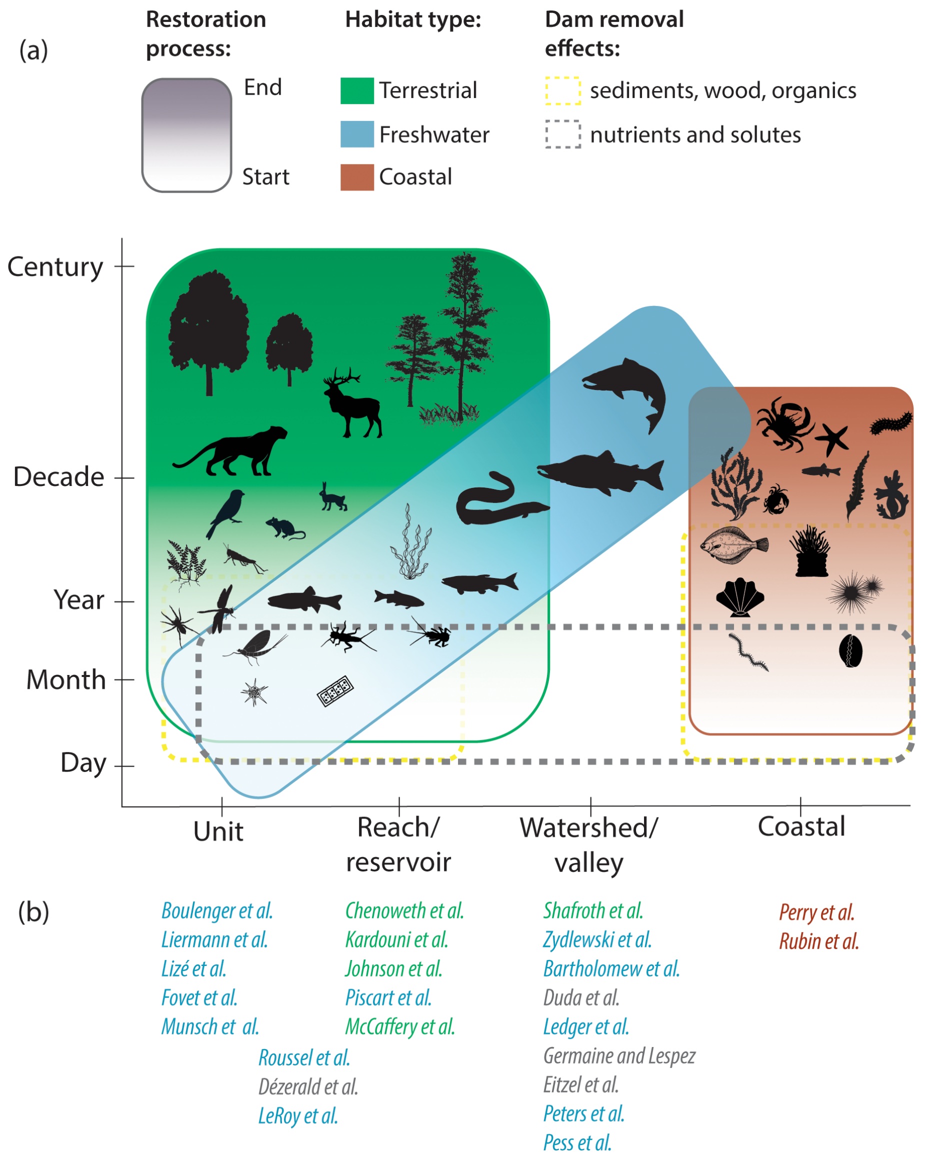

FIGURE 1
(A) Large dam removal influences multiple ecosystems over large spatial and temporal scales. Restoration processes are expected to occur from a span of days to decades and extend from microhabitats in the terrestrial and aquatic environments to trans-ecosystem influences. Processes include abiotic changes in sediment, wood, and water quality as well as diverse biotic and successional changes in freshwater aquatic, terrestrial, and coastal/marine ecosystems. **(B)** The papers in this Research Topic span riverine, terrestrial, and coastal ecosystems, examining dam removal issues and impacts in the first decade following large dam removal. The font colors highlight whether each paper covers freshwater (blue), terrestrial (green), coastal (brown), or multiple (grey) ecosystems.

and Europe. This Research Topic informs ongoing, long-term ecological restoration and monitoring projects related to dam removal as well as to upcoming large dam removal projects. Most of the papers focus on two large dam removal systems. The first is the Elwha River in Washington State, USA, where researchers have had 10 years or more to study post-dam removal outcomes using several scientific lenses. The second is the Sélune River in Normandy, France, where two dams were removed in 2019 and 2022. Finally, the Research Topic includes a review of dam-related challenges to fish and how removal of two dams mitigated some passage problems for the Penobscot River, Maine, USA; a modeling tool developed and tested on the Touques River in Normandy, France, to assess diadromous fish runs in restoration projects; and an exploration of how current removal of four dams on the Klamath River in California and Oregon, USA, could impact fish and fish disease dynamics.

2 Ecosystem ecology and water quality

The role of connections between ecosystems has long been acknowledged in ecological science, questioning the simplistic vision of compartmentalization of ecological processes (Summerhayes and Elton, 1923; Odum et al., 1979). The emergence of the meta-ecosystem framework (Loreau et al., 2003; Angeler et al., 2023), which considers flows of energy across ecosystem boundaries, highlights how adjacent ecosystems depend on each other across spatial and temporal scales. Conversely, alterations of ecological continua and transfers between ecosystems can affect their sustainability and resilience (e.g., Ward and Stanford, 1995; Baxter et al., 2004). In this first section, six articles address the multiple effects of large dams and their removal on the terrestrial–freshwater–marine continuum, highlighting perceptible impacts on water quality, plant and animal communities, and ecosystem functions. Roussel et al. report that the retention of sediment and nutrients in reservoirs can modulate the balance between detritus-based and algal-based food chains, altering the patterns of carbon flow in aquatic food webs along the river continuum. Fovet et al. demonstrate that fluxes of nutrients and sediments restore quickly after dam removal and become available again to aquatic life downstream after decades of sequestration into reservoirs. LeRoy et al. focus on a functional aspect of riverine ecosystem response by studying the decomposition of terrestrial-derived leaf litter by aquatic fungal and macroinvertebrate communities and show how this ecosystem function varies along the upstream-downstream gradient after dam removal. Similarly, Piscart et al. observe a rapid reestablishment of benthic macroinvertebrates in river segments within the footprint of a former reservoir, but also point out that fine sediment and instability of benthic habitats can delay the restoration of the whole river metabolism. Looking beyond the river itself, Dézerald et al. document the fast and simultaneous recovery of aquatic invertebrate, riparian invertebrate, and vegetation communities after reservoir dewatering, while demonstrating ongoing changes between communities as systems go through transient recovery phases. Finally, Rubin et al. illustrate the variable ecological responses among subtidal communities of kelp, benthic invertebrates, and fish following a massive sediment export after dam removal and the restoration of natural rates of terrestrial sediment transfer toward marine habitats.

3 Diadromous and migratory fish populations

There is keen interest in the response of fish populations to increased longitudinal connectivity from dam removal (Branco et al., 2014, Magilligan et al., 2016; Thieme et al., 2023). The bulk of the current dam-removal literature deals with documenting fish passage, estimating the amount of longitudinal habitat access restored, and changes to upstream fish assemblage structure. Most of these studies are of relatively short duration, a characteristic of most dam removal (Bellmore et al., 2016) and river restoration (Bernhardt et al., 2005) efforts. Several papers in the large dam removal Research Topic go beyond these structural-style studies and delve into topics that deal with fish functional responses to dam removal. Ledger et al. use genetic tools and a riverscape approach to examine the spatial structure of neutral genes and two genes associated with early migration timing in Steelhead and Chinook Salmon, finding limited genetic spatial structure in both populations (a result documented in pre-dam removal studies) and an increase in early return timing alleles in *Oncorhynchus mykiss* (i.e., Rainbow Trout and Steelhead) samples. Munsch et al. explore how restoring connectivity through dam removal goes beyond simply providing access to river kilometers of habitat upstream; it also can provide a portfolio of different habitats and environmental conditions within which life history diversity of fish populations can emerge and diversify. Such diversity has been shown to promote resistance to environmental disturbance and long-term resilience of populations (Schindler et al., 2010, Moore et al., 2014, Munsch et al., 2022). Pess et al. examine 10 years of during- and post-dam removal data focused on Steelhead and Chinook Salmon, two species listed under the U.S. Endangered Species Act. They show that dam removal, hatchery production, and harvest restrictions interacted and contributed to population response, including increasing population size, spatial extent, and life history diversity. In another long-term study from the east coast of the U.S. with a different assemblage of diadromous fish, Zydlewski et al. highlighted seven influences of dams on fish populations and how dam removal reversed some of these effects. Lizé et al. establish baseline levels of carbon stable isotopes in a diadromous fish community prior to dam removal, using the data to examine dietary niche partitioning and levels of interactions and overlap before the river is free flowing again. Bartholomew et al. discuss the potential for dam removal to change river conditions—especially with regards to temperature and flow regimes—and how this might affect the ecology and dynamics of parasites and their salmonid hosts.

Two papers in the Research Topic contain methodologies and modeling approaches that can be used in fish abundance estimation for adults (Boulenger et al.) and juveniles (Liermann et al.), techniques that can be employed for restoration projects, including dam removal. Boulenger et al. used independent, synchronous data from acoustic cameras to estimate detection probabilities and daily fish passage estimates. Liermann et al. created a model to relate water temperature, spawning location data, growth, and movement models to predict the emergence timing and size of outmigrating juvenile Chinook Salmon.

4 Terrestrial ecology

In contrast to fish restoration and ecosystem ecology, restoration of terrestrial plant and wildlife communities following dam removal has received relatively little attention (Bellmore et al., 2016; Wieferich et al., 2021). However, the sediment pulse generated by large dam removal and the exposure of dewatered reservoir beds creates new surfaces both in the former reservoirs and downstream of dam sites for diverse plant and animal species to establish and subsequently influence restoration trajectories (McCaffery et al., 2018). There is also interest in understanding the ecological impacts of active revegetation efforts (e.g., seeding and planting native plants and removing invasive species) and how those interact with natural plant establishment to inform future restoration efforts. Finally, patterns of terrestrial wildlife use and activity are closely linked to changes in vegetation, restoration of fish populations (Call, 2015; Tonra et al., 2015), and response of aquatic biodiversity in these systems.

This Research Topic contains several papers examining aspects of revegetation following dam removal—both natural and managed—as well as one paper examining wildlife responses. First, Shafroth et al. provide an overview of vegetation response throughout the Elwha River watershed, explaining the rapid changes that occurred due to the sediment pulse that moved through the watershed as the dams were removed and how those are expected to attenuate as sediment dynamics stabilize. Chenoweth et al. provide a complete review of natural plant establishment as well as active revegetation efforts on the dewatered reservoir beds, including initial predictions and actual patterns of revegetation. In Kardouni et al., authors focus specifically on the impacts of riverbank lupine (*Lupinus rivularis*) seeding efforts on ecosystem dynamics in the dewatered reservoirs in the Elwha River. Staying in the dewatered reservoir habitat, Johnson et al. describe how strategic placement of large wood as part of the restoration process can potentially enhance tree growth by mitigating moisture and nutrient limitations as well as protecting planted seedlings from ungulate browsing. Dézerald et al. describe the rapid establishment of new vegetation communities in the immediate years following dam removal, while highlighting the dynamic nature and rate of change present in these areas. Moving downstream to the coastal environment, Perry et al. describe vegetation establishment on new surfaces created by sediment mobilization during dam removal relative to existing coastal vegetation communities, and how those surfaces have changed as sediment dynamics stabilized in the 10 years since dam removal. Finally, turning to terrestrial wildlife, McCaffery et al. used camera traps to investigate mammalian wildlife use of dewatered reservoirs in the Elwha River ecosystem as restoration approaches the 10-year mark, demonstrating differences in species use by season and study reach.

5 The human connection: social science, political ecology, and economics

There are far fewer studies of social aspects of dam removal than those focused on physical and ecological outcomes (but see Sneddon et al., 2017; Leisher et al., 2022; Lutter et al., 2024), and most focus on local controversies (e.g., Jørgensen and Renöfält, 2013; Fox et al., 2016; Germaine and Lespez, 2017; Magilligan et al., 2017), management concerns (Tullos et al., 2016), or economic elements related to cost or property values (Loomis, 1996; Lewis et al., 2008). In this Research Topic, several case studies highlight the intersection of ecological, sociological, and natural resource management involved with dam removal and the recovery of a river and its valley. They also indicate that each component of the ecosystem can respond at a different pace, sometimes at large spatial scales, during the restoration period. The outcomes of large-scale dam removal projects inevitably affect the human communities living upstream and downstream of the dam to be removed, and they should be prepared and familiar with the details of the process as early as possible. Germaine and Lespez compare dam removal implementation details and social settings of the Elwha River (most of the watershed in a National Park) and the Sélune River (a rural European setting), stressing the importance of incorporating human relationships and attachment to local places as part of the dam removal context. Based on the Elwha River experience, Eitzel et al. give useful recommendations for successfully involving citizens in dam removal scientific studies, using a participatory science approach. Setting up large-scale dismantling programs also questions our capacity to cope with divergent management goals among partners and stakeholders, as pointed out by Peters et al. regarding the adaptive management of Endangered Species Act-listed salmonid populations on the Elwha River. Finally, on the economic level, Duda et al. describe a database of 668 dam removals in the USA with reported costs and cost drivers, creating a model of dam removal cost as a function of parameters such as the size of the dam, river, and project complexity based on the presence of cost items related to construction, mitigation, and post-removal outcomes.

6 Conclusion

At its simplest, the removal of a large dam from a river is about linear reconnection, restoring the unimpeded downstream flow of water, sediment, and nutrients while restoring the ability of aquatic organisms to move freely upstream, downstream, and out to the ocean as their life histories dictate. But the reality is much more complex, in ways we are only starting to fully appreciate. The research in this Research Topic and other recent synthesis efforts (Magilligan et al., 2016; Tonitto and Riha, 2016; Foley et al., 2017; Major et al., 2017; Bellmore et al., 2019) show that rivers and their denizens can respond quickly to large dam removal and the resulting restored longitudinal connectivity. Although scientists have a much better understanding of the initial and often large response to the act of dismantling a large dam from a river, the tail of the response distribution has been neglected (Figure 1). Recovery can start quickly for physical processes (e.g., flow, sediment, and temperature regimes) and some organisms with short lifespans like invertebrates, while riparian communities and fish populations can take longer to recover or document a signal from often noisy data. This Research Topic also highlights underappreciated restoration and responses of areas far from the location of large dam removal, such as coastal and subtidal ecosystems. This highlights the far-reaching, cross-boundary nature of restoration following dam removal and showcases broad linkages across ecosystems.

Despite our widespread advertising requesting submissions of large dam removal studies to be included in this Research Topic, only a small number were available to answer the call. The number of case studies, their geographic representation, and the temporal scale of impacts to river systems remains limited, highlighting the importance of continued research in the long term into this understudied area of river restoration. With such expansion, future synthesis efforts can draw from a larger pool of case studies, identifying unique features, generalities, and overarching lessons that can inform future practice and prioritization. Strategic implementation of comprehensive, long-term studies of key large dam removal efforts can be combined with efforts to document the location, focal species, dam characteristics, removal timeline, methods, costs, and associated drivers for all dam removal projects. Together such efforts could provide essential guidance to widespread efforts to restore river ecosystems and recover imperiled species.

Author contributions

RM: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. JD: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. LS: Conceptualization, Writing – original draft, Writing – review & editing. J-MR: Conceptualization, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research 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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Effects of large dams on the aquatic food web along a coastal stream with high sediment loads

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The contribution of two basal energy sources – detrital organic matter and primary producers – as part of aquatic food webs varies typically along river continua. A host of barriers to river flow increase the water residence time and sediment and nutrient retention in reservoirs worldwide, and potentially alter the balance between detritus-based and algae-based energy pathways in the downstream food webs. We explored this issue on the Sélune River (Normandy, France), a small coastal stream that drains an agricultural catchment with high sediment runoff. Seasonal measurements of the following parameters were compared upstream and downstream of the reservoirs of two large dams (16 m and 36 m high): sediment fluxes, nutrient and chlorophyll *a* concentrations, algal communities in the epilithic biofilm (taxonomic composition, biomass and growth), and benthic invertebrate communities (abundance and trophic guild structure). As anticipated, annual sediment fluxes were much lower downstream of the reservoirs, where significant decreases in water turbidity, phosphate and silicate concentrations were recorded. A higher chlorophyll *a* concentration in water and a higher contribution of pelagic algae taxa to the photosynthetic biofilm suggested drifting and deposition of reservoir-borne phytoplankton downriver. Photosynthetic biofilm growth was higher downstream of the reservoirs in spring and fall, and so was the abundance of herbivores in the invertebrate community, notably scrapers and algae eaters. Energy pathways within riverine food webs were traced using stable isotope analyses of carbon (C) and nitrogen in the tissues of aquatic consumers (invertebrates and fish). Mixing models revealed a discontinuity in the origin of the C entering the food webs along the river continuum, confirming a greater contribution of algal C to aquatic consumers downstream of the reservoirs. These results illustrate mechanisms whereby large reservoirs can modulate C flow in food webs along a small coastal river with high sediment loads, and make it possible to anticipate the effects of dam removal on the future river ecosystem.

KEYWORDS

nutrient concentrations, sediment fluxes, photosynthetic biofilm, benthic invertebrates, fish, stable isotope analysis, mixing models, carbon flow

1 Introduction

Two major energy pathways exist in river food webs. On the one hand, dissolved nutrients and inorganic carbon (C) fuel primary producers, namely phytoplankton, benthic algae and aquatic plants (Elser et al., 2007; Bumpers et al., 2017). The organic C resulting from photosynthesis is called autochthonous C. It is available to herbivores and other consumers at higher trophic levels, and fuels the algae-based pathway. The dissolved inorganic carbon (DIC) that enters this energy pathway is a mix of terrestrial (HCO_3 and dissolved CO_2 from chemical weathering, soils and groundwater), aquatic (ecosystem respiration) and atmospheric (diffusion of CO_2 at the air–water interface) sources (Mook and Tan, 1991; Finlay, 2003; Liu et al., 2011). Algae provide high-quality food resources to primary consumers (Guo et al., 2016a; Guo et al., 2016b), and the prevalence of algae-derived C in aquatic consumers has been reported in many river food webs (Mayer and Likens, 1987; Thorp and Delong, 2002; Lau et al., 2009; Brett et al., 2017). On the other hand, the detritus-based pathway involves primary consumers (fungi, bacteria and invertebrates) relying on dissolved or particulate organic C, notably fragments of dead plants, animals and feces. The available pool of detrital C is a combination of autochthonous C from aquatic organisms and allochthonous C from terrestrial ecosystem inputs, notably leaf litter from riparian trees (review by Marks, 2019). The influence of the detritus-based pathway on aquatic food web functioning is expected to vary along the river continuum. In theory, detrital C should prevail in headwater reaches receiving high allochthonous inputs from riparian trees ("river continuum concept" (RCC), Vannote et al., 1980). For instance, in small tributaries where a dense tree canopy strongly limits solar radiation, aquatic consumers mostly rely on C derived from riparian inputs (Roussel et al., 2021). According to the RCC, aquatic primary producers mostly support river food webs further downstream in intermediate reaches, while detrital and terrestrial C become dominant again in large rivers where primary production is hampered by water depth and turbidity. This pattern has been debated for large river ecosystems subjected to seasonal flooding, where macrophytes and/or floodplain plants can be a major C source in food webs ("flood pulse concept", Junk et al., 1989). Various case studies in the literature support different predictions on the predominant C sources and energy pathways in large river food webs (Hoeinghaus et al., 2007; Roach, 2013; Soto et al., 2019; Wang et al., 2021).

In addition to natural variations along the river continuum, human activities can modify the expected balance between the algae-based and detritus-based pathways in river food webs. By stimulating primary production, anthropogenic nutrient inputs – notably N and P – have major effects on freshwater ecosystems, including algal blooms (Galloway et al., 2004; Diaz and Rosenberg, 2008; Paerl et al., 2011; Penuelas et al., 2013). Such an increase of the primary producer biomass can reduce the DIC concentration, promote the diffusion of atmospheric CO_2 into the water (Portielje and Lijklema, 1995; Schindler et al., 1997), and ultimately change the origin of C cycling in aquatic environments (Brenner et al., 1999; Roussel et al., 2014). Anthropogenic nutrients from non-point-source pollution also change microbial activity on detrital C and its assimilation by primary consumers (Rosemond et al., 2015; Guo et al., 2016b) and modulate the detritus-based pathway. Another obvious impact of human activity on river food webs is observed when a large amount of organic waste offers alternative resources of high nutritional value to primary consumers in benthic invertebrate communities (Camargo, 1992; Guilpart et al., 2012) and enhances the detritus-based pathway downstream of the inputs (Roussel et al., 2018; de Carvalho et al., 2020). The algae-based and detritus-based pathways within river food webs are under the influence of a complex balance that depends on the position along the river continuum and anthropogenic pressures. Therefore, the origin of the C inputs at the base of river food webs and C flow to higher trophic levels can significantly change when the availability of detrital C and/or nutrients to aquatic organisms is altered.

A host of barriers constrain natural river flows worldwide (Grill et al., 2019). In a recent review, Belletti et al. (2020) concluded to a mean density of 0.74 barrier per kilometer of river in Europe. By creating impoundments, barriers to river flow increase the water residence time and have major consequences on the natural process of sediment transfer. Using satellite imagery analyses on major rivers, Dethier et al. (2022) estimated that dams have halved the global sediment flux from lands to seas in the northern hemisphere. Large dams and reservoirs can trap and store huge quantities of suspended materials, including detrital C that is no longer available to downstream river ecosystems, estuaries and marine coastal areas

(Syvitski et al., 2005; Zarfl and Dun, 2022). Moreover, large reservoirs affect nutrient biogeochemistry and strongly modulate the downriver transfer of dissolved nutrients (review by Maavara et al., 2020). Phosphorus (P) is essential to freshwater primary producers in its dissolved inorganic form, but uptake by phytoplankton in reservoirs alter its availability to downstream food webs (Lu et al., 2016; Bao et al., 2018). After decades of impoundment, sediments trapped in reservoirs contain large quantities of legacy P, which can be released through various physical and biogeochemical processes (Orihel et al., 2017). Similarly, the blooming and sinking of silica diatoms in reservoirs deplete the dissolved silicon (DSi) available downriver and in marine areas (Tréguer and de la Rocha, 2013) during specific periods of the year (Chen et al., 2014). The intensity of depletion is correlated with the water residence time in reservoirs (Ma et al., 2018). In some cases, large dams and reservoirs massively reduce all dissolved nutrients (P, N, DSi) down to the ocean (Gupta et al., 2021). The diversity of patterns reported in the literature outlines that the complex biochemical processes occurring in large reservoirs alter both particulate and solute fluxes, and in turn (theoretically) the balance between the algae-based and detritus-based pathways and C flow in downriver aquatic food webs. However, literature on this issue mostly relies on the study of dams and reservoirs on large rivers, but the ecological processes at play in small river catchments have retained less attention to date.

We explored the effect of two large dams and their reservoirs on aquatic communities and the energy flow in the food web of a small coastal stream – the Sélune River, an 85-km stream discharging into the Bay of Mont Saint-Michel (Normandy, France). In the early 20th century, two large hydropower dams (16 and 36 m high) were constructed in the lower third of the catchment, resulting in two consecutive reservoirs that covered 19 km of the initial river course. Agriculture is a dominant activity in the catchment; annual rainfall and erosion result in high quantities of suspended sediment and dissolved nutrients reaching the river (Fovet et al., 2020). In this context, we expected that high inputs of terrestrial organic matter and water turbidity would drive the aquatic ecosystem toward detritus-based functioning. We predicted that by hindering the transfer of suspended sediment, the dams and reservoirs could enhance the algae-grazer pathway and the contribution of algal C to aquatic biota downriver. Seasonal measurements of sediment fluxes, nutrient concentrations, photosynthetic activity, benthic algae and invertebrate communities together with stable isotope analyses of aquatic fauna were performed upstream and downstream of the reservoirs to test these assumptions. The broader goal of this work was to establish a baseline pattern of the food web of the Sélune River with its two reservoirs in order to evaluate river recovery after the scheduled removal of the two dams.

2 Materials and methods

2.1 Study site and context

The Sélune is a 85 km long river that drains a 1,083 km^2 watershed and flows into the Mont Saint-Michel Bay in Normandy

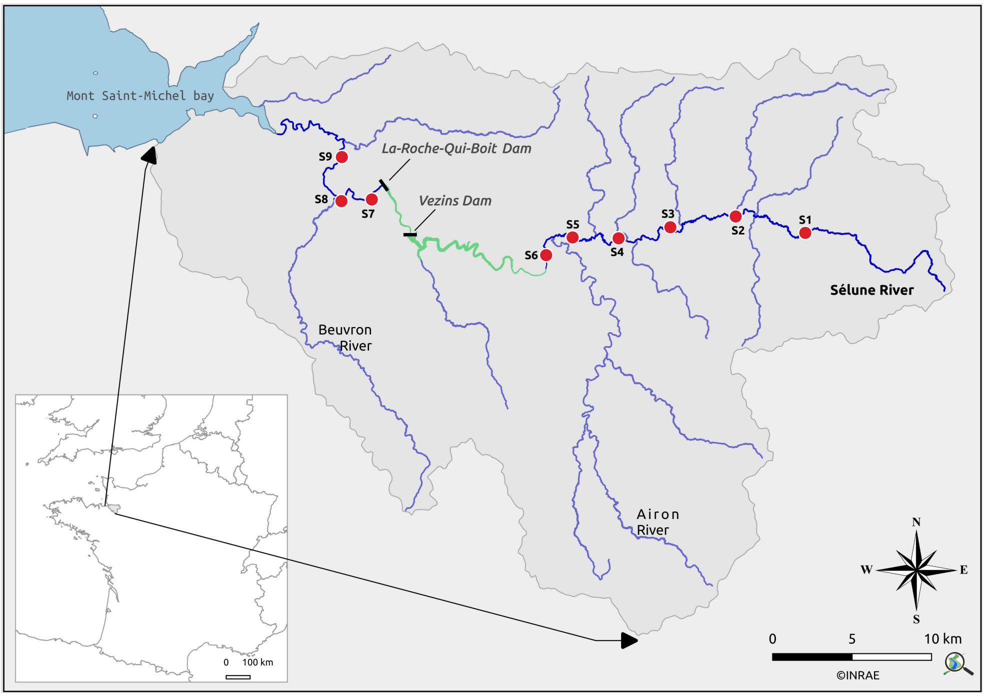

FIGURE 1
The Sélune River watershed, with two dams (black rectangles), two reservoirs (in green) and the study sites (red dots, S1 to S9). Distances, from source (0 km) to bay (85 km): S1 (15 km), S2 (23 km), S3 (29 km), S4 (34 km), S5 (39 km), S6 (42 km), Vezins dam (57 km), La-Roche-Qui-Boit dam (61 km), S7 (62 km), S8 (65 km), S9 (70 km).

(France) (Figure 1). Climate is oceanic, with mean annual rainfall of *ca*. 800 mm, and high and low flow periods occurring in winter and early fall, respectively. The median daily flow is 5 $m^3 \cdot s^{-1}$, the total monthly flow varies from 10^6 $m^3 \cdot month^{-1}$ during severe summer drought up to $120 \cdot 10^6$ $m^3 \cdot month^{-1}$ during high flood in winter (Fovet et al., 2020). The bedrock is composed of granite and Brioverian schist. Mixed crop–livestock farming covers 85% of the watershed area, with arable land covering 46% of this surface and grassland 39% (https://www.theia-land.fr/en/product/land-cover-map/). The watershed is vulnerable to soil erosion, hence high water turbidity and sediment loads are recorded (Vongvixay et al., 2018). In the early 20th century, two large hydropower dams (Figure 1) were built on the river: La-Roche-qui-Boit (16 m high and 125 m long, reservoir volume $90 \cdot 10^3$ m^3) and Vezins (36 m high and 278 m long, $18 \cdot 10^6$ m^3). Depending on the season, the mean water residence time varied from 1 to 4 days in La-Roche-Qui-Boit, and from 14 to 47 days in Vezins (Fovet et al., 2020). The two reservoirs covered a total distance of 19 km, which is more than 20% of the initial river course (Figure 1). Owing their volume, spatial coverage and high water residence time, they were considered as large reservoirs on such a watershed. Water in the reservoirs was nutrient-rich; the mean summer nutrient concentrations varied between 7.4 and 16.5 $\mu g \cdot L^{-1}$ P-PO_4 and between 4.0 and 5.3 $mg \cdot L^{-1}$ N-NO_3 along the water column (Fovet et al., 2020).

Considering the low hydropower capacity (27 GWh) of the two dams, potential safety issues because of the condition of their structure, periodic toxicity events in summer associated with cyanobacterial blooms in the reservoirs, and law on diadromous fish species, dismantling was decided by the French government in 2009. Operations started in spring 2017 by emptying Vezins reservoir, while dismantling of Vezins dam was completed by summer 2020. The same procedure for La-Roche-Qui-Boit started in 2021 and ended in early 2023. A long-term multidisciplinary scientific program (2012–2027) aims at evaluating the Sélune River restoration processes after dam removal (https://programme-selune.com). The present study is part of this program, and focuses on the pre-removal period, *i.e.* before spring 2017. The overall work took place at nine flowing sites located along the river continuum (Figure 1). For financial reasons it was not possible to record all variables (*i.e.* water discharge, sediment and nutrient concentrations, algal communities in epilithic biofilm and benthic invertebrate communities; see below for description) at each site. However, for each variable, the sampling design allowed comparisons between sites located upstream and downstream of the reservoirs. The choice of a site was constrained by specific criteria. For sediment and water chemistry, auto-samplers needed power supply and support made of concrete on bankside, whereas biofilm was studied with fragile glass slides installed mid-channel in sunny, shallow but not too fast-flowing habitats to avoid damage. For benthic invertebrate collection, we favored easily wadable sites with a great variety of substrates. An overall criterion was that the habitat conditions at upstream and downstream sites were as similar as possible for each variable. This explains why S5 or S6 (upstream), and S7 or S8 (downstream) sites were chosen depending on the variable to record (Figure 1). These sites (S5 and S6; S7 and S8) were very close (about 2 km) one from another, and we did not expect any bias coming out of this. The Airon tributary increases the Sélune River discharge between S5 and S6, but it does not cause major differences in dissolved nutrients as it drains an area with similar soils and land use pattern on the Sélune River catchment. Finally, we extended our sampling to eight sites for stable isotope analysis on animal tissues to get a clearer picture of food web shifts along the river gradient (see Section 2.5).

2.2 Sediment and solutes

Water, sediment and solutes were monitored at S6 (upstream the reservoirs) and S8 (downstream the reservoirs) from January 2015 to March 2017 (Figure 1). The water level, temperature and turbidity were recorded at a (sub-)hourly time step (1h at S6; 6 min at S8) using dedicated sensors (Hach Lange SOLITAX sc). Water discharge was computed from the measured water level using a rating curve established and kindly provided by DREAL 50 (State office in charge of hydrometric monitoring) and EDF (Electricité de France, the hydropower company). At both sites, grab samples were collected weekly, and ISCO autosamplers collected 10–20 samples (800 mL each) during storm events (see Fovet et al., 2020 for details). In the laboratory, a subsample from each sample was filtered at 0.45 µm on nitrate cellulose filters, dried at 105°C and weighed. The filtered volume (at least 350 mL) was measured to determine the suspended solids (SS) concentrations (EN 872:2005, 2005). A 30-mL aliquot of filtered water was used to measure NO_3 concentrations by ionic chromatography (Dionex ICS3000, EN 10304-1:1995, 1995), and dissolved silica (DSi) and orthophosphate (PO_4) concentrations by colorimetry (Seal Analytical AQ2, NF T 90-007:2001, 2001; EN 6878:2004, 2004). Another subsample was filtered at 0.45 µm on glass fiber filters and used for analyzing the carbon (C) and nitrogen (N) contents in SS particles using an Elemental Analyzer (Thermo Finnigan FLASH EA 1112).

Data were pooled by site (S6 and S8) and season: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Specific discharge was calculated by dividing the discharge values ($m^3 \cdot s^{-1}$) by the drained surface (629 km^2 at S6 and 777 km^2 at S8) to compare discharge between sites. The molar C:N ratio of SS was used as a proxy of the origin of particulate organic matter, considering that values above or below eight suggest terrigenous or phytoplanktonic origin, respectively (Hedges et al., 1997; Kendall et al., 2001; Balakrishna and Probst, 2005). We fitted a regression between the SS concentrations and the turbidity values at S6 and S8 to estimate the SS fluxes from turbidity time series. Regression coefficients and their 95% confidence intervals were used to compute instantaneous loads of SS and uncertainty associated with the regression coefficients, and then cumulated over the water years. “Site” (upstream or downstream the reservoirs) and “season” (winter, spring, summer and fall) effects were tested with two-way ANOVAs followed by Tukey’s *post-hoc* test ($p < 0.05$) on the following response variables: water discharge, turbidity, SS concentrations, the C:N ratio, phosphate, nitrate and dissolved silicon.

2.3 Phytoplankton and photosynthetic biofilm

Phytoplankton biomass was measured monthly at S5 (upstream the reservoirs) and S8 (downstream the reservoirs) by fluorescence using a multiparametric probe (Idronaut Ocean Seven 316Plus CTD, Milan, Italy) from January 2015 to October 2016. Water samples were collected monthly at the sub-surface and in mid-channel to measure chlorophyll *a* concentrations after filtration on Whatman GF/F glass-fiber filters and extraction overnight at 4°C in 90% acetone (Lorenzen, 1967). Absorbance was measured at 665 nm and 750 nm with a spectrophotometer, before and after acidification, following Lorenzen's method (Lorenzen, 1967).

The photosynthetic biofilm was studied from January 2015 to October 2016 on a monthly basis. Four glass slides (30 × 10 × 3 mm) were installed vertically in opened plastic boxes with perforated sides to allow water flow. The boxes were covered with a plastic mesh (2 cm mesh size) to prevent large debris from entering. They were anchored in the middle of the riverbed at S5 and S8, and the glass slides were changed every month, *i.e.* after one month of incubation (Biggs, 1988; Morin et al., 2008). The boxes were occasionally inaccessible due to high water flow, or damaged. However, we successfully retrieved glass slides in winter (once at S8), spring (six times at S5 and six times at S8), summer (six times at S5 and six times at S8), and fall (one and two times at S5 and S8, respectively). Chlorophyll *a*, ash-free dry mass (AFDM), taxa and photosynthetic activity were evaluated on separate glass slides.

For chlorophyll *a*, the glass slide was scraped on both sides using a razor blade to retrieve the biofilm, which was immediately stored in a plastic tube, kept in the dark in a cooling box in the field, and then freeze-dried in the laboratory. Overnight extraction with acetone was performed before spectrophotometric measurements following Lorenzen's method (Lorenzen, 1967). The chlorophyll *a* concentration ($\mu g \cdot L^{-1}$), the incubation duration and the glass slide surface were used to calculate the biofilm biomass increase in time, expressed in $\mu g \cdot cm^{-2} \cdot d^{-1}$. For AFDM, the biofilm was scraped in the same way as for chlorophyll *a*, oven-dried at 105°C for 48 h to get total dry mass (algae, bacteria, fungi, and detritus, in $g \cdot m^{-2}$), and then burnt for 1 h at 500°C to obtain AFDM. The percentage of organic matter was expressed as the AFDM:dry mass ratio. The photosynthetic biomass:total biomass ratio corresponding to the autotrophic index (Weber, 1973) was calculated to describe the trophic nature of the biofilm (autotrophic *versus* heterotrophic). For taxonomic identification, the biofilm was scraped off from the slide, immediately fixed in Lugol solution and kept in the dark at 4°C. Microalgae were identified and counted using a light microscope (Leica DM4000B) and a Nageotte counting chamber. Taxa were classified as benthic, benthopelagic, planktonic, or unknown according to the literature (Germain, 1981; Bourrelly, 1990; John et al., 2002; Rimet and Bouchez, 2012) and the Diatoms of North America online database (https://diatoms.org/).

Finally, we measured the photosynthetic activity of the biofilm on the fourth glass slide right after its removal from the river. Repeated measurements of fluorescence signals were performed using a four-wavelength-excitation pulse amplitude modulation fluorometer (Phyto-PAM, Heinz Walz® GmbH, Effeltrich, Germany) equipped with an emitter-detector fiberoptics unit. The fiber device was placed at 2 mm from the glass slide surface with a 4-cm diameter adapter to control irradiance. The PAM calculates photosynthesis as the relative electron transport rate (rETR) through photosystem II ($\mu mol\ e^{-} \cdot m^{-2} \cdot s^{-1}$) at different levels of light (Kromkamp and Forster, 2003). After 15 min of dark adaptation, rapid photosynthesis-light curves (RLC) were performed in triplicate with increasing light intensities (16 to 265 mmol $photons \cdot m^{-2} \cdot s^{-1}$), with a 20 s time interval (Jakob et al., 2005). The light-saturated maximum rETR was calculated by applying the nonlinear least squares regression model of Eilers and Peeters (1988) to fit the rETR-irradiance curves. "Site" and "season" effects were tested separately with two-way ANOVAs followed by Tukey's *post-hoc* test ($p < 0.05$) for chlorophyll *a*, AFDM, taxonomic identification and photosynthetic activity.

2.4 Benthic invertebrates

A Surber net sampler (0.05 m^2, 0.5 mm mesh size) was used to collect benthic invertebrates at S5 (upstream the reservoir) and S7 (downstream the reservoir) in fall (October 2014 and 2015) and spring (April 2015 and 2016), following the NFT 90-333 protocol and the Water Framework Directive (2000/60/EC). Twelve samples were collected *per* date and site to encompass the diversity of aquatic habitats in the river channel (96 samples in total, all dates and sites included). The samples were fixed with 96% ethanol and stored. In the laboratory, each sample was sorted under a binocular microscope, and taxa were identified down to the genus or species level (crustaceans, molluscs, insect larvae) or family/tribe levels (Diptera); Nematoda and Hydracarina were not identified further.

Following Tachet et al. (2010), two traits associated to invertebrate diet were considered: food items (9 modalities) and feeding behavior (8 modalities). For a given taxon and diet trait, an affinity score was assigned to each modality, ranging from "no affinity" (zero) to "high affinity" (3 for feeding behavior, 5 for food items). These values provide information on the intensity of the link between the taxa and each modality (*i.e.* low or high affinity) and the amplitude of the preference or tolerance of the taxon (*i.e.* the number of modalities used). We retained 8 modalities connected to the diet of primary consumer taxa for further analysis: deposit feeder, shredder, filter feeder, scraper (feeding behavior traits), small (<1 mm) and large (>1 mm) organic debris, and algae and macrophytes (food item traits). For each site and season, the diet trait modality affinities of the taxa (expressed as frequencies) weighted by their abundances were summed to determine the number of individuals in each modality at the community level (see Usseglio-Polatera et al., 2000 for further details). We run PERMANOVA on log(x +1) transformed data to test differences in community structure according to the diet traits (feeding behavior and food items). Then we tested for differences in the number of individuals in each modality to identify which modalities drove the difference observed for each diet trait, using non-parametric analysis of variance of aligned rank transformed data (Wobbrock et al., 2011) since the data did not meet the assumptions of parametric ANOVA. "Site" (2 levels), "season" (2 levels) and their interactions were considered in both PERMANOVA and non-parametric analysis of variance. The vegan 2.5-7 (Oksanen et al., 2020) and ARTool 0.11.1 (Kay et al., 2021) R packages were used for PERMANOVA and variance of aligned rank transformed data, respectively.

2.5 Stable isotope analysis

Primary and secondary consumers were sampled in summer (July 2014 and July 2015) at sites upstream (S1, S2, S3, S4, S5) and downstream (S7, S8, S9) of the reservoirs (Figure 1). A Surber sampler was used to collect benthic invertebrates, which were identified at the family level and sorted into three feeding behavior categories: herbivores, detritivores, and omnivores (see Table S1 for list of taxa) following Tachet et al. (2010) and Usseglio-Polatera et al. (2000). Each invertebrate was cleaned and stored individually in a microtube. For the smallest taxa, up to 10 specimens were pooled to reach the minimum weight for stable isotope analyses (see below). Six to 18 samples *per* feeding group were collected at each site and date, depending on availability. Small invertivorous fish were caught by electrofishing in shallow, coarse substratum habitats (see Table S1 for list of taxa). Depending on their availability, 10–30 individuals were collected at each site, their total body length ranging between 50 and 129 mm. Lamprey larvae were caught by electrofishing in the soft substrate habitats where they had buried; catch success and body length varied greatly among sites (1–10 individuals, 60–160 mm, respectively). Crayfish were caught by electrofishing at sites S1 and S5 only (60 and 54 samples, respectively, body length 15–41 mm from rostrum to telson). Fish and lamprey were anaesthetized using a benzocaïne bath, and all animals (fish, lamprey, crayfish) were euthanized and kept in a cooler in the field. The experiment complies with the French regulations on animal care and ethics (license number R-2012-JLB-02 and 201602051204637 delivered to INRAE) and electrofishing survey (permit number 2014-DDTM-SE-0036 and 2015-DDTM-SE-0019 delivered to INRAE).

Dorsal muscle (fish) or abdominal muscle (crayfish) samples were dissected in the laboratory, with special attention to avoid skin, scales and bones. Invertebrate and muscle samples were freeze-dried, ground to a homogenous powder using a mixer mill, weighed (*ca.* 0.9–1.1 mg) and encapsulated in tin foil. ^{13}C:^{12}C, ^{15}N:^{14}N and C:N ratios were measured by continuous-flow isotope-ratio mass spectrometry, using mass spectrometers (Delta Plus XP and Delta V Plus, Thermo Finnigan) interfaced with elemental analyzers (Carlo Erba NC2500 and Costech 4010, Thermo Finnigan). Isotopic ratios were expressed using the conventional δ notation as parts *per* thousand (‰). Five hundred and five samples were run in four separate batches. Repeat analyses of 12–15 certified standards showed maximum standard deviations (SD) of 0.29 ($\delta^{13}C$) and 0.38 ($\delta^{15}N$). Thirty-two samples were analyzed twice (*i.e.* 32 duplicates); the SD values of the duplicates were constantly lower than the SD values of the standards. All stable isotope analyses were performed at the Stable Isotopes in Nature Laboratory, University of New Brunswick (Canada).

C:N ratios were checked to identify possible lipid bias in $\delta^{13}C$ values (Post et al., 2007). When C:N ≥ 3.5, the $\delta^{13}C$ value was corrected using the equations of Post et al. (2007) for aquatic organisms. $\delta^{13}C$–$\delta^{15}N$ biplot and the standard ellipse areas (SEAc, sample size-corrected for $n < 30$) that integrated 75% of the sample variance (also called isotopic niche breadths) were drawn to visualize the isotopic niches of aquatic consumers upstream (S1 to S5) and downstream (S7 to S9) of the reservoirs, using SIBER (Jackson et al., 2011). The tRophicPosition package (Quezada-Romegialli et al., 2018) was used to estimate the trophic position of consumers and the discrimination factor between C of algal and detrital origins (α), *i.e.* the contribution of each C source to the feed of consumers. Calculations were based on Bayesian models using stable C and N isotopes and combined with Markov chain Monte Carlo simulations (60,000 iterations). A two-baseline model with trophic enrichment factors on C and N was run for each site separately, using isotopic values of herbivores (primary consumers of algal C) and detritivores (primary consumers of detrital organic C) as end-members. The diet-tissue fractionation values of +3.7 ‰ $\delta^{15}N$ between mixed invertebrate diet and fish proposed by Bunn et al. (2013) for streams and rivers, and of +0.4 ‰ $\delta^{13}C$ *per* trophic level (Post, 2002) were used. Because mixing models are highly sensitive to variations in discrimination factors (Bond and Diamond, 2011), we kept the high SDs (± 2.4 for $\delta^{15}N$ and ±1.3 for $\delta^{13}C$) proposed as priors in Bayesian models in the literature to better reflect uncertainties in posterior estimates.

3 Results

3.1 Sediment and solutes

The median seasonal values of specific discharge were similar downstream (S8) and upstream (S6) of the reservoirs (Figure 2A), in line with the dam management rules whereby the water flow downstream of the dams should mimic the natural flow variations recorded upstream. Median seasonal turbidity varied between 0 and 1098 NTU and was lower downstream (Figure 2B). Similarly, the seasonal suspended solid (SS) concentrations were 85–88% lower downstream (Figure 2C). R-square values for the fitted regressions between turbidity and SS were 0.96 and 0.84 at S6 and S8, respectively. Using regressions, the estimated sediment fluxes were 19.2 $t{\cdot}km^{-2}{\cdot}yr^{-1}$ (±11%) upstream and 11.6 $t{\cdot}km^{-2}{\cdot}yr^{-1}$ (±14%) downstream for the September 2015–August 2016 water year (Table 1). The average (± SD) C:N molar ratios of SS were higher upstream, notably in spring (11.1 ± 0.97 *vs.* 7.54 ± 0.83) and summer (9.43 ± 0.94 *vs.* 7.82 ± 1.47), indicating a greater contribution of phytoplankton-derived particles to organic matter in the SS downstream of the reservoirs (Figure 2D). The mean NO_3, PO_4 and DSi concentrations (Figures 2E–G) varied seasonally. P concentrations were significantly and systematically lower downstream ($p < 0.001$) except in winter, whereas between-site variations in N concentrations were not consistent. Similarly, DSi was lower downstream in all seasons except winter ($p < 0.001$).

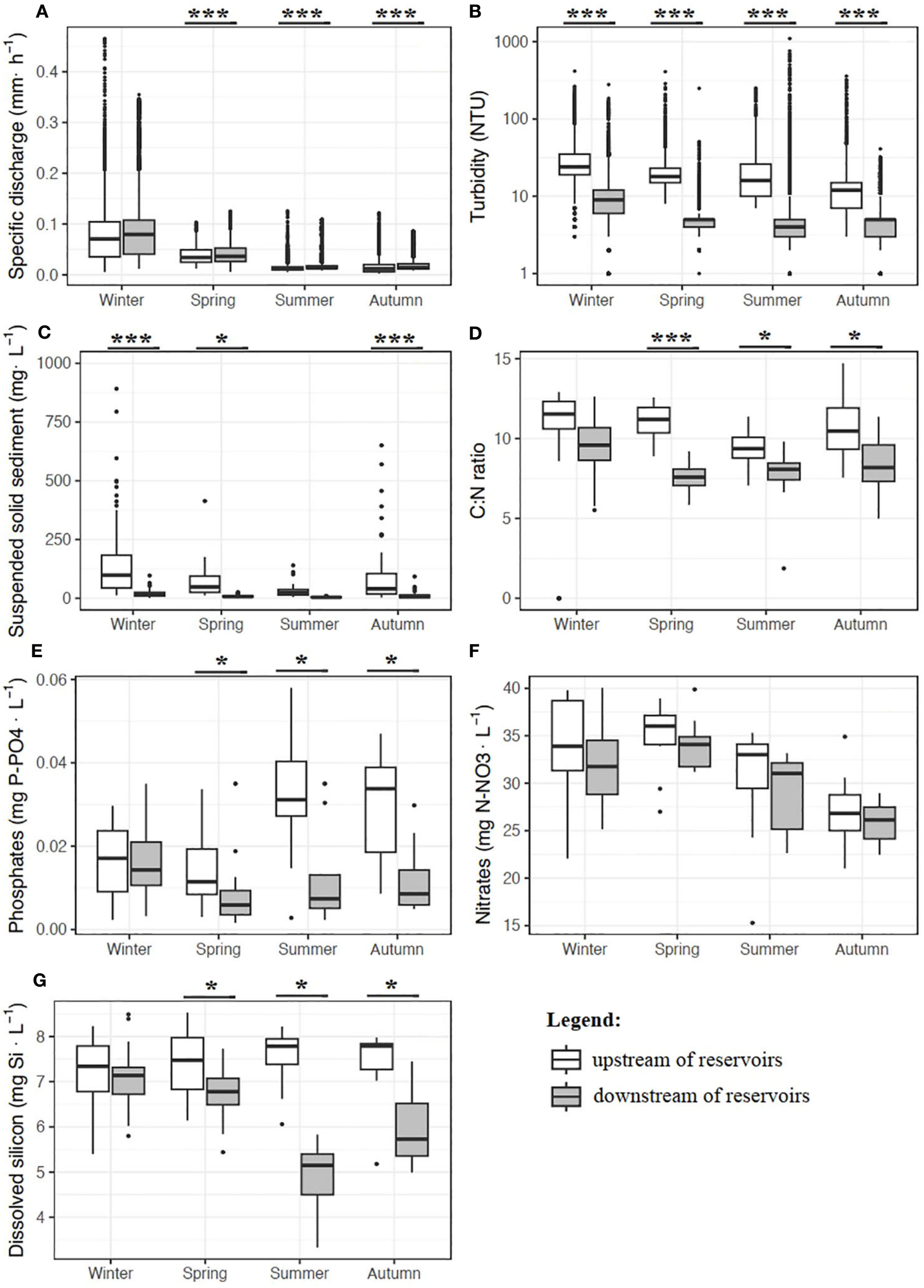

FIGURE 2
Seasonal variations of specific discharge **(A)**, water turbidity **(B)**, the suspended solid concentration **(C)**, the molar ratio of particulate C:N **(D)**, phosphates **(E)**, nitrates **(F)** and dissolved silicon **(G)** concentrations in the Sélune River, upstream (white) and downstream (gray) of the reservoirs. Each box plot shows the 25th and 75th percentiles around the median; vertical lines represent 1.5 times the interquartile range and dots are outliers. Stars indicate significant differences between upstream and downstream sites (***$p < 0.001$; *$p < 0.05$).

3.2 Photosynthetic biofilm

The chlorophyll *a* concentration in the water was higher downstream of the reservoirs irrespective of season, and the difference was significant in summer (Figure 3A; $p < 0.01$). The N:P molar ratio based on N-NO_3 and P-PO_4 concentrations ranged from 180 to 10,300 between sites and seasons (Figure 3B) and were significantly higher downstream of the reservoirs in summer and fall ($p < 0.001$), indicating potential P limitation for primary producers downstream. The percentage of organic matter in the biofilm samples was significantly lower upstream in spring ($p < 0.001$), indicating more inorganic sediment embedded in the biofilm matrix (Figure 3C). The biofilm algal community upstream of the dams mostly contained benthic species (85.6 ±

TABLE 1 Total rainfall and estimated runoff and sediment flux upstream and downstream of the Sélune River dams from January 2015 to March 2017.

	Total rainfall (mm)	Upstream dams (S6)		Downstream dams (S8)	
		Total runoff (mm)	Total sediment flux ($t{\cdot}km^{-2}$)	Total runoff (mm)	Total sediment flux ($t{\cdot}km^{-2}$)
Jan.2015–Aug.2015	522	248	12.8 (±11%)	311	5.2 (±18%)
Sep.2015–Aug.2016	758	355	19.2 (±11%)	443	11.6 (±14%)
Sep.2016–Mar.2017	324	61	1.5 (±17%)	76	0.5 (±29%)

Percentage values in parentheses represent the deviation between the mean and the 95% CI values estimated from linear regressions.

10.9%) and a few planktonic (2.9 ± 1.2%) and benthopelagic (6.1 ± 5.8%) species (Figure S2). Conversely, the contribution of planktonic and benthopelagic species increased downstream to average 8.2 ± 6.6% and 17.6 ± 19.4%, respectively (Figure S2). Algal biomass growth (chlorophyll *a*, $\mu g{\cdot}cm^{-2}{\cdot}d^{-1}$) and photosynthetic activity (maximum rETR, $\mu mol\ e^{-}{\cdot}m^{-2}{\cdot}s^{-1}$) in the biofilm decreased in fall and winter to reach values close to zero (Figures 3D, E). Biomass growth was higher in spring and fall downstream of the reservoirs, yet not significantly so. The maximum rETR values were very similar upstream and downstream of the reservoirs. Median values of the autotrophic index ranged between 1.9 and 2.3 in spring and summer upstream and downstream the reservoirs, indicating a biofilm where autotrophy and heterotrophy were balanced (Figure 3F), while values tended to increase toward heterotrophy in fall and winter upstream of the reservoirs ($p < 0.02$).

3.3 Benthic invertebrates

Irrespective of season, the abundance of benthic invertebrates caught in Surber net samples was higher downstream (12,273 individuals in spring; 17,267 in fall) than upstream (8,927 in spring; 6,613 in fall). A total of 45,080 individuals were sorted and identified. Among them, 39,653 (88.0%) and 36,332 (80.6%) were identified as primary consumers according to their feeding behavior trait (deposit feeder, shredder, filter feeder, scraper) or food item trait (small or large organic debris, algae, macrophytes), respectively. The most influential taxa are listed in Table S3.

The community structure of invertebrate primary consumers significantly differed between sites for the food item trait (PERMANOVA, Site pseudo-F = 15.26 and p = 0.001; Season pseudo-F = 1.41 and p = 0.2; Station × Season pseudo-F = 0.69 and p = 0.5) and for the feeding behavior trait (Site pseudo-F = 16.59 and p = 0.001; Season pseudo-F = 1.28 and p = 0.2; Station × Season pseudo-F = 1.0 and p = 0.3) but not between seasons (Figure 4). Primary consumer taxa were significantly more abundant downstream than upstream of the reservoirs, regardless of the modalities and traits (analysis of variance on aligned rank transformed data, see Table 2). No significant seasonal variation was detected except for filter feeders that were more abundant downstream the reservoirs in fall only. Scrapers and algae eaters were the two most abundant modalities found among primary consumers irrespective of season.

3.4 Stable isotopes and food web analyses

The isotopic values of the samples collected along the Sélune River ranged from –21.3‰ to –32.6‰ and from 0.8‰ to 16.9‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (Figure 5A). Invertebrate herbivores (grazers and scrapers pooled) were consistently ^{13}C-depleted compared to detritivores (shredders), while omnivores and crayfish displayed intermediate values. As expected, invertivorous fish were ^{15}N-enriched compared with invertebrates. The isotopic niche breadths (ellipses including 75% of the variance) upstream of the dams (sites S1 to S5 pooled) and downstream of the dams (sites S7 to S9 pooled) mostly overlapped for invertebrates but not for fish and lamprey (Figure 5A).

Using invertebrate herbivores and detritivores as end-members for Bayesian mixing models, invertebrate omnivores showed trophic positions of 2.5, and C of algal and detrital origin equally contributed to their tissues (Figure 5B). Crayfish followed a similar pattern, with a slightly higher trophic position (2.7). Simulations confirmed that fish had the highest trophic position (>3), and revealed that fish and juvenile lamprey shifted toward a higher algal-C contribution downstream of the dams. Posterior distributions of coefficient α at each site showed that detrital C dominated in aquatic fauna only at the most upstream site S1, whereas algal C prevailed downstream of the dams at S7 and S8, and equal contributions of detrital and algal C were observed at S2, S3, S4, S5 and S9 (Figure 5C).

4 Discussion

In the study, we explored the mechanisms whereby two sequential large dams and their reservoirs can control the balance between detritus-based and algae-based energy pathways in aquatic food webs along a river continuum. Investigations were made on the Sélune River (Normandy, France), a small-coastal stream draining an agricultural catchment with high sediment runoff and discharging into the Mont Saint-Michel Bay (France). The river has been impounded by two dams (16 and 36 m high) in its lower part for a century. As anticipated, the two reservoirs significantly retained sediments, phosphates and silicates for which concentrations were much lower downstream of the reservoirs. There were no large tributaries flowing into the reservoirs, nor was there a specific land use pattern in the vicinity of the reservoirs, that could have influenced water discharge and dissolved nutrient

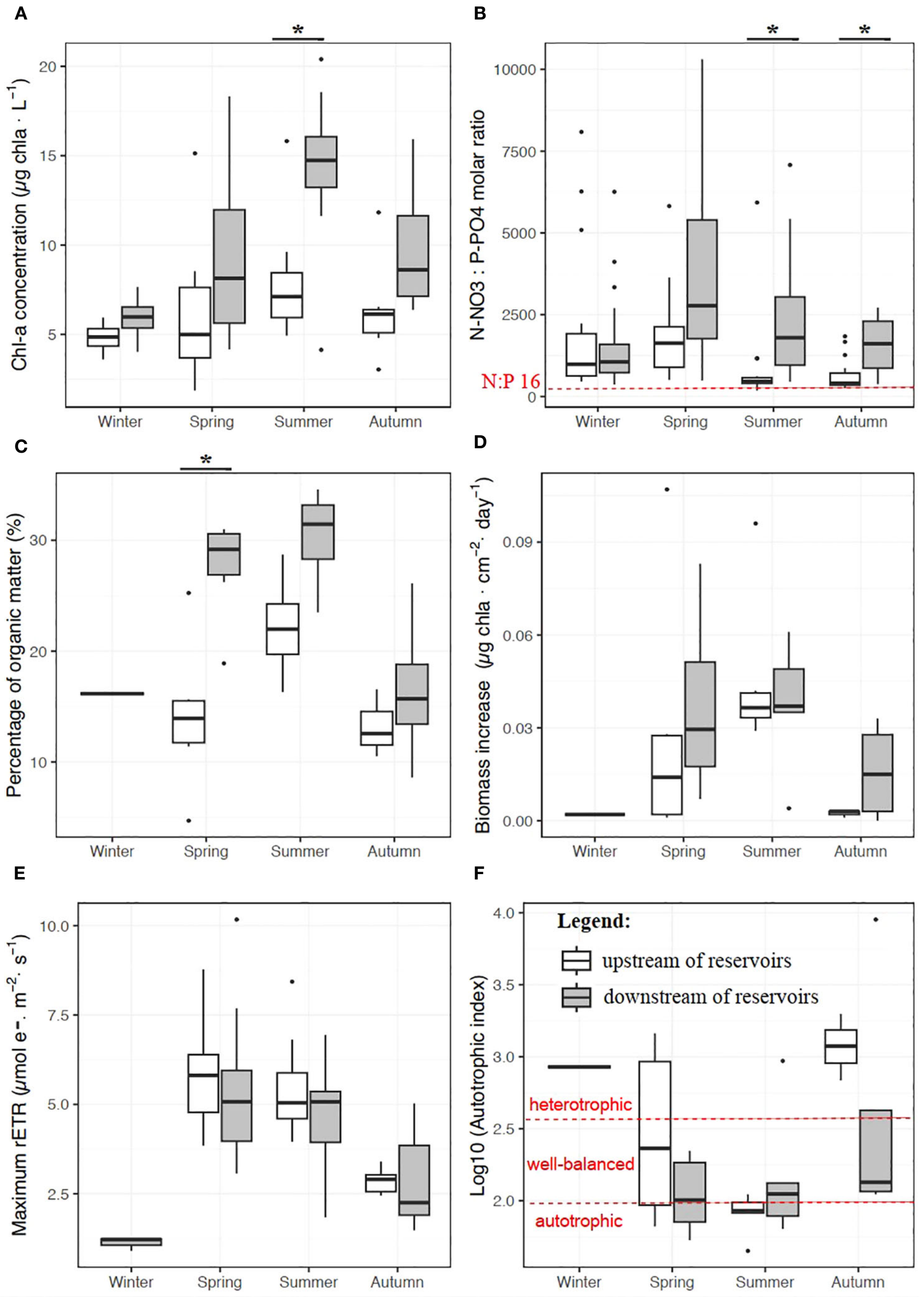

FIGURE 3
Seasonal variations of the chlorophyll *a* concentration in water **(A)** and of the dissolved N:P molar ratio based on N-NO_3 and P-PO_4 concentrations **(B)**, and, for the photosynthetic biofilm: the percentage of organic matter **(C)**, the biomass increase per day **(D)**, photosynthetic activity **(E)** and the autotrophic index **(F)** in the Sélune River, upstream (white) and downstream (gray) of the reservoirs. Stars indicate significant differences between the upstream and downstream sites (*$p < 0.05$).

concentrations. Measures of the photosynthetic activity in epilithic biofilm showed no clear differences, but their biomass growth tended to be higher downstream of the reservoirs in spring and fall, and so was the abundance of herbivores in the benthic invertebrate community. A greater contribution of algae-based energy to aquatic invertebrates and fish downstream of the reservoirs was corroborated by stable isotopes analysis, clearly suggesting that the dams caused a major discontinuity in the origin of C entering and flowing in aquatic food webs along the river continuum.

Identifying the relative importance of different energy sources is a basic prerequisite for understanding river food web dynamics and ecosystem restoration. Aquatic primary consumers rely on two major basal sources defined by the origin of their C component – aquatic (autochthonous) or terrestrial (allochthonous) primary producers. The contribution of these two C sources to higher

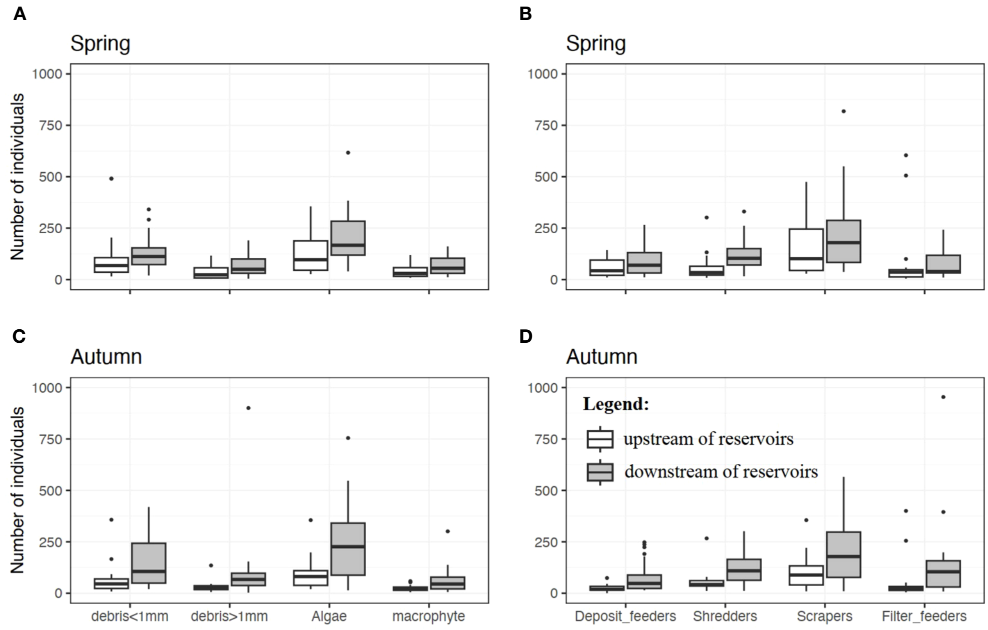

FIGURE 4
Abundance of invertebrate primary consumers in the Sélune River upstream (white) and downstream (gray) of the reservoirs. Box-plots display the spring **(A, B)** and fall **(C, D)** values according to the food items they ingest **(A, C)** and their feeding behavior **(B, D)**. Each box-plot shows the 25th and 75th percentiles around the median; the vertical line represents 1.5 times the interquartile range, and dots are outliers.

trophic levels, notably fish, depends on the position along the upstream–downstream gradient (Vannote et al., 1980; Finlay, 2001; Hoeinghaus et al., 2007). Several studies have illustrated significant contributions of terrestrial C to small headwater streams and large rivers, where terrestrial organic matter inputs from riparian trees (headwater streams) and floodplains (large rivers) supply the aquatic food webs (Reid et al., 2008; Wang et al., 2014; Soto et al., 2019; Roussel et al., 2021; Wang et al., 2021). Seasonal variations in discharge, local stream geomorphology and riparian communities also drive the food web reliance on C sources (Ou and Winemiller, 2016; Venarsky et al., 2020), outlining the complex balance of allochthonous and autochthonous C supply to the biomass of primary consumers and transfer to higher trophic levels. In this context, artificial barriers to river flow and related impoundments have major effects on the downstream ecosystem metabolism. Chowanski et al. (2020) observed that the gross primary production in a large, temperate, oligotrophic river increased downstream of a large reservoir, and postulated that sediment retention and lower water turbidity downriver increased light availability to aquatic producers. Such a pattern seems to be commonplace in literature on dams. In Mediterranean rivers, artificially stable flow regimes below dams promoted a shift from detritus-based to algae-based food webs (Mor et al., 2018). In large tropical rivers as in the Mekong basin, a seasonal combination of algae and terrestrial energy sources supports fish production, but the contribution of algal C appears greater below dams (Ou and

TABLE 2 Analysis of variance (aligned rank transformed data) of the food items and feeding behavior of benthic invertebrates showing the effect of "site" (upstream or downstream of the dams), "season" (spring or fall) and their interaction.

Food items	Organic debris, large (>1 mm)		Organic debris, small (<1 mm)		Algae		Macrophytes	
	$F_{1,90}$	p	$F_{1,90}$	p	$F_{1,90}$	p	$F_{1,90}$	p
Site	12.80	**0.0006**	23.51	**<0.0001**	15.94	**0.0001**	12.52	**0.0006**
Season	0.10	0.7	0.51	0.5	0.003	1	1.56	0.2
Site x Season	1.11	0.3	0.77	0.4	1.19	0.3	0.06	0.8
Feeding behavior	Deposit feeder		Shredder		Filter feeder		Scraper	
	$F_{1,90}$	p	$F_{1,90}$	p	$F_{1,90}$	p	$F_{1,90}$	p
Site	10.19	**0.002**	32.30	**<0.0001**	18.0	**<0.0001**	7.68	**0.007**
Season	2.88	0.09	2.29	0.1	3.95	**0.05**	0.47	0.5
Site x Season	0.01	0.9	2.33	0.1	4.27	**0.04**	0.15	0.7

Significant p-values are in bold.

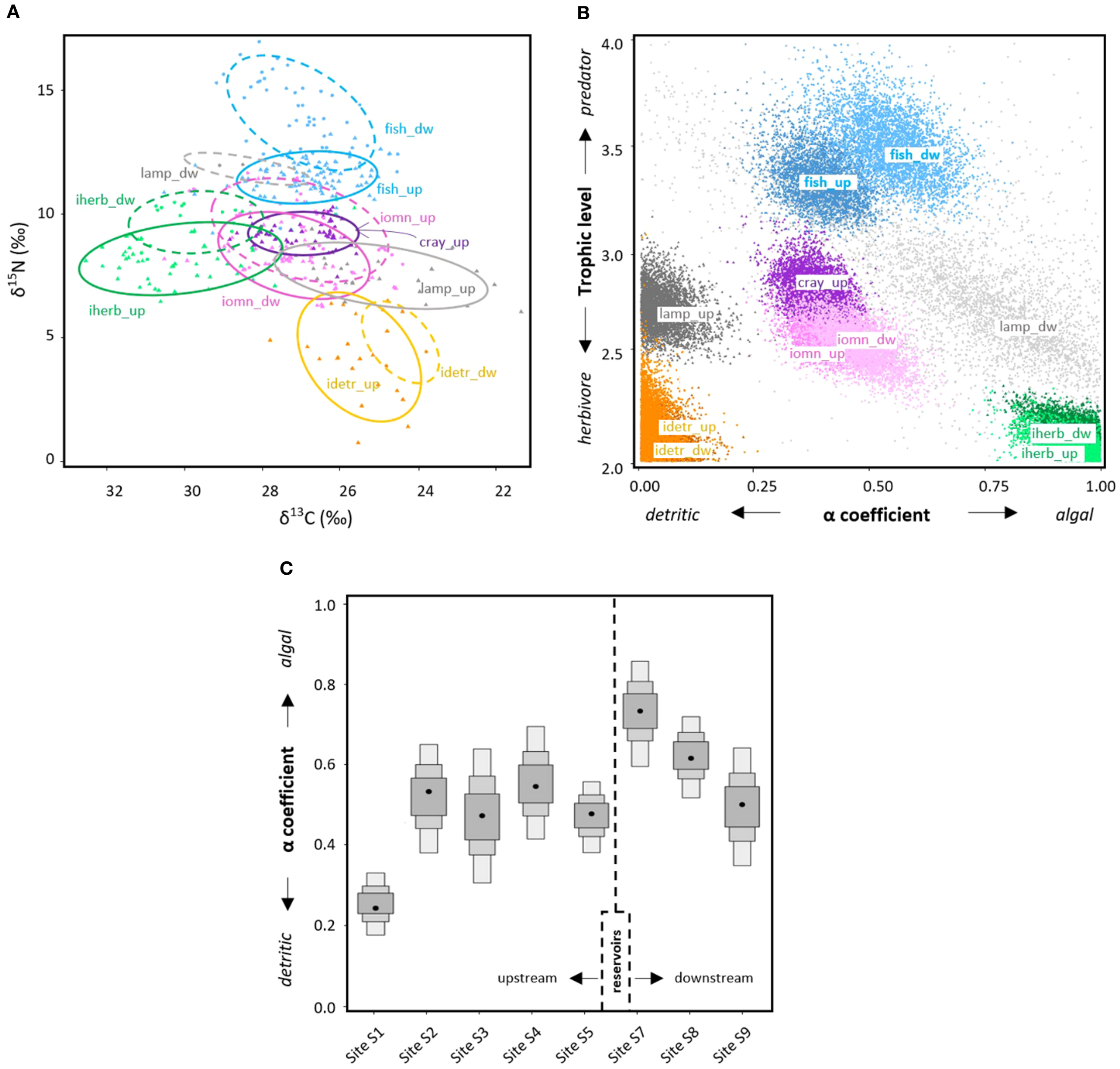

FIGURE 5
δ^{13}C and δ^{15}N values of samples collected in the Sélune River **(A)**. Isotopic niche breadths (SEAc) of each invertebrate consumer group (iherb, herbivores; idetr, detritivores; iomn, omnivores), crayfish (cray), lamprey (lamp) and fish are depicted for sites located upstream (up, solid ellipses) and downstream (dw, dashed ellipses) of the dams. Simulated values of the trophic position and carbon-origin discrimination coefficient (α) obtained from end-members Bayesian mixing models for consumers upstream and downstream of the dams **(B)**. The dual contributions of algal *vs.* detrital C origin to aquatic fauna is displayed along the Sélune River profile **(C)**, each box indicating 50%, 75% and 95% Bayesian credibility intervals around the median (dot); the dashed line shows the position of the reservoirs.

Winemiller, 2016). Similarly, algae contribute more to the diet of macroinvertebrates in the Colorado River below Glen Canyon dam, while terrestrial-based food increases further downstream with increasing water turbidity and organic matter inputs from tributaries (Wellard Kelly et al., 2013). Various case studies in both temperate and tropical ecosystems highlight a shift toward greater assimilation of algal C by aquatic consumers downstream of reservoirs in large rivers. However, little attention has been given to the pattern of C flow in small stream food webs below such large reservoirs.

Carbon and N stable isotope ratios of invertebrate and fish tissue samples were used to estimate the contribution of basal sources supporting aquatic food webs along the course of the Sélune River. Using long-lived (>6 months) primary consumers in mixing models to limit stochastic isotopic signatures of basal sources (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999), we found a 3-fold variation in the contribution of the algal energy pathway within a 70-km-long stretch of river. At 15 km from the source, 75% of the food web C was derived from terrestrial detritus assimilated by invertebrate shredder species, notably Limnephilidae (*Halesus* sp., *Chaetopteryx* sp., *Limnephilus* sp., *Potamophylax* sp.) and Sericostomatidae (*Sericostoma* sp.). Consistent with theory (Vannote et al., 1980; Junk et al., 1989; Finley 2001; Hoeinghaus et al., 2007), this result confirms the dominant role of terrestrial supplies in the upstream reaches of the Sélune River (Site S1, Figures 1, 5C). However, the contribution of algal C equalled the detrital contribution at most sites, indicating that autochthonous and allochthonous sources of energy together sustained aquatic food webs in most of the river course. This result was somehow unexpected owing to the high sediment load and water turbidity in the river supposed to hamper primary production. Our simulations may have exaggerated the contribution of algae-derived C in the river food webs because we collected our samples in shallow, fast-flowing habitats where primary production is known to be at its maximum in rivers (Finlay, 2004). However, many studies have shown that agriculture in industrialized countries is a major source of nutrients in rivers and coastal waters, involving a number of effects including the increase in biomass of primary producers (*e.g.* Paerl et al., 2011; Grizzetti et al., 2012; Dupas et al., 2015; Boardman et al., 2019). Accordingly, the high concentration in nutrients is a favorable background to aquatic primary producers in the Sélune River, and this likely promotes the influence of the algae-based pathway in aquatic food webs despite high water turbidity and sediment loads.

The annual flux of sediment estimated in the Sélune River upstream of the reservoirs (19.2 $t.km^{-2}.yr^{-1}$) is consistent with the observed pattern of European Atlantic rivers with a similar catchment size (Vanmaercke et al., 2011). Despite greater uncertainty about the sediment load estimates downstream of the dam where suspended sediment quantities were sometimes very low and more difficult to measure accurately, the annual flux of sediment dropped (11.6 $t.km^{-2}\cdot yr^{-1}$) downstream of the reservoirs. This corresponds to an amount of 12,077 $t\cdot yr^{-1}$ and 9,013 $t\cdot yr^{-1}$ upstream and downstream of the dams, respectively, meaning that the reservoirs trapped and stored about $3\cdot 10^3$ tons of sediment from September 2015 to August 2016. With 758 mm rainfall, this water year was consistent with the inter-annual variability observed on the river. One immediate consequence was a drastic drop in water turbidity downstream of the reservoirs irrespective of season (Figure 2B) that set off a chain reaction in the entire river food web, from epilithic biofilm to invertivorous fish. The percentage of inorganic sediment in the epilithic biofilm samples was lower downstream of the reservoirs. Seasonal biofilm dynamics were substantial everywhere, with higher biomass and productivity in spring and summer. Biofilm growth on a virgin glass support measured as the increase in chlorophyll *a per* day was slightly, but not significantly, higher downstream than upstream of the reservoirs in spring and fall. Moreover, the trophic nature of the biofilm estimated using the autotrophic index (Weber, 1973) remained similar to the autotrophic threshold downstream irrespective of season, whereas heterotrophy prevailed upstream of the reservoirs in fall. This result was corroborated by measurements of the C:N molar ratio of suspended sediment. The ratio of organic matter exported from soils was close to the expected values (Kendall et al., 2001) upstream of the reservoirs, but it strongly decreased downstream in spring and summer when solar radiation, water turbidity and water temperature were most favorable to primary producers. It indicates that the reservoirs produced a fraction of organic matter – algae-derived C drifting downstream – as also supported by continuous monitoring of the chlorophyll *a* concentration in the water column downstream of the reservoirs (Fovet et al., 2020), hence the presence of pelagic forms (notably diatoms) in the epilithic biofilm matrix downriver. Therefore, the composition of the epilithic biofilm differed remarkably downstream of the reservoirs as a response to lower water turbidity, siltation, and the input of pelagic microalgae drifting from the reservoirs.

In the Sélune River, the higher abundance of herbivores (algae eaters, scrapers) within invertebrate communities downstream of the reservoirs suggests an enhancement of the algal pathway. The shift from detritivores to herbivores in invertebrate communities has been reported in river food webs downstream of large reservoirs (Mor et al., 2018). Stable isotope analysis of aquatic consumers, invertebrates and fish, gives support to this assumption. We estimated that an average 75% of the C flowing into the river food web 1 km downstream of the reservoirs was derived from aquatic primary producers, *i.e.* + 25% compared to the river food web just upstream of the reservoirs. This effect was still perceived 4 km downstream of the reservoirs (60% of algae-derived C in the food web) and stopped further downstream where equal contributions of autochthonous and allochthonous C were found. Phytoplankton that drifted from the reservoirs and deposited on the epilithic biofilm likely contributed to higher algal C contribution in the downstream food web, as reported in other studies (Angradi, 1993; Hoeinghaus et al., 2007; Doi et al., 2008; Ru et al., 2020). According to methodological recommendations (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999), invertebrate primary consumers (herbivores and shredders) were used in our mixing models, and it was not possible to estimate the contribution of a specific basal food sources (*i.e.* phytoplankton *vs.* phytobenthos). However, nine kilometers downstream of La-Roche-Qui-Boit reservoir (Site S9, Figure 1), equal contributions of algal C and detrital C to aquatic consumers were reported, meaning that the effect of the dams on C flow in the aquatic food webs had disappeared. This suggests that terrestrial-based food sources increased in the lower reaches of the Sélune River, outlining the possible influence of organic matter inputs from downstream tributaries, notably the Beuvron River (Figure 1).

In our analysis, values of nutrient concentrations, benthic algal and invertebrate communities and stable isotope ratios on aquatic organisms were considered jointly, revealing subtle interactions between C and nutrient biogeochemical cycles in the Sélune River. It also outlines mechanisms whereby large dams and reservoirs can affect these cycles and food web functioning in a small agricultural stream. Primary producers rely upon dissolved inorganic C (DIC) that originates from the terrestrial ecosystem (*e.g.* HCO_3 and dissolved CO_2 from chemical weathering and soils), respiration of the aquatic ecosystem, and diffusion of atmospheric CO_2 into water (Mook & Tan, 1991; Finlay, 2003; Liu et al., 2011). During photosynthesis, algae preferentially assimilate ^{12}C (Hecky and Hesslein, 1995), but when productivity is high and DIC concentration is depleted, less discrimination against ^{13}C can lead to higher $\delta^{13}C$ values in primary producers. Moreover, a lower DIC concentration can promote the diffusion of atmospheric CO_2 into water. Since the $\delta^{13}C$ value of atmospheric CO_2 is high (about −8‰, Keeling et al., 2010), primary producers are expected to be ^{13}C-enriched in more productive rivers (Roussel et al., 2014). In the Sélune River, the contribution of algal C to aquatic food webs was higher downstream of the reservoirs, but we did not find higher

δ^{13}C values in herbivorous invertebrates (Figure 5A). Fluorescence measurements on the epilithic biofilm did not reveal higher photosynthetic activity downstream of the reservoirs, and it is likely that the observed higher algal-C contribution to the aquatic food web downstream of the reservoirs was a consequence of a lower detrital-C contribution rather than higher primary production. Indeed, both PO_4 measurements and the N:P molar ratios in water samples showed that phosphorus availability decreased downstream of the reservoirs. Phosphorus is essential to freshwater primary producers, but the blooming and sinking of phytoplankton in reservoirs can massively reduce its availability to downstream food webs during specific periods of the year (Chen et al., 2014; Lu et al., 2016; Bao et al., 2018), notably in large reservoirs where water residence time is high (Ma et al., 2018). Therefore, we argue that low phosphorus availability restricted primary production in reaches downstream of the reservoirs in the Sélune River, despite less water turbidity and better light availability. Taken together, those results illustrate how large reservoirs on a small, agricultural stream with high nutrient concentrations and sediment loads could affect the balance between the algae-based and the detritus-based energy pathways, and modulate C flow in the riverine food webs from primary producers to predators.

Finally, our study outlines some of the drivers of the reliance on different C sources in the food web of a small, coastal stream with high sediment loads. We notably highlighted mechanisms whereby large dams and reservoirs can induce a major discontinuity in the natural process of C flow in aquatic food webs and along the river continuum. By changing the downstream transfer of suspended particulate matter and dissolved nutrients, the two dams on the Sélune River artificially maintained environmental conditions that promoted the contribution of the algae-based pathway the riverine food webs. This conclusion comes from data and samples collected between 2015 and 2017, before the removal of the two dams. The dismantling operations were completed by early 2023, and the downstream transfer of sediment and solutes are being restored after a century of disruption (Fovet et al., 2023). Profound impacts on the river ecosystem are expected from now, and our results will help understand how nutrients and C flow in food webs will change during the river restoration process. We anticipate that the prevalence of algal C in aquatic consumers should fade out rapidly downstream of the reservoirs. Except in the upstream reaches and headwater tributaries where detrital C may prevail, equal contributions of algal and detrital C to the aquatic food web should be observed along the Sélune River continuum. Moreover, the expected return of diadromous species, *e.g.* Atlantic salmon and sea lamprey (*Salmo salar*, *Petromyzon marinus*), will disseminate marine-derived nutrients throughout the watershed, as observed in the Elwha River and the Penopscot River (Duda et al., 2011; Tonra et al., 2015; Zydlewski et al., 2023). European eel (*Anguilla anguilla*) will also colonize the headwaters, and this species is known to have a large impact on other fishes in the Sélune River (Lizé et al., 2023). These new driving forces will require attention in order to understand how the river ecosystem and the aquatic food webs will be restored along the Sélune River over the next decade.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by "Comité rennais en matière d'éthique et d'expérimentation animale". The study was conducted in accordance with the French legislation and institutional requirements on animal care and ethics.

Author contributions

J-MR conceived the idea, supervised the project and wrote the manuscript. OF and AC (sediment and solutes), AP and CG (photosynthetic biofilm), HR-P and CP (macroinvertebrates) and J-MR (stable isotopes and food web) designed the project, collected the samples, co-supervised the work and wrote the corresponding text sections of early drafts. MP, CG, GF, DH contributed to data and sample collection in the field, processed the samples in the laboratory and prepared the data. OF, CG, AP, HR-P, OD and J-MR analyzed the data, prepared the illustrations, and revised the manuscript. AT and MC developed and managed the geographic information system SISélune; SF and LS managed the project. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1250892/full#supplementary-material

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Early assessment of effects of dam removal on abiotic fluxes of the Selune River, France

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The Water Framework Directive set for European Union countries the objective of restoring the ecological and/or sediment continuity of rivers, as the latter is relevant for providing suitable habitats for the former. Indeed, abiotic fluxes and variables shape riverine ecological habitats and are likely to be modified by barriers such as dams. Two dams were removed from the Selune River (northwestern France) from spring 2017 to summer 2022. The objective of this study was to describe and quantify how the dams modified abiotic parameters and fluxes, as well as the dynamics of these fluxes during dam removal. We monitored coarse and fine sediments, water temperature and nutrient concentrations in the Selune River from upstream to downstream of the dams from 2015 to 2023. The results showed that coarse sediments of the riverbed are a legacy and that current hydrodynamic conditions are not sufficient to move them much, with or without the dams. In addition, it appears that at this early stage after the removal some downstream parameters, especially nutrient concentrations and water temperature, have already converged towards upstream signals, while fine sediment stored in the dam's reservoirs are still destocking. Restoring ecological continuity of the Selune River will involve dynamics of abiotic parameters over longer time scales, in response to removal of the dams, and over larger spatial scales, in response to climate and other global changes.

KEYWORDS

sediments, biogeochemistry, water temperature, nutrients, river restoration

1 Introduction

Many environmental policies, such as the Water Framework Directive set for European Union (EU) countries the objective of restoring river ecological and sediment continuity. Dams, especially large ones, alter the geomorphology of rivers by deposition of bed and suspended sediments upstream from them which causes a sediment deficit that commonly leads to incision and development of a river bed sediment coarsening (pavement) downstream from them (Kondolf, 1997; Brandt, 2000; Rollet et al., 2014). However, predicting effects of dam removal on geomorphology remain difficult because i) these effects depend on local configurations (Foley et al., 2017a), ii) few references are available (Bellmore et al., 2017) and iii) time scales of response are uncertain but likely to be on the order of decades (Pizzuto, 2002; Graf, 2005). The recovery trajectories are known to be dynamic and likely to lead to ecological conditions similar or different to the ones before impoundment (Bellmore et al., 2019). A meta-analysis on dam removal studies over the United States that include pre-removal and post-removal data emphasized the large influence of landscape features on the biophysical response to dam removal and highlighted the limitation of our understanding due to a limited range of landscapes in the existing studies (Foley et al., 2017b).

Based on data from dam removals in the United States (United States), Foley et al. (2017a) concluded that physical variables generally changed rapidly after the removal of large dams, and that physical connectivity quickly became effective again. In the Elwha River (United States), dam removal was managed to use the river to naturally erode and transport sediments (Warrick et al., 2012). After 2 years of monitoring this emblematic removal operation, Warrick et al. (2015) estimated that 90% of the sediments initially stored in the former reservoir had been flushed to coastal waters, some of which had been deposited in the river's mouth. They also observed that the deposition was dominated by coarse and sandy sediments, but also contained large amounts of fine sediments. Additional monitoring for the next 3 years showed that the first 2 years contained most of the sediment and geomorphic signal (Ritchie et al., 2018). Dam removal is expected to reverse the disturbances the dam created by eroding sediments stored in the upstream reservoir and transporting and depositing them in downstream reaches (Brandt, 2000; Doyle et al., 2005). Fine sediments are expected to respond more rapidly than coarse sediments (Doyle et al., 2005). Dams influence river water temperature greatly (Poirel, 2010; Olden and Naiman, 2010). Depending on how reservoir water is released, downstream water can be either cooled (release of deep layers of stratified water) or warmed (release of the surface layer). Reservoirs also tend to smooth out daily and/or annual temperature variations (Ward, 1985). These disturbances of the thermal signal are observed directly downstream of a reservoir and can persist for several tens of km depending on factors such as the structure of the dam or riparian vegetation cover (ZaidelCaissie, 2006; 2021).

Other abiotic parameters are also likely to respond strongly to dam removal (Bednarek, 2001; Doyle et al., 2005), such as nutrients that are retained by dams, including nitrogen (N) (mainly due to denitrification) (Stanley and Doyle, 2002; von Schiller et al., 2016) and phosphorus (P) (usually trapped in reservoirs) (Doyle et al., 2003; Fovet et al., 2020). Geomorphologic changes can modify these retentions by modifying particle deposition (and thus P retention), the extent of the water-sediment interface, the size of particles and the potential to denitrify N (Stanley and Doyle, 2002; Doyle et al., 2003). For instance, 14 days after dam removal in the Chishui River (China), Lei et al. (2023) observed an increase in P concentration and a decrease in N concentration, suggesting higher N retention soon after the removal, when active erosion was observed. Doyle et al. (2003) concluded that removing small dams from the Koshkonong River (United States) decreased P retention in the reach that contained the former reservoir, but did not stop it completely, and increased the P concentration downstream. Bohrerova et al. (2016) measured concentrations in the reach of the Olentangy River (United States) upstream of the Fifth Avenue Dam before and after it was removed, and highlighted higher in nitrate concentrations and lower phosphate concentrations when the impounded portion was restored as running water. Velinsky et al. (2006) observed no significant effects of a small dam on Manatawny Creek (United States) or its removal on the concentrations and forms of carbon (C), N or P; they concluded that the residence times were too short and the thermal stratification too weak to influence nutrient cycling. Abbott et al. (2022) monitored dissolved oxygen concentration continuously for 3 weeks in summer at 15 river sites in the United States before and after removal of their small dams; they found that the reservoir's oxygen signal returned to the upstream reference at 80% of sites within 1 year of the removal. Riggsbee et al. (2012) used experiments to quantify nutrient fluxes before and after removal of a dam on the Little River (United States) and identified that vegetation had a significant influence on N and P leaching during the first growing season after removal and that it likely would have a larger influence in the long term.

These studies of effects of dam removal on abiotic parameters are less common than those of effects on biotic parameters (Pizzuto, 2002; Bellemore et al., 2017), limited in space (reservoir and downstream), or limited to a few abiotic parameters, especially sediment dynamics (Warrick et al., 2012; Foley et al., 2017a; Basilico et al., 2021). The present study's objective was thus to measure the response of a variety of abiotic parameters, including coarse and fine sediments, temperature and nutrient concentrations, to the removal of two consecutive dams on the Selune River, a lowland low-energy river in northwestern France. This study provided 1) reference data on effects of dam removal, 2) evidence to help interpret and understand the processes involved in ecological restoration of the Selune River after dam removal and 3) a complete monitoring program that helped understand abiotic parameters, especially sediment dynamics.

2 Materials and methods

2.1 Study site

The Selune River flows for 91 km into the Bay of Mont Saint-Michel (Figure 1). It drains a watershed area of 1,083 km^2 and once had two hydroelectric dams: Vezins and Roche-Qui-Boit (RQB) (36 and 16 m high, respectively) (Table 1). The watershed's climate is oceanic, with a low temperature amplitude and rainfall distributed throughout the year. The annual mean (± standard deviation) rainfall is 794 (±209) mm (2015–2022). Rainfall is highest in December (111 ± 68 mm) and lowest in July (39 ± 29 mm). Rainfall and evapotranspiration variations cause seasonal fluctuations: a period of high flow in winter and low flow in summer. Mean monthly discharge at Ducey (39°38′22.4545″E, 12°13′9.7918″S, WGS84) is equal to 10.9 m^3 s^{-1} in average and varies between 4 m^3 s^{-1} in September and 21.1 m^3 s^{-1} in February.

The watershed's Armorican bedrock consists of Brioverian sedimentary formations in the center (schists and sandstones) surrounded by granitic layers to the north and south (Cadomian). Due to the low permeability of this substrate, groundwater bodies are particularly shallow, which results in hydromorphic soils in bottomlands. The hillsides have well-drained Cambisols. Most slopes are moderate and less than 3%, but can reach 13% in the river gorge and in the valleys of some tributaries. The watershed is dominated (89% of the area) by agriculture, with arable land and grassland for mixed (summer/winter) crops and livestock.

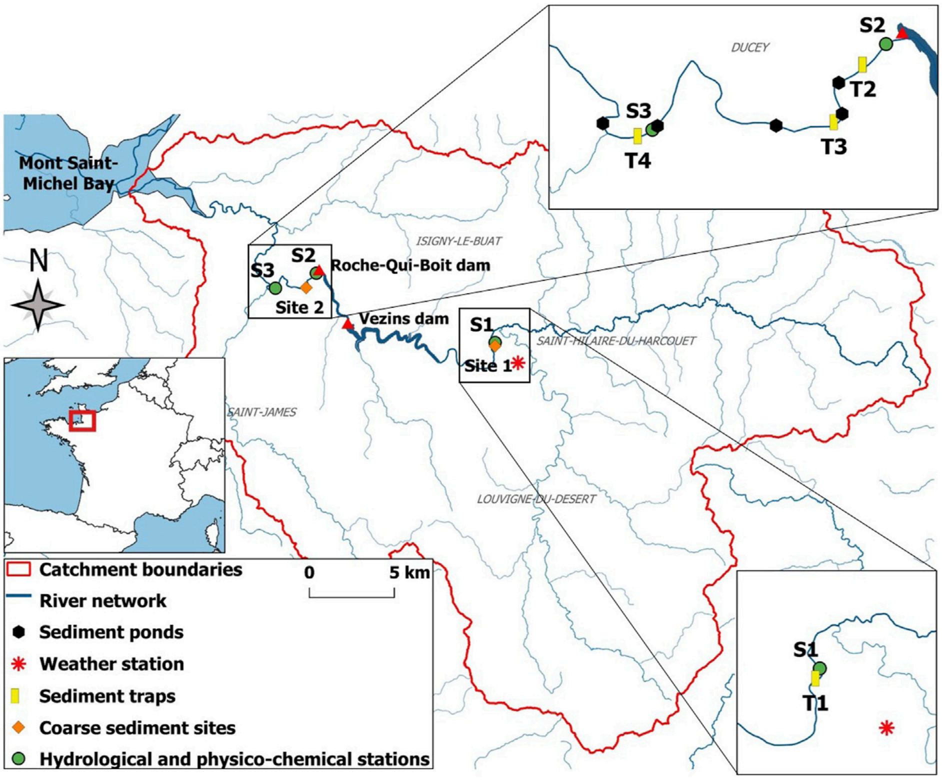

FIGURE 1
Map of the Selune River watershed and location of stations. The inset maps show only sediment traps and ponds.

TABLE 1 Characteristics of the 2 dams removed from the Selune River, from (SEPIA CONSEIL, 2002). Mean residence times were computed by averaging over each period the daily residence times obtained by dividing the reservoir volume (in m^3, measured and provided by the dam manager) by the average daily discharge measured downstream the dam (in m^3.day^{-1}, measured by us or the dam manager).

Characteristic	Vezins	Roche-Qui-Boit
Year of construction	1932	1919
Surface area (km^2)	1.70	0.29
Maximum volume of the reservoir (m^3)	18,000,000	90,000
Maximum depth of the reservoir (m)	31	16
Mean depth of the reservoir (m)	12.0	3.1
Mean residence time of the reservoir (days)	14 (Nov.-Apr.)	1 (Nov.-Apr.)
	47 (Jun.-Sept.)	4 (Jun.-Sept.)

In 2009, the French government decided to remove the 2 dams. Removal operations on the Vezins dam began in March 2017, and the dam was dismantled from April 2019 to June 2020. The RQB dam was dismantled from June 2022 to January 2023. Hydro-sedimentary continuity of the river was effective in May 2022.

The amount of sediments stored in the 2 dam reservoirs was estimated as 1,800,000 m^3 (IDRA, 2012). To keep this massive amount of sediments from moving and clogging the river downstream, much of it was dredged and stored in ponds built with gabions and dykes made from *in-situ* sediments (Berrée, 2019). After the reservoirs had emptied and the sediments had dried, the gabions were removed. To our knowledge, this kind of sediment management using heavy civil engineering was unprecedented in the history of dam removal (French Water Agency, personal communication; Germaine and Lespez, 2017; Schiermeier, 2018).

A multidisciplinary scientific program (https://programme-selune.com/fr/) was established in 2012 to assess impacts of removal of the dams on the river and its restoration. An observation network was established in 2015 to monitor physical and chemical parameters and fluxes of water, sediments and dissolved elements.

2.2 Coarse-sediment measurement and transport monitoring

Coarse sediments of the riverbed were traced using 150 RFID transponders. Two injection sites were selected, one upstream of the Vezins dam (site 1) and the other downstream of the RQB dam (site 2) (Figure 1). Difficulty in accessing certain sections (in particular because of the steep valley), preference for sectors with shallow water to allow for prospection on foot and difficulty in finding sites without direct human influence (i.e., weirs) led us to select sites with slightly different geomorphological characteristics. Site 1 had a significantly lower slope than site 2 (Table 2).

TABLE 2 Characteristics of the coarse-sediment tracing sites upstream of the Vezins dam (site 1) and downstream of the Roche-Qui-Boit dam (site 2).

Site	1	2
Watershed area (km^2)	627	761
Slope (m.m^{-1})	0.0007	0.0018
Bankfull width (m)	17.1	21.0
Specific stream power (W.m^{-2})	15.22	39.80

Sediments equipped with a transponder had a median particle size similar to that measured at the two sites (D50 of 39–55 mm). Only particles smaller than 22 mm, which represented 10% (site 1) and 23% (site 2) of the particles on the riverbed, were too small to be used. Tracers were injected in July 2015 along 2 transects at the 2 sites, spaced 20 cm apart, taking care to mimic the natural intermingling of the sediments as well as possible. Thus, 50 and 100 tracers were injected at sites 1 and 2, respectively. They were surveyed annually, over seven water years from 2015 to 2022 (denoted P0 to P6 in Figure 2), and their location was recorded using DGPS (Differential Global Positioning System). Given the diameter of the detection antenna (50 cm) and the precision of DGPS (3 cm after processing), the mean margin of error, after several tests, was 1 m. We thus considered the tracers that moved more than 1 m per year to be mobile.

Travel distances were measured using GIS. The locations of the tracers were projected on a central line of the channel, and only the longitudinal movements were measured. Given the low representativeness of the movements recorded during the first year after injection (due to the risk of overexposure of sediments and imperfect nesting), only monitoring results obtained beginning in August 2016 are presented. The hydrological characteristics of the monitoring periods were obtained from the Signy measuring station S3 (described below) (Figures 1, 2).

2.3 Monitoring physico-chemical variables and fluxes

The monitoring scheme is the result of a collaboration between research units, the EDF group that was in charge of energy production via the dams, and the Regional Directorate of the Environment (DREAL 50). Two stations, one upstream and one downstream of the dams (Figure 1), have been equipped with sensors since 2015 to continuously monitor the water level (pressure sensor with ceramic cell PLS, OTT HydroMet), water temperature (PLS, OTT HydroMet), turbidity (Solitax ts-line sc, 0.001-4000 FNU/NTU, TSS: 0.001 mg L^{-1}–50 g L^{-1}, HACH) and conductivity (C4E, 4 electrode measurement, AQUALABO). River discharge was estimated using a rating curve established for each station by DREAL 50. The upstream station, Virey (S1), which

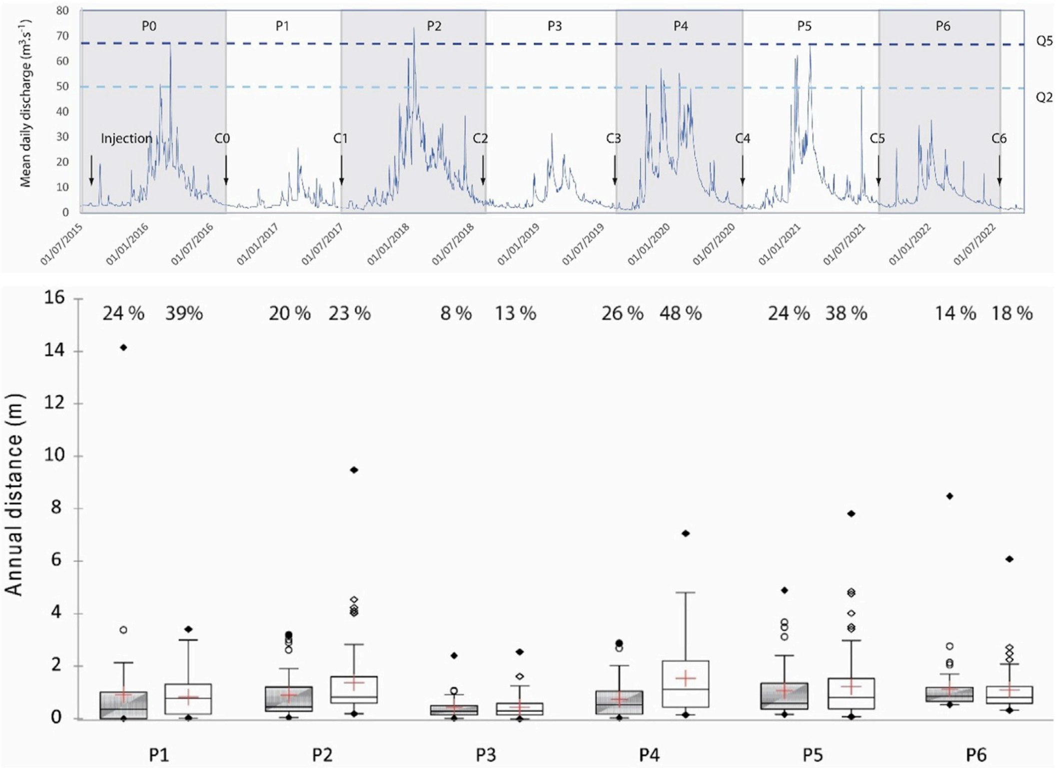

FIGURE 2
(top) Stream flow dynamics during the monitoring period and tracer-monitoring surveys (C0-C6) performed at the end/start of hydrological years (P0-P6) and (bottom) tracer mobility results at the upstream site (Site 1 - Virey) (grey box plots) and downstream site (Site 2 - Pont de Bateau) (white box plots) for each survey. The percentages over the box plots indicate the annual sediment mobility rate. Whiskers indicate 1.5 times the interquartile range.

is managed by EDF, is located 14.7 km upstream of the Vezins dam and drains a watershed area of 629 km^2. Its sensors take measurements every 1 h. The downstream station, Signy (S3), which we managed, is located 4 km downstream of the RQB dam and drains 777 km^2. Its sensors take measurements every 6 min. Turbidity and water-level data from the EDF station located immediately downstream of the RQB dam (Pont de Bateau, S2), whose sensors take measurements every 1 h, were also used in this study.

Since 2015, 1 L grab-samples of water have been taken once per week at the upstream and downstream stations (S1 and S3). These stations also have automatic samplers (ISCO) that sample several flood events per year. These samples are analyzed at the analytical laboratory. Of each sample, 500 mL are filtered at 0.45 µm, dried and then weighed to determine the concentration of suspended sediments (SS) (ISO, 2019b). From half of the samples, a subsample is filtered through a fiberglass membrane and then used to measure C and N concentrations using an elemental analyzer (CN FLASH EA 1112, Thermo Finnigan). For each sample, a bottle of unfiltered water is used to measure the total P concentration via colorimetry (ISO, 2018). Finally, for each sample, a subsample is filled with 0.45 µm filtered water to measure the concentrations of major ions (Cl^-, NO_3^- SO_4^{2-}) via ionic chromatography (ICS-3000, DIONEX) (ISO, 2021) and PO_4^{3-} (ISO, 2018), ammonium (ISO, 2019a) and dissolved silica (Si) (AFNOR T90-007) by colorimetry (SmartChem 200, AMS Alliance). Since April 2022, ca. 28 grab-samples of water have also been taken at station S2, four of them during flood events, to measure concentrations of SS. Hourly rainfall data were provided by Météo France from the station in Saint-Hilaire-Du-Harcouet (no. 50484002).

2.4 Data analysis

2.4.1 Data acquisition and treatment

This study examined different phases of the removal project. For the pre-removal period, data from 2015 to March 2017 were used. The dams had not yet been completely dismantled, but hydro-sedimentary continuity of the River Selune was recovered (May 2022) when most of the RQB dam was removed. Monitoring continues, and measurements collected until 1 March 2023 were included in this study. However, emptying of the reservoir behind the RQB dam (from 15 May to 1 September 2022) displaced a large volume of stored sediments. This period was therefore considered separately when analyzing the turbidity signal and calculating sediment loads.

The high-frequency data acquired by the sensors were visualized, examined and validated using the OTT software Hydras 3 (version 2.91.0). Punctual outliers due to factors such as micro-cuts (i.e., shorter than 30 min) were removed and replaced by the mean of the previous and subsequent values. If a sensor drifted for several hours or days, the period was removed. For station S3, hourly time series were extracted from the original data (6-min measurements) for homogeneity with the other stations. For concentrations of chemical elements measured by laboratory analyses, extreme values below or above the 1st and 99th percentiles, respectively, were removed.

Statistical analyses were performed using the *stats* package (version 4.2.2) of R software (version 4.2.2) (R Core Team, 2022). Graphs were made using the *ggplot2* package (version 3.4.1).

2.4.2 Relation between suspended sediment concentration and turbidity

Turbidity represents the cloudiness of water due to SS smaller than 1 mm in size. It is related mainly to the concentration of SS (SSC) but also on the size and type of the particles. Turbidimeter probes are more sensitive to concentrations of fine particles, while measurements of SSC are related mainly to the mass of suspended loads (Thollet et al., 2013). Fine suspended loads were calculated from high-frequency turbidity measurements using a relation calculated between *in-situ* measurements of SSC and turbidity. To establish this equation between turbidity and SSC, a simple linear regression was used (see, *e.g.*, Minella et al., 2007; Gray and Landers, 2014; Vongvixay et al., 2018):

$$\mathrm{SSC}\,[\mathrm{mg/L}] = \mathrm{a} \times \mathrm{tubidity}\,[\mathrm{NTU}] + \mathrm{b} \tag{1}$$

where a and b are the coefficients of the calibration equation.

One SSC-turbidity relation was determined per station by selecting relevant events: a regression was calculated for each flood event and selected for the station's regression if its coefficient of determination (R^2) exceeded 0.6. Uncertainty in the calibration equations was calculated as a 95% confidence interval. As the removal operations (e.g., sediment management, dismantling) may have directly influenced the downstream station, data from the pre-removal and removal periods were separated, and one SSC-turbidity relation was determined for each.

2.4.3 Monitoring the emptying of the reservoir behind the RQB dam

Sediment loads at station S3 from 15 May-1 September 2022 were calculated separately from those for the rest of the year, for several reasons. First, the turbidity during the emptying was higher than that usually observed (up to 1,400 nephelometric turbidity units). Second, the particles resuspended by removing the dam likely differed from those that crossed the RQB dam. Finally, a large amount of turbidity data (ca. 1 month in total) was missing at S3 during this period due to technical problems and because the probe became buried under massive sediment deposits. During this period, sediment loads were estimated at the two stations downstream of the dam (S2 and S3) to estimate the amount of sediment that left the dam immediately and that was deposited along the 4 km between the two stations.

A SSC-turbidity relation was established for each station from the samples from this period (6 SSC-turbidity pairs for S2 and 26 for S3). The turbidity data were then divided into four periods (i.e., phases) that had different dynamics: increase, plateau, recession and stabilization. When turbidity data were missing, we used a relation between SSC at stations S2 and S3 established from SS data of the same phase. The mean temporal shift between the two stations, estimated as 3 h, was considered in this relation (Supplementary Figure S1).

2.4.4 Measurement of sand and suspended-solid particle sizes

To highlight effects of dams on the particle-size distribution of sediments that moved downstream, one of two protocols was applied depending on the mode of movement. For SS, water samples at S1 and S3 were analyzed before and after dam removal. The particle-size distribution of SS was measured using a laser particle-size meter (CILAS 1180). Before measurement, each sample was passed through a 1 mm sieve, and an H_2O_2 solution was added to dissolve the organic matter. Once dissolved, a hexametaphosphate solution was added to prevent particles from aggregating, and an ultrasonic treatment was applied to the bath of the particle-size meter for 1 min.

To sample sediments that moved a few cm above the riverbed, we built sediment traps that were fixed to the riverbed and collected every 2 weeks if the water level was sufficiently low. The traps were made from plastic bottles, which slowed the water flow. Each bottle contained a honeycomb structure that trapped the sediments that passed through. As the inlet of the bottle had a diameter of 3 cm, only small gravel or sand could be trapped, but in practice, the largest sediment caught was a few mm in size. The sediment caught in each trap was dried in an oven and then passed through a set of 6 sieves (from 50 to 2 mm). Traps were installed at S1 in September 2021, before hydro-sedimentary continuity had been restored, and at T1-T4 after May 2022, to assess sediment trapping by large pools downstream of RQB (Figure 1). As the velocity of water passing through the traps was not measured, the sand concentration or mass flow could not be calculated. The size of sand particles in the traps was thus considered as a qualitative indicator of the size of particles that moved near the riverbed.

3 Results

3.1 Coarse sediments are a legacy and moved little

Hydrological conditions varied greatly during the monitoring period. The 2 years flood - Q_2 (50.3 m^3 s^{-1}) was exceeded during 3 of the 6 observation periods, and the 5-years flood - Q_5 (67.2 m^3 s^{-1}) was exceeded during 2 of the periods. However, no extreme flows (decennial or greater) were recorded after injecting the tracers (Figure 2). The tracers' recovery rates during the surveys (92%-100%) were much higher than those reported in the literature, due to their low mobility, regardless of the site or period considered (Figure 2). Despite floods at which morphogenic processes can theorically occur (>2 years flood), all mobility rates were lower than 40%, which indicated partial mobilization of the bottom of the riverbed, even for flows that reached those of a 5-year flood. Once mobilized, 75% of the tracers moved less than 2 m y^{-1}. Even when considering the maximum distances, mobility behaviors differed little among periods and did not exceed 15 m. Despite this low mobility, hydrology and tracer mobility were correlated. The median distances were slightly higher during periods P2, P4 and P5, which experienced either more intense floods (P2 and P5) or more frequent floods (P4). Mobility rates and annual distances changed simultaneously at both sites as a function of discharge, which appeared to be the dominant controlling factor (Figure 2). Finally, sediment had slightly higher mobility at site 2 than at site 1 due to the difference in specific stream power.

3.2 Water temperature and solute concentrations recovered their upstream signals quickly after removal

Water temperature usually increased from upstream (S1) to downstream (S3), especially in summer (Figure 3), and the usually negative difference between them (S1 minus S3) decreased in 2022 once the Selune River flowed freely (Figure 3). In autumn and winter (September to March), the mean difference in water temperature between S1 and S3 relative to mean water temperature at S1 was −9.8% for the pre-removal period and 0.61% for the 2022-2023 hydrological year. Variations in water temperature at S3 were also much lower during the pre-removal period, with a mean daily relative amplitude (i.e., daily maximum minus daily minimum, divided by the daily mean) equal to 11.6%, while for 2022–2023 it reached 18.8% (Figure 3A).

Before the dams were removed, nitrate and dissolved Si concentrations differed between stations S1 and S3, while after removal, concentration dynamics at S3 rapidly converged towards those at S1 (Figure 4). The concentration dilutions observed for all flow events at S1 were absent at S3 before removal but became similar after removal (Figure 4). Baseline concentrations were slightly lower at S3 than at S1 in spring/summer for nitrate and much lower for dissolved Si. These baseline concentrations differed between S1 and S3 in summer 2015 (29.8 vs. 28.4 mg NO_3. L^{-1} and 7.6 vs. 5.2 mg Si. L^{-1}, respectively) and summer 2016 (34.1 vs. 31.0 mg NO_3. L^{-1} and 7.6 vs. 4.2 mg Si. L^{-1}, respectively). Such differences did not occur after dam removal began, since the dissolved concentrations at S3 became similar to those at S1. In contrast, river discharge differed little between the two stations (Figure 4).

3.3 Toward full recovery of sediment transfer

3.3.1 Impact of the dams on sediment loads

Before the dams were removed, SS and turbidity signals at S3 were lower than those at S1 (Figure 5; Supplementary Figure S2). In particular, SSC usually peaked during storm events at S1, while no peaks were observed regularly at S3 before May 2022. Only the most intense storm events increased turbidity and SSC at S2 and S3. Similarly, the annual suspended load varied from 4,089–41,954 t (6.6–66.6 t km^{-2} y^{-1}) at S1 and 1,476–14,297 t (1.9–18.8 t km^{-2} y^{-1}) at S3, proportional to the annual rainfall and specific runoff (Figure 6; Supplementary Figure S3). On average, 73% (±6%) of the suspended load was stored in the reservoirs from 2015 to 2021. This estimate did not consider fluxes of sand (>50 μm) that moved near the riverbed, since the monitoring equipment could not quantify this component of the sediment flux accurately. However, reservoirs effectively trap sediments larger than 20 μm. Analysis of the SS particle-size distribution at S1 and S3 highlighted that sediment larger than 20 μm did not cross the dams (Figure 7). Assuming that 10% of the total volume of sediment (1,800,10^3 m^3) that settled in the

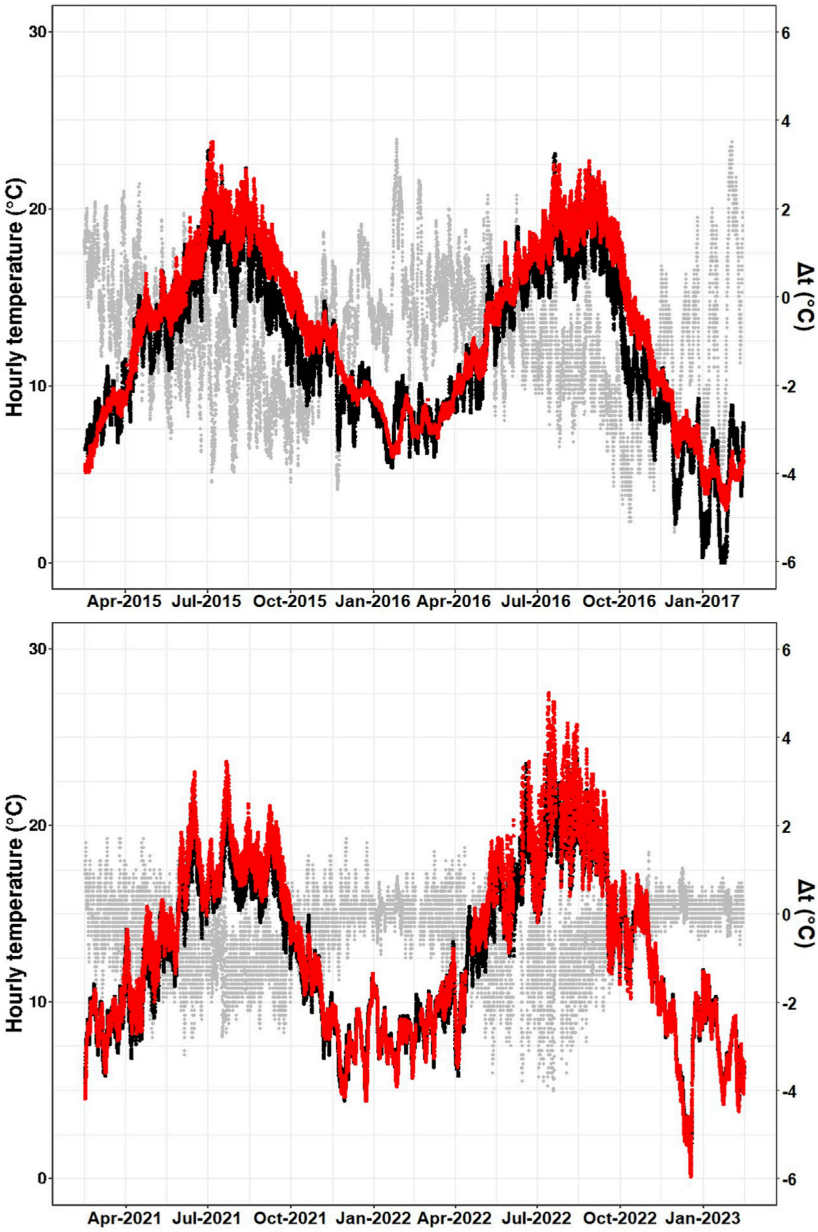

FIGURE 3
Water temperature at stations S1 (black dots) and S3 (red dots), and the difference between them (S1 minus S3) (grey dots), for the period (top) before dam removal (2015–2017) and (bottom) after dam removal (2021–2023).

two reservoirs in the past 90 years was larger than 50 µm (IDRA, 2012), the annual sand flux at S1 could be estimated. Based on sample data (IDRA, 2012) and a sediment density of 1.5 g cm^{-3} (to convert sediment volume to mass), we estimated a time-averaged sand flux at S1 of 3,000 t y^{-1} (4.8 t km^{-2} y^{-1}).

3.3.2 Initial period of physical continuity

After hydro-sedimentary continuity was restored (15 May 2022), high peaks of SS and turbidity were observed at S2 and S3 (Figure 5, Supplementary Figures S1, 2), without similar dynamics at S1. Estimated fluxes of suspended load for 15 May–September 2022 were 3.2, 17.9 and 11.3 t km^{-2} at S1, S2 and S3, respectively, which did not follow the linear relation between suspended load and specific discharge observed at S1. Therefore, they could not have come from a sediment source in the upper part of the watershed. Although these estimates had high uncertainties, they highlighted deposition of large amounts of fine sediments between S2 and S3. Six weeks after removal, the turbidity at S3 stabilized to values similar to those at S1. Nevertheless, large deposits of fine sediments are still being observed along the banks of the Selune downstream from the dismantled dams (Figure 8). Hydrological conditions varied little during winter 2022–2023 (Figure 5). After 15 May 2022, sandy sediments were also trapped at T2 but not at T1 (Supplementary Figure S4). Because there was no major storm event from 15 May-15 September 2022, the main sediment source at T2 and T4 during this period corresponded to the finite and easily mobilizable sediment that had been stored behind the RQB dam.

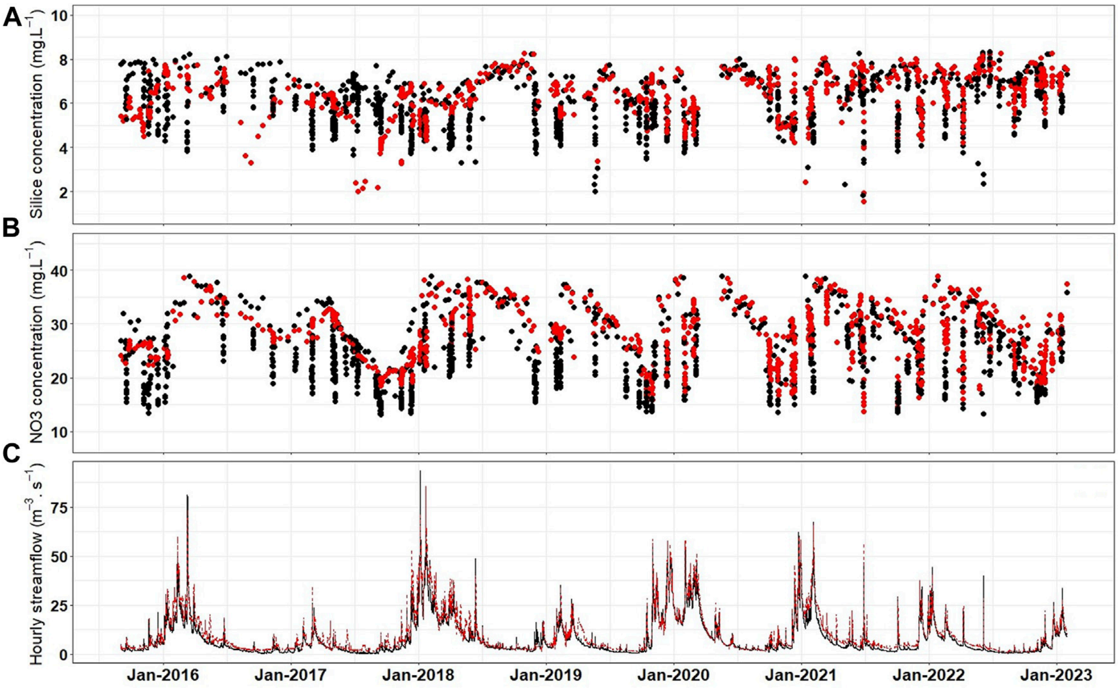

FIGURE 4
Time series of **(A)** dissolved silica concentration, **(B)** nitrate concentration and **(C)** river discharge at stations S1 (black dots) and S3 (red dots).

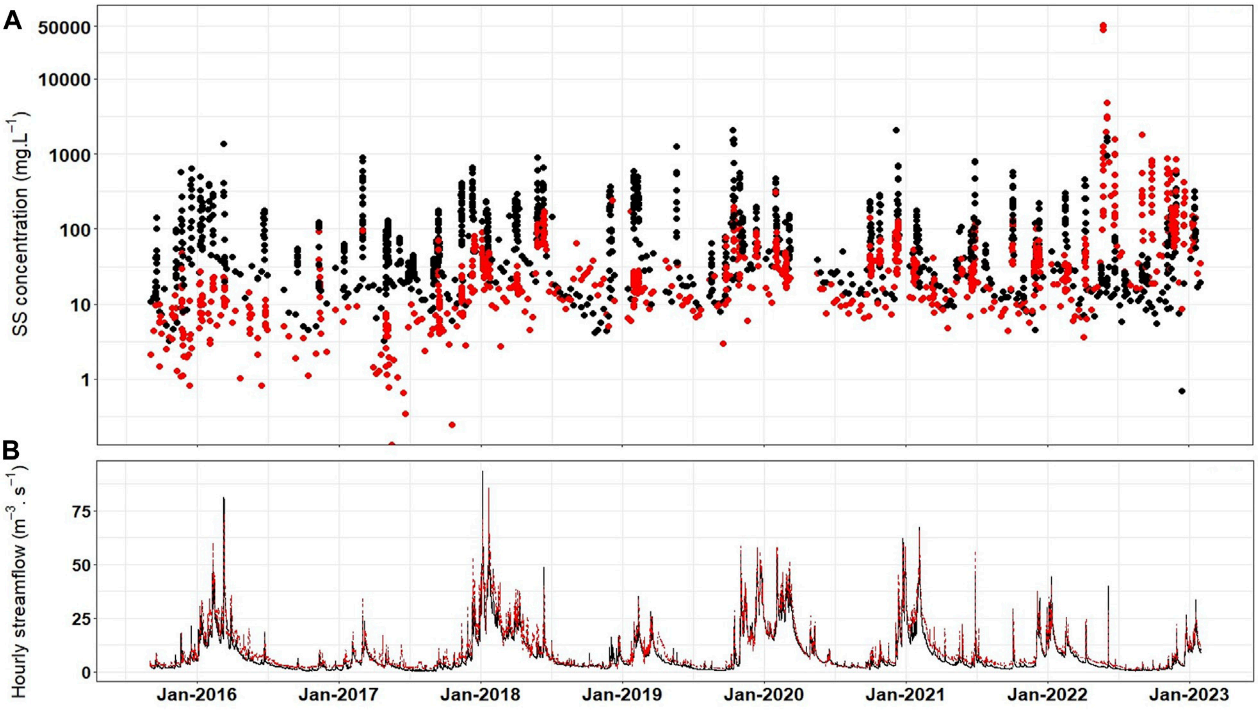

FIGURE 5
Time series of **(A)** suspended sediment (SS) concentrations (note the $\log_{10}$ scale) and **(B)** river discharge at stations S1 (black dots) and S3 (red dots), combining weekly grab-samples with flow-event samples from auto-samplers.

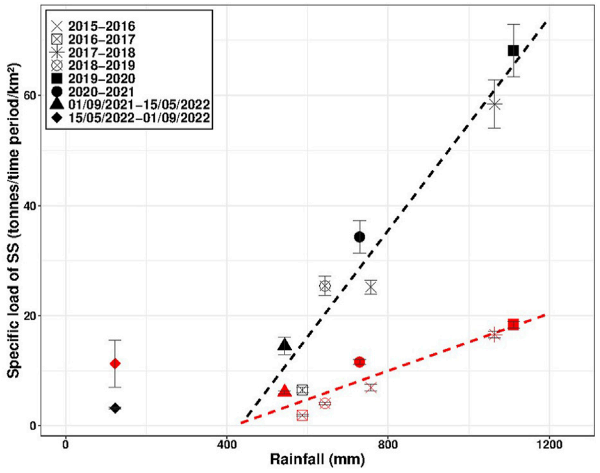

FIGURE 6
Estimated annual specific fluxes of suspended sediment at stations S1 (black symbols) and S3 (red symbols) as a function of annual rainfall for successive hydrological years from 2015 to 2022. Each symbol form corresponds to a given period, usually a water year: *e.g.*, 2015-2016 stands for 1 September 2015 -31 August 2016. The period 1 September 2021-15 May 2022 was that before the last dam was dismantled, while 15 May-1 September 2022 was the period when hydro-sedimentary continuity became effective.

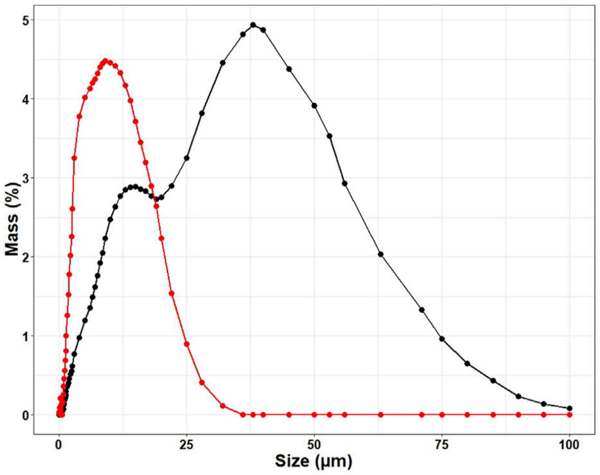

FIGURE 7
Particle-size distribution of suspended sediments at the Virey and Signy stations before the dams were removed.

4 Discussion

4.1 Restoring sediment continuity vs. increasing the turbidity of habitats

The Water Framework Directive lies at the heart of decisions to remove dams, since they are removed to restore ecological and sedimentary continuity; however, bed-load and fine-sediment issues of the latter are rarely distinguished. Restoration of the bed load is targeted because the bed load strongly influences the morphodynamic equilibrium of rivers (Kondolf, 1997) and creates the river forms that support ecological diversity (Pitlick and Wilcock, 2001; Thomson et al., 2001). However, increased fine sediment transfer is associated with the risk of clogging and pollutant transfers, whether in urban or agricultural watersheds (Taylor and Owens, 2009). Tracing coarse-sediment load revealed that the riverbed of the Selune River has low mobility. Furthermore, no morphological indicators (e.g., sediment size, geometry) downstream of the dams indicated that the river had changed in response to a sediment deficit, as observed in many contexts (Kondolf, 1997; Brandt, 2000; Phillips, 2003). This low mobility of the riverbed resulted from two factors: the low energy of this type of river (mean specific power <30 W m^2) and its particularly coarse bottom sediment (D50 of 45–50 mm), which it inherited from the Pleistocene (Beauchamp, 2018). Similar sedimentary functioning has also been observed in other rivers in granitic hydrological areas in Normandy (e.g., Orne River, Vire River), whose inherited bottom load no longer corresponds to current hydraulic conditions and thus has low mobility. These rivers now have nearly no coarse sediment input, as their watersheds have produced essentially only fine matter since they were transformed for agriculture in the Middle Ages (Beauchamp, 2018). Moreover, these types of rivers correspond to the "stable bed aggrading bank" model developed by Brown and Keough (1992) and demonstrated by Beauchamp (2018) for the Selune River. Consequently, the banks, little eroded, contain only fine sediments and cannot serve as sources of coarse-sediment load. Thus, concerns about restoring the sediment load and their dynamics in these rivers are low.

4.2 Rapid recovery of abiotic parameters: implications for future resilience of the river

The results show that the dynamics of most nutrient concentrations and water temperature have become more similar between S1 and S3 since the dismantling started. Removing the dams decreased the warming of the downstream sections in warmer seasons, even during summer 2022, which was the hottest summer of the monitoring period. This result is of interest for ecological continuity, especially in the context of climate change. Moulin et al. (2022) identified this warming effect of the dam by decomposing the water temperature signal using independent component analysis. They concluded that the warming caused by the heat accumulated in the reservoirs was associated more with the Vezins dam than the RQB dam. They distinguished seasonal and daily components, and the former had the highest contribution and amplitude. Particular attention must be paid to the amplitude of this seasonal component, especially maximum temperatures in summer, since many organisms do not tolerate high temperatures well, such as Atlantic salmon. Warm season co-occurs with spawning migration (during spring to autumn) of adults for which critical temperature are estimated closed to 25°C (Breau, 2013) and which are likely to be physiologically affected by the warming of river (Lennox et al., 2018). One strategy for surviving heat waves could be to migrate further upstream the main river course (Frechette et al.,

FIGURE 8
Photographs of fine-sediment deposits along the banks of the Selune River in June 2022 downstream from the dismantled dams (between S2 and S3). The presence of decomposing leaves trapped below the sediment layer indicates that the deposits were not associated with a hydrological event.

2018) where the water is cooler, which is possible now that continuity has been restored.

Nutrient concentration dynamics recovered rapidly at both the event and seasonal scales. Like for water temperature, the Vezins dam had the larger and more biologically active reservoir (Fovet et al., 2020; Rodriguez-Perez et al., 2021); thus, as soon as removal operations started, they directly modified the levels of the reservoirs and changed their biological activity. These dynamics of nutrient concentrations are important for downstream ecosystems, which respond to nutrient ratios (especially the C:N:P:Si ratio) until reaching the ocean (Winton et al., 2019). For instance, Fried and Wuest (2002) illustrated such effects on diatom communities in the Danube River (Germany). Although the chemical continuity of the Selune River seems to have been restored, the fine sediments deposited along it downstream of the dismantled dams are now a source of P. The fate of this stored P will depend strongly on that of the fine sediments, along with pH and variations in redox and temperature, which control the mobilization of P (Parsons, 2017; Gu et al., 2019).

4.3 Long-term monitoring is needed to understand the restoration process

These early results after removal of the Selune dams highlight the relevance of long-term monitoring of abiotic parameters, especially fine-sediment fluxes. The remaining issue for the final phase of restoration is the fate of the sediments that were dredged and stored at the former reservoirs or/and that were deposited downstream at S2 after the reservoir behind RQB was emptied. It is likely that the time required to reach similar dynamics of fine-sediment fluxes between upstream and downstream sections will depend on the hydrological conditions (e.g., Martinez-Carreras et al., 2012; Misset et al., 2019). The frequency of extreme events will strongly influence how rapidly fine-sediment fluxes are restored. Given the locations of S1, S2 and S3, the dynamics of multiple sediment stocks can be monitored. Eventually, S1, S2 and S3 should have similar responses of annual specific suspended load (load divided by the watershed area). The winter of 2022–2023 was relatively calm hydro-dynamically and dry. Indeed, rainfall in Normandy was 28% lower than the winter mean for 1991–2020 (Météo France 2023). Monitoring needs to continue to determine whether this stock will be mobilized within a winter, a year, or a longer period. Additionally, we have begun to analyze sediment tracers using particulate organic markers (Jeanneau et al., 2018), which should help identify remobilization of the deposited sediment more precisely. In particular, it could help distinguish whether sediments come from drained land, riverbanks or eroding reservoir storage.

The results of this study are likely limited to similar rivers (Foley et al., 2017a), first because the response to dam removal also depends on specific characteristics of the dam's reservoir. For instance, N retention was not high in this study, but other reservoirs can act as active N sinks (Friedl and Wuest, 2002). Second, the response also depends on geomorphological dynamics of the river; as a lowland low-energy river, the Selune River is typical of other hydrosystems in northwestern France (Rollet et al., 2014). Thus, although the river's coarse sediments were not mobile with or without the dams, it already has favorable habitats for aquatic ecosystems and migratory species.

5 Conclusion

In the Selune River, a lowland low-energy and relatively turbid river in northwestern France, we found the following:

i) coarse sediments moved little before or after the dams were removed
ii) water temperature and solute concentrations downstream of the dams recovered their upstream signals quickly after dam removal
iii) fine sediments responded rapidly, with large amounts mobilized and deposited downstream of the former reservoir and stabilization of water turbidity after 6 weeks
iv) the need to observe the restoration process over periods longer than a year to determine the dynamics and fate of fine sediments, both those dredged and stored in ponds upstream and those mobilized and deposited during the rapid response.

Respectively, they could have the following implications for ecological dynamics during restoration:

i) little influence of coarse sediments, since favorable habitats in aquatic communities are already present
ii) improvement in the river's water temperature, since removing the dams decreases exposure of downstream reaches to overwarming in the context of climate change
iii) yet-to-be-determined influence of fine sediments, since increased transfer of fine sediments, even punctual, risks clogging habitats.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://geosas.fr/geonetwork/srv/fre/catalog.search#/metadata/6c581e6a-dfd1-4d33-877d-3cd7b302f428.

Author contributions

OF, AC, and A-JR designed the study. FM and OF wrote the first outline of the manuscript. FM, A-JR, and J-MC acquired most of the data with the support of AC, OF and other contributors (see the acknowledgements). FM created the figures and performed the statistical analyses. FM, AC, A-JR, and OF wrote the first draft. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research 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

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Leaf litter decomposition and detrital communities following the removal of two large dams on the Elwha River (Washington, USA)

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Large-scale dam removals provide opportunities to restore river function in the long-term and are massive disturbances to riverine ecosystems in the short-term. The removal of two dams on the Elwha River (WA, USA) between 2011 and 2014 was the largest dam removal project to be completed by that time and has since resulted in major changes to channel dynamics, river substrates, in-stream communities, and the size and shape of the river delta. To assess ecosystem function across the restored Elwha watershed, we compared leaf litter decomposition at twenty sites: 1) four tributary sites not influenced by restoration activities; 2) four river sites downstream of the upper dam (Glines Canyon Dam); 3) four river sites within the footprint of the former Aldwell Reservoir upstream of the lower dam (Elwha Dam); 4) four river sites downstream of the lower dam; and 5) four lentic sites in the newly developing Elwha delta. Three major findings emerged: 1) decomposition rates differed among sections of the Elwha watershed, with slowest decomposition rates at the delta sites and fastest decomposition rates just downstream of the upper dam; 2) aquatic macroinvertebrate communities establishing in leaf litterbags differed significantly among sections of the Elwha watershed; and 3) aquatic fungal communities growing on leaf litter differed significantly among sections. Aquatic macroinvertebrate and fungal diversity were sensitive to differences in

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canopy cover, water chemistry, and river bottom sediments across sites, with a stronger relationship to elevation for aquatic macroinvertebrates. As the Elwha River undergoes recovery following the massive sediment flows associated with dam removal, we expect to see changes in leaf litter processing dynamics and shifts in litter-dependent decomposer communities (both fungal and invertebrate) involved in this key ecosystem process.

KEYWORDS

dam removal, leaf litter decomposition, aquatic–terrestrial interaction, macroinvertebrate communities, fungal communities, aquatic decomposition, ecological restoration

1 Introduction

Dams have long been known to negatively influence river systems (Stanford and Ward, 2001; Morley et al., 2008; Pess et al., 2008; Colas et al., 2016), but in recent decades, as dams are decommissioned and removed, there are both short-term disturbances caused by dam removal, as well as long-term benefits of reconnected watersheds (Bednarek, 2001; Stanley and Doyle, 2003; Duda et al., 2016; Bellmore et al., 2019; Ding et al., 2019; Morley et al., 2020; Atristain et al., 2023). Dams impede the flow of water, sediment, and organic matter from upstream to downstream reaches (Minear and Kondolf, 2009; Atristain et al., 2023), causing changes upstream of dams to flow velocity, stream water temperature, and the deposition of sediment and organic material (Warrick et al., 2015; Warrick et al., 2019). Downstream, dams often create sediment starvation conditions, reduce discharge, increase velocity, reduce allochthonous material transport (Salomão et al., 2019; Tabucanon et al., 2019; Li et al., 2020; Kasahara et al., 2022), scour the riverbed, and alter nutrient cycling (Maavara et al., 2020). During and following dam removals, watersheds can experience significantly greater sediment and organic matter loads as material deposited in reservoirs is mobilized and transported downstream (Bednarek, 2001; Foley et al., 2015; Foley et al., 2017a; Peters et al., 2017; Bellmore et al., 2019), contributing a greater proportion of finer-grained sediments than before dam removal (Kibler et al., 2011; Tullos et al., 2014; East et al., 2018). Dam removal can flood sediment- and resource-starved reaches with excessive sediment and potentially either overwhelm decomposer communities with too much organic material or create anoxic conditions throughout watersheds, both of which could alter rates of organic matter processing (Muehlbauer et al., 2009).

Organic matter processing is a key ecosystem function that links terrestrial and aquatic communities in riverine habitats (Cummins et al., 1973; Benfield, 1996; Wallace et al., 1997) and has been predicted to show longitudinal patterns in riverine systems according to the River Continuum Concept (RCC; Vannote et al., 1980), with modifications predicted by the Riverine Productivity Model (RPM; Thorp and Delong, 1994). Rivers and streams partially depend on allochthonous inputs of organic matter from riparian forests, especially in forested headwaters, along tributaries, and when in-stream autochthonous (algal) resources are diminished. However, inputs of organic matter from the floodplain, side channels, and tributaries can also provide valuable resources for larger rivers (Junk et al., 1989; Thorp and Delong, 1994). Inputs of woody debris (Flory and Milner, 1999; Milner and Gloyne-Phillips, 2005; Wootton, 2012), leaf litter (Cummins et al., 1973; Petersen and Cummins, 1974; Webster and Benfield, 1986), and plant reproductive structures (Flory and Milner, 1999; Garthwaite et al., 2021) are all important resources for a variety of in-stream decomposers (microbial and invertebrate) and support stream food webs (Cummins and Klug, 1979; Cummins et al., 1989; Graça, 2001; Hayer et al., 2022). The establishment of microbial communities on organic matter conditions tissues and alters stoichiometry, making the organic matter more nutritious for macroinvertebrate shredders, grazers, and collectors that feed on biofilms on leaf surfaces (Arias-Real et al., 2018). Finally, the processing of organic matter and breakdown of material from coarse particulate organic matter (CPOM; leaves, flowers, twigs, wood) to fine particulate organic matter (FPOM; leaf and wood fragments, feces) feeds a diverse downstream community of filtering and collecting organisms (Kaushik and Hynes, 1971; Cummins and Klug, 1979; Vannote et al., 1980; Petersen et al., 1989). Organic matter decomposition rates are predicted to be fastest in shady headwaters with macroinvertebrate communities dominated by shredders, and slower in larger reaches of rivers dominated by collectors and grazers (Vannote et al., 1980). However, decomposition rates may still be relatively fast along the edges of large rivers where woody debris entrains litter, benthic macroinvertebrates have peak densities (Thorp and Delong, 1994), and some studies have reported high percentages of shredders (Chauvet, 1997). Processing of organic matter is predicted to be slow in large order rivers where sediment deposition leads to anoxic and unstable conditions (Thorp and Delong, 1994) and physical fragmentation rates may be lower (Chauvet, 1997).

Dam removals can be large but temporary disturbances, and the release of sediment and organic matter may alter environmental conditions for decomposers as well as the available stocks of organic matter for processing (Muehlbauer et al., 2009; Atristain et al., 2023). After 100 years of impoundment, two dams on the Elwha

River (WA, USA) accumulated an estimated 21 million m^3 of sediment, of which ~50% was fine organic and inorganic particles (Warrick et al., 2019). The removal of these dams was the largest controlled-sediment release in history, and it occurred in concurrent increments between 2011 to 2014 to balance the severity and duration of sediment pulses during key life stages for salmon. Throughout 2011–2016, large sediment pulses altered substrate and organic matter stocks throughout the Elwha watershed (Warrick et al., 2015; Ritchie et al., 2018; Morley et al., 2020), and shifting water quality parameters showed greater turbidity, nitrate, ammonium, and phosphate (Foley et al., 2017b). At the same time, anadromous fish were able to access upstream spawning areas for the first time in a century.

In this study, we examined how leaf litter decomposition varied across different sections of the Elwha River following the sediment-pulse stage of dam removal. Our primary response variables were litter decomposition rate and associated macroinvertebrate and fungal community composition. Due to the mosaic of effects during and following dam removal throughout the watershed, we hypothesized that: 1) decomposition rates would differ throughout the watershed, with fastest rates in low-order tributaries and slowest rates at the new Elwha delta (as predicted by the RCC and RPM and based on expected high rates of sediment deposition at downstream locations); 2) decomposition rates would be influenced by environmental variables across sites (for example, decomposition rates may be negatively influenced by fine sediment deposition and positively influenced by numbers of shredders and temperature); 3) decomposer communities (fungal and invertebrate) would differ among sections of the watershed, with highest diversity at tributary sites and lowest diversity in the new Elwha delta (as predicted by the RCC and RPM and based on expected high rates of sediment deposition at downstream locations); and 4) decomposer community metrics would be influenced by environmental variables across sites, but the variables influencing fungi and macroinvertebrates may vary.

2 Materials and methods

2.1 Site description

The Elwha River basin ranges in elevation from approximately 1372 m at the headwaters inside Olympic National Park to sea level at the delta, where it drains into the Strait of Juan de Fuca (Figure 1). The Elwha drains a large, mostly protected watershed of over 833 km^2, 83% of which resides inside Olympic National Park. The geology of the watershed consists of sandstone/shale bedrock in the upper basin and alluvial deposits/glacial till in the lower basin (Duda et al., 2008). Riparian forest vegetation includes bigleaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and various shrub understory assemblages.

This study took place at 20 locations throughout the Elwha watershed (Figure 1; four additional sites were used for just a subset of the study) distributed across five distinct river sections: 1) four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 2) four river sites downstream of the upper Glines Canyon Dam; 3) four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 4) four river sites downstream of the lower Elwha Dam; and 5) four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). An additional four sites were located in the Elwha River upstream of the Glines Canyon Dam in the former Mills reservoir footprint and were used for only a subset of this study due to issues with access (see Section 2.2). Leaf litter experiments were carried out in the autumn of 2016 and 2017, with decomposition rates calculated in 2016 and fungal litter colonization assessed in 2017. The study was designed with both decomposition rates and fungal colonization to take place in 2016, but a freezer failure destroyed fungal samples from 2016 and new samples were incubated for fungal establishment in 2017.

2.2 Leaf litter decomposition study

In fall of 2016, we examined bigleaf maple (*A. macrophyllum*) litter decomposition rates at the 20 primary sites within the Elwha River watershed post-dam removal. Bigleaf maple was chosen as a litter source because it is common throughout the Elwha watershed and it has moderate decomposition rates (not as fast as alder, not as slow as conifer needles, both of which are also common throughout the watershed). Naturally abscised leaves were collected from bigleaf maple stands at 5 source locations within 5 km of the Elwha River. Leaves were air-dried, petioles were removed, and 4.00 g +/− 0.10 g quantities were placed into coarse-mesh (6.4-mm openings) litterbags to allow invertebrate access (n = 60 bags per maple source; N = 300). During litterbag preparation, we counted the number of maple tar spots (*Rhytisma punctatum*, a common fungal endophyte) on leaves in each bag because this fungal infection has been shown to influence decomposition rates in other studies (LeRoy et al., 2011; Wolfe et al., 2019). Litterbags were then randomly assigned both a harvest date and one of 20 locations within the five sections in the Elwha watershed. Fifteen litterbags were placed at each site in pools near monitored riffles, attached to 2-m rings of steel cable, and anchored into place using sandbags. Litterbags were placed in late August 2016, and five replicate litter bags were harvested from each location after 2, 5, and 6 weeks (specific dates varied slightly depending on sample location and retrieval logistics; final harvest date was determined by the onset of high flows). Harvested litterbags were placed into individual polyethylene zipper bags and transported on ice to the laboratory for processing.

Litterbags were processed within 12 hours of harvesting. Sediment and macroinvertebrates were rinsed from leaf fragments and sieved through 250-µm nets for preservation in 70% ethanol. At the week 5 harvest, leaf punches were collected for microbial analysis (but those samples were lost in a freezer accident, so we repeated this aspect of the study in 2017 for fungal amplicon sequencing, see below). Remaining leaf material was oven-dried at 70°C for 72 hours then ground, and 0.25 g subsamples were combusted at 500°C for one hour to determine ash-free dry mass

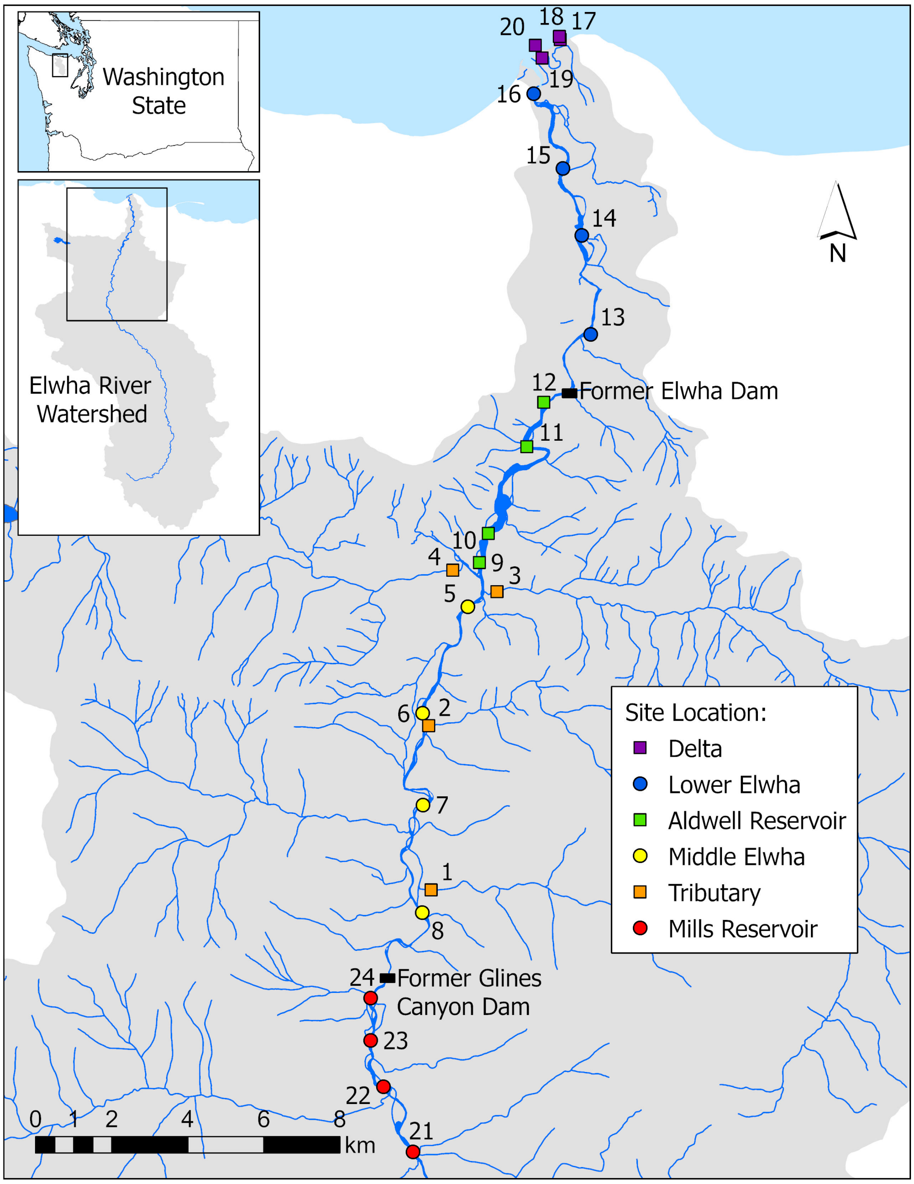

FIGURE 1
Map of all 24 study locations across six sections of the Elwha River watershed following the removal of two major dams: 1) Orange squares: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 2) Yellow circles: four river sites downstream of the upper Glines Canyon Dam; 3) Green squares: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 4) Blue circles: four river sites downstream of the lower Elwha Dam; and 5) Purple squares: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). An additional four sites (Red circles) were located in the Elwha River upstream of the Glines Canyon Dam in the former Mills reservoir footprint and were used for only a subset of this study (see Section 2.2).

(AFDM). A follow-up incubation of additional litterbags (n = 4) at each of the full 24 locations (including the former Lake Mills Reservoir) was used to evaluate fungal colonization of leaf litter in August–September 2017 (with 1-week and 3-week incubations, see Section 2.4).

2.3 Aquatic macroinvertebrates

Preserved macroinvertebrate samples from the first harvest date were sorted into three major categories for further identification: EPT taxa (Ephemeroptera, Plecoptera, Trichoptera), other insects (members of families other than EPT), and non-insects (i.e., Arachnida, Oligochaeta, Mollusca, and other non-insect invertebrates). Functional feeding groups were determined for each taxon. Litterbags at all locations retained sufficient leaf litter at the first harvest date to provide substrate, habitat, and food resources for invertebrates. All macroinvertebrate identifications were made using a dissecting microscope, to the lowest taxonomic level possible (typically genus to family for insects and class to order for non-insects) using Merritt et al. (2019) and Thorp and Covich (2009). Samples from locations 9 and 10 were accidentally combined during processing and samples from locations 14 and 15 were so large they were subsampled (25% was sorted and identified and then estimated to the whole sample size). Prior to analysis, rare taxa were consolidated at the family level. Reference specimens are stored in the LeRoy Aquatic Ecology Lab at The Evergreen State College.

2.4 Fungal amplicon sequencing

Subsamples (25 mg) of lyophilized leaf litter from litterbags collected on two harvest dates (1- and 3-week 2017 litterbag incubations at 24 locations) were weighed into vials, and microbial DNA was extracted using a DNeasy PowerSoil Pro kit (Qiagen) following the manufacturer's instructions. Subsamples were transferred to 96-well plates along with controls to detect contamination during bacterial and fungal library preparation.

Genomic DNA was amplified using an ITS barcoded primer set, adapted for the HiSeq2000 and MiSeq systems (Illumina). These primers were designed by Kabir Peay's laboratory at Stanford University (Smith and Peay, 2014). The reverse amplification primer also contained a twelve base barcode sequence that supports pooling of up to 2,167 different samples in each lane (Caporaso et al., 2011; Caporaso et al., 2012). Each 25 µL PCR reaction contained 9.5 µL of PCR Water (MO BIO, certified DNA-Free), 12.5 µL of AccuStart II PCR ToughMix (QuantaBio, 2× concentration, 1× final), 1 µL Golay barcode tagged Forward Primer (5 µM concentration, 200 pM final), 1 µL Reverse Primer (5 µM concentration, 200 pM final), and 1 µL of template DNA. The conditions for PCR were as follows: 94°C for 3 min to denature the DNA, with 35 cycles at 94 °C for 45 s, 50 °C for 60 s, and 72 °C for 90 s; with a final extension of 10 min at 72 °C to ensure complete amplification. Amplicons were quantified using PicoGreen (Invitrogen) and a plate reader. Once quantified, different volumes of each of the products were pooled into a single tube so that each amplicon was represented equally. This pool was then cleaned up using AMPure XP Beads (Beckman Coulter), and then quantified using a fluorometer (Qubit, Invitrogen). After quantification, the molarity of the pool was determined and diluted down to 2 nM, denatured, and then diluted to a final concentration of 6.75 pM with a 10% PhiX spike for 2 × 251 bp sequencing on the Illumina MiSeq (Argonne National Laboratories).

Sequences were demultiplexed at Argonne National Laboratories using QIIME (Bolyen et al., 2019). Similar sequences were assigned to operational taxonomic units (OTUs) by clustering sequences at a 97% similarity threshold with reference to the UNITE full fungal database (Nilsson et al., 2019). OTUs were filtered to remove singletons and summarized to list taxonomic levels down to species. Unassigned taxa were filtered from the OTU table in QIIME. A phyloseq object containing the OTU-by-sample matrix, sample metadata, and taxonomic information was combined for downstream analyses (McMurdie and Holmes, 2013). We removed OTUs that were present in less than 1% of samples and normalized for variable sequencing depth by calculating the proportional abundance of OTUs within each sample (McMurdie and Holmes, 2014) prior to community analysis.

2.5 Environmental covariates

Study sites were measured in the summer/fall of 2016 and 2017 for a variety of in-stream habitat, water quality, and biological variables (Table S1) following the methods of Morley et al. (2008; 2020) and Duda et al. (2011); for more details, please see these previous studies. Briefly we measured wetted width (m using a laser range finder, Impulse), depth at sample location (cm), canopy cover (measured using a modified convex spherical densiometer, %), benthic chlorophyll-a (for algae scrubbed and rinsed from five cobbles per site, filtered onto 47 mm glass fiber filters [1 µm pore size] and measured using fluorometry, µg cm^{-2}), water temperature and specific conductivity (measured using a model 85 multiprobe, YSI, °C and µS cm^{-2}, respectively), total N, total P, NO_3^--N, NH_4^+-N, NO_2^- N, PO_4^{3-}-P, and SiO_4^{4-}-Si (µg L^{-1}; measured using a continuous flow RFA/2 system, Alpkem), fine sediments and substrate diameters (measured using pebble counts, % and D_{50} [median sediment size], respectively), benthic macroinvertebrate density (measured using a slack sampler [500 µm mesh, 0.25 m^2 frame; Moulton et al., 2002], number m^{-2}), shredders (% of total invertebrates in the benthos), and organic and inorganic matter density in both rock cobbles and in seston (µg cm^{-2} and µg L^{-1}, respectively). For all measurements, values were averaged across five locations at each site. We determined elevation (m above sea level) and river distance (km) using ArcInfo 9.1 (Earth Systems Research Institute Redlands, CA). In addition, these sites were assessed for fine sediment (<3.35 mm diameter) and salmonid spawning gravels (3.35–75 mm diameter) from a population of riffle crests available in 2016 and 2017 to coincide with biological sampling (see methods in Peters et al., 2017). Briefly, three subsamples were collected from each riffle crest, dried, sieved (mesh openings of 75, 26.5, 13.2, 9.5, 3.35, 2.0, 0.85, and 0.106 mm), and weighed to the nearest 0.001 kg. Fine sediments (< 0.0106 mm) were determined from water column collections before and after sediment collection using gravimetric methods (Peters et al., 2017). The data from the three subsamples were combined to produce a summary of the riffle conditions.

2.6 Statistical analysis

We used permutational (Monte Carlo) statistical tests for all analyses in R (R version 4.3.1; R Core Team, 2021) due to unequal variances and non-normality for some variables. Analysis of leaf litter decomposition rates (k day^{-1}) required a natural log-transformation of percent AFDM remaining to determine exponential decay rates by regressing ln % AFDM remaining by harvest day (Olson, 1963; Petersen and Cummins, 1974; Benfield, 1996). Decay constants ($-k$) were compared using permutational analysis of covariance (ANCOVA) where significant interactions with time reflected significant differences in decomposition rates (slopes). We used a permutational three-way ANCOVA to compare maple litter sources, river sections, days in stream, and all possible interactions. Litter sources did not differ and so all litter sources were pooled and a follow-up two-way ANCOVA was used to determine significant differences in decomposition rates (section*day interaction) among river sections. We used Tukey's Honest Significant Difference (HSD) test to make pairwise comparisons of decomposition rates among river sections. We used permutational linear regressions to test for linear relationships between k values and a large suite of environmental variables (physical, chemical, biological, sedimentary variables, and individual decomposer taxa; see Table S1), and the total number of *Rhytisma punctatum* stromatal infections in each litterbag. We used Principal Components Analysis (PCA) to combine environmental factors into six principal components that we used to explain variation in k, but none of the principal components explained significant fractions of the variation in k, so were excluded from analysis. Statistical analyses were conducted using the package *lmPerm* (*aovp*, *lmp*; Wheeler and Torchiano, 2016), and figures were produced using the R-package *ggplot2* (Wickham et al., 2023).

We calculated simple diversity metrics for decomposer communities in each litterbag (macroinvertebrates after 2 weeks of incubation and fungi after 1 and 3 weeks of incubation). For benthic macroinvertebrates, we calculated total abundance (total number of individuals per litterbag), taxa richness (number of unique taxa per litterbag), % EPT taxa, % shredders, and Shannon's diversity index (H′ per litterbag) using the *vegan* package, but for microbial communities we used the *iNext* package (Hsieh et al., 2016; Chao et al., 2022; Hsieh and Chao, 2022), which uses rarefaction to account for unequal sequencing depth for fungal OTUs to estimate fungal richness (counts of OTUs per litterbag) and Shannon's diversity index (H′ per litterbag). To examine relationships between fungal OTU richness and diversity among harvest dates (1-week and 3-week) and river sections, we first used permutational two-way ANOVAs with harvest*section interactions. For fungal communities, harvest was not a significant effect in any model, so we ran follow-up permutational one-way ANOVAs by river section with Tukey HSD *post hoc* tests. For macroinvertebrates from the 2-week harvest, we ran permutational one-way ANOVAs by river section with Tukey HSD *post hoc* tests. We examined linear relationships among invertebrate and fungal community metrics, decomposition rates, and environmental variables (listed above) using permutational simple linear regressions. We used Principal Components Analysis (PCA) to combine environmental factors into six principal components that we used to explain variation in community metrics, but none of the principal components explained significant fractions of the variation, so were excluded from analysis.

To examine broader patterns in decomposer community composition, we used two-way permutational multivariate analyses of variance (PerMANOVAs) and we visualized differences among assemblages using non-metric multidimensional scaling (NMDS) ordinations with Bray-Curtis distance measures using the package *vegan* in R (Oksanen et al., 2022). For fungal OTUs, we used a 2-way PerMANOVA with harvest, section, and the harvest*section interaction. Harvest was not a significant effect in this model, so we ran a follow-up one-way PerMANOVA to determine the influence of river section on fungal community composition. Similarly, we ran a one-way PerMANOVA to determine the influence of river section on macroinvertebrate community composition. We used Bonferroni-corrected pairwise comparisons to determine significant differences among sections. We ran follow-up permutational tests for homogeneity of multivariate dispersion (PermDisp) to examine whether communities in each section of the Elwha were equally dispersed. Fungal OTU counts were converted to proportional abundances using the R-package *phyloseq* (McMurdie and Holmes, 2013; Morgan and Ramos, 2023) and macroinvertebrate abundances were log(x+1) transformed to preserve zeros (McCune et al., 2002). Correlations between NMDS ordination axes and environmental variables (listed above) were conducted using the R-package *vegan*. Indicator Species Analysis (ISA) determined which members of the macroinvertebrate community were significantly associated with a particular river section, which we performed with the R-package *vegan*. A slightly different approach was used to determine which fungal community members were associated with a particular river section. We used the R-package *ALDEx2* (Fernandes et al., 2013) to perform differential abundance tests following central log ratio (CLR) transformations to lower false positive discovery rates (McMurdie and Holmes, 2014). OTUs were considered indicators when mean proportions were significantly different between one section and all others based on Benjamini-Hochberg corrected p-values from Wilcoxon rank sum tests, and comparing *ALDEx2* effect sizes (Gloor et al., 2017).

3 Results

3.1 Leaf litter decomposition

Maple leaf litter decomposition rates differed significantly among sections of the Elwha watershed (Figure 2; section*days: $F_{(4,384)} = 8.87$, $p < 0.0001$). In particular, litterbags placed in the newly formed Elwha Delta decomposed slowest, and litterbags placed in the middle reaches of the Elwha, just downstream of the upper dam, decomposed fastest. Decomposition rates for specific locations ($n = 4$ per section) across the watershed ranged almost two orders of magnitude from −0.00631 at one of the Delta sites to −0.09521 for one of the Aldwell Reservoir sites (Table 1). Decomposition rates were not significantly influenced by differences in litter quality among the five maple sources used to create litterbags (source*days: $F_{(4,384)} = 0.19$, $p = 0.999$), but decomposition rates were negatively influenced by the number of endophyte-infected stromatal patches of *Rhytisma punctatum* on the initial leaf litter ($F_{(1,18)} = 7.92$, $p = 0.0115$). Decomposition rates across the twenty locations were not significantly related to any physical, chemical, or substrate variables across the watershed, but were positively related to %EPT taxa ($F_{(1,18)} = 4.85$, $p = 0.0409$; Table 2). When we statistically account for the number of *Rhytisma* patches, there are negative linear relationships between decomposition rates and both the smallest sediment size (<0.0106 mm [Sed1]; $F_{(1,14)} = 8.96$, $p = 0.0096$) and the inorganic material in the sediment ($F_{(1,14)} = 5.35$, $p = 0.0365$; Table S2), but no other environmental variables were significantly related to k. However, although the mechanisms for relationships with decomposition rates may not always be clear, a suite of invertebrates and fungi were significantly related to k (Table S2).

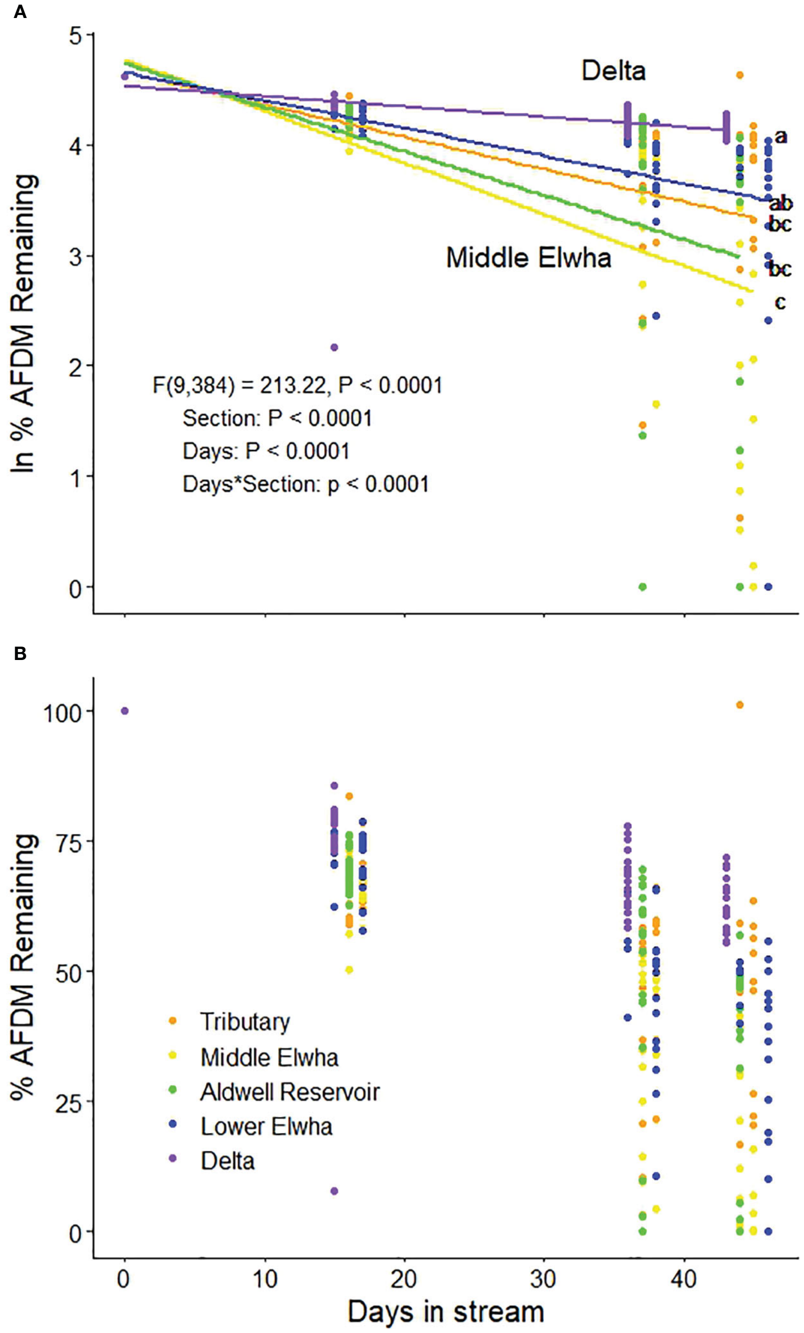

FIGURE 2
(A) Regression lines showing ln percent ash free dry mass (AFDM) remaining through time showing decomposition rates (slopes of exponential regression lines) for bigleaf maple leaf litter, and **(B)** percent ash free dry mass remaining through time for bigleaf maple litter decomposing in five sections of the Elwha River watershed following the removal of two major dams in 2014: 1) Orange circles: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 2) Yellow circles: four river sites downstream of the upper Glines Canyon Dam; 3) Green circles: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 4) Blue circles: four river sites downstream of the lower Elwha Dam; and 5) Purple circles: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). Lower case letters represent decomposition rates that differ significantly ($p < 0.05$).

3.2 Macroinvertebrates

We identified 37 macroinvertebrate taxa in leaf litter bags, from a total of 32 families and 11 orders. The abundance, richness, and diversity of macroinvertebrates in leaf litterbags varied among river sections and were related to several environmental variables across the watershed. The abundance of macroinvertebrates was significantly different across sections ($F_{(4,15)} = 2.97$, $p = 0.001$), with highest abundances at Lower Elwha sites and lowest abundances at Tributary sites (Figure 3A). The richness of macroinvertebrate taxa was significantly different among sections ($F_{(4,15)} = 4.77$, $p = 0.0114$), with highest richness at sites in the

TABLE 1 Decomposition rates at each of twenty locations across five sections of the Elwha watershed post-dam removal.

Location	Section	$-k$ (day^{-1})	Standard error	p-value
1	Tributary	0.015385	0.0013	0.0001
2	Tributary	0.012980	0.0010	0.0001
3	Tributary	0.037153	0.0101	0.0018
4	Tributary	0.054106	0.0138	0.0011
5	Elwha Middle	0.018219	0.0013	0.0001
6	Elwha Middle	0.062376	0.0123	0.0001
7	Elwha Middle	0.072687	0.0149	0.0001
8	Elwha Middle	0.032707	0.0040	0.0001
9	Aldwell Reservoir	0.013816	0.0011	0.0001
10	Aldwell Reservoir	0.012282	0.0017	0.0001
11	Aldwell Reservoir	0.021132	0.0014	0.0001
12	Aldwell Reservoir	0.095203	0.0126	0.0001
13	Lower Elwha	0.043913	0.0097	0.0002
14	Lower Elwha	0.024219	0.0028	0.0001
15	Lower Elwha	0.014815	0.0010	0.0001
16	Lower Elwha	0.016088	0.0015	0.0001
17	Delta	0.009289	0.0008	0.0001
18	Delta	0.006310	0.0068	0.3678
19	Delta	0.009767	0.0011	0.0001
20	Delta	0.011725	0.0006	0.0001

Values represent decomposition rate constants ($-k$ day^{-1}) and associated standard errors and p-values from exponential regression analysis.

former Aldwell Reservoir and Lower Elwha, compared to lowest taxa richness at the Elwha Delta (Figure 3B). Shannon's Diversity Index values for litter bag macroinvertebrates were significantly different among sections (Figure 3C; $F_{(4,15)} = 8.38$, $p = 0.0026$), with highest diversity at the Tributary sites, followed by the Middle Elwha and Delta, and lowest diversity at the Aldwell Reservoir and Lower Elwha sites. The percentage of EPT taxa differed significantly among river sections ($F_{(4,15)} = 22.89$, $p < 0.0001$) with highest values at the Tributary and Middle Elwha sites, with increasingly lower values at Aldwell Reservoir, Lower Elwha, and Delta sites. The percentage of shredders did not differ among sections ($F_{(4,15)} = 1.95$, $p = 0.1205$).

The abundance of macroinvertebrates was positively related to algal biomass (chl-a: $F_{(1,18)} = 4.98$, $p = 0.0386$; Table 2), and both organic ($F_{(1,14)} = 7.74$, $p = 0.0147$) and inorganic material in the sediment ($F_{(1,14)} = 7.03$, $p = 0.0189$). The richness of macroinvertebrate taxa was positively related to sediment size (D_{50}; $F_{(1,18)} = 10.43$, $p = 0.0046$) and negatively related to the proportion of fine sediments ($F_{(1,18)} = 5.86$, $p = 0.0263$) and water temperature ($F_{(1,18)} = 8.78$, $p = 0.0083$). The diversity of macroinvertebrate taxa was positively related to the elevation ($F_{(1,18)} = 6.23$, $p = 0.0225$) and river distance of the site ($F_{(1,18)} = 5.19$, $p = 0.0352$), canopy cover ($F_{(1,18)} = 8.67$, $p = 0.0087$), and nitrate ($F_{(1,14)} = 6.27$, $p = 0.0253$), while being negatively related to both latitude ($F_{(1,18)} = 5.55$, $p = 0.0300$) and longitude ($F_{(1,18)} = 8.15$, $p = 0.0150$), both the organic ($F_{(1,14)} = 6.87$, $p = 0.0201$) and inorganic material in the sediment ($F_{(1,14)} = 11.85$, $p = 0.0040$), and algal biomass on rock surfaces ($F_{(1,18)} = 4.70$, $p = 0.0438$).

The structure of macroinvertebrate communities establishing in leaf litterbags was also significantly different across river sections (Figure 4; $F_{(4,15)} = 5.21$, $p < 0.0001$, stress = 0.0547), with Delta communities clearly separated from other sections of the Elwha watershed. Macroinvertebrate communities did not differ in terms of multivariate dispersion ($F_{(4,15)} = 1.47$, $p = 0.2690$). Environmental variables such as elevation, canopy cover, specific conductance, nitrate, and increased macroinvertebrate diversity were correlated with macroinvertebrate communities found at Tributary sites. Variables like organic matter in seston and increasing taxa richness and abundance were correlated with macroinvertebrate communities found at the Aldwell Reservoir and Lower Elwha sites, with only temperature correlated with macroinvertebrate communities found at Delta sites (Figure 4). There were several significant indicator taxa, with the mayfly *Baetis* sp. associated with the Middle Elwha, while Oligochaeta, Chironomidae, and the stonefly *Zapada* sp. were associated with the Lower Elwha, and only a Physidae gastropod was associated with the Elwha Delta (Table 3).

TABLE 2 Significant linear relationships among community and environmental variables across 20–24 locations in the Elwha watershed.

Response variable	Explanatory variable	Pos / Neg	df	*F-ratio*	p-value	Adj R^2
k (decomposition rate)	*Rhytisma* patches (# per litterbag)	–	1, 18	7.58	0.0131	0.2573
	Sediment < 0.0106 mm (Sed1, kg)	–	1, 14	5.76	0.0304	0.2422
	EPT taxa (%)	+	1, 18	4.81	0.0409	0.2123
Invert Abundance	Organic matter in sediment (mg cm^{-2})	+	1, 14	7.74	0.0147	0.3099
(# per litterbag)	Inorganic matter in sediment (mg cm^{-2})	+	1, 14	7.03	0.0189	0.2869
	Algal biomass (chl-a, µg cm^{-2})	+	1, 18	12.36	0.0025	0.3743
Invert Taxa Richness	Fine sediment (%)	–	1, 18	5.86	0.0263	0.2038
(taxa per litterbag)	Sediment D$_{50}$ (mm)	–	1, 18	10.43	0.0046	0.3318
	Water temperature (°C)	–	1, 18	8.78	0.0083	0.2905
Invert Diversity (H′)	Organic matter in sediment (mg cm^{-2})	–	1, 14	6.87	0.0201	0.2814
(per litterbag)	Inorganic matter in sediment (mg cm^{-2})	–	1, 14	11.85	0.0040	0.4198
	Canopy cover (%)	+	1, 18	8.67	0.0087	0.2875
	Algal biomass (chl-a, µg cm^{-2})	+	1, 18	4.70	0.0438	0.1631
	Nitrate (NO$_3^-$, µg L^{-1})	+	1, 14	6.27	0.0253	0.2598
	Elevation (m.a.s.l.)	+	1, 18	6.23	0.0225	0.2159
Fungal Taxa Richness	Specific conductance (µs cm^{-1})	–	1, 46	4.98	0.0306	0.0781
(taxa per litterbag)	Water temperature (°C)	–	1, 46	8.17	0.0064	0.1324
	Algal biomass (chl-a, µg cm^{-2})	–	1, 46	4.26	0.0446	0.0649
Fungal Diversity (H′)	Inorganic matter in sediment (mg cm^{-2})	+	1, 38	4.43	0.0421	0.0807
(per litterbag)	Inorganic matter in seston (mg cm^{-2})	+	1, 46	4.33	0.0432	0.0661
	Canopy cover (%)	+	1. 46	8.36	0.0059	0.1353
	Total P (phosphorus, µg L^{-1})	+	1, 38	6.48	0.0151	0.1231
	Total N (nitrogen, µg L^{-1})	+	1, 38	5.31	0.0267	0.0996

Values represent degrees of freedom (df) associated with F-ratios, p-values, and adjusted coefficients of determination (R^2) from permutational simple linear regressions among variables. We used Principal Components Analysis (PCA) to condense variables into six PCA axes, but they did not correlate with these response variables. Invert, invertebrate; Pos, positive linear relationship; Neg, negative linear relationship; H', Shannon's diversity index.

3.3 Fungal decomposers

Leaf litter from across the Elwha watershed was colonized by 326 aquatic fungal taxa (OTUs). There were no significant differences in fungal taxa richness (F$_{(1,36)}$ = 2.95, p = 0.0708) or Shannon's Diversity Index (F$_{(1,36)}$ = 0.27, p = 0.7843) by harvest date (1 versus 3 weeks), nor significant interactions between harvest date and river section (richness: F$_{(1,36)}$ = 1.16, p = 0.3383; diversity: F$_{(5,36)}$ = 0.72, p = 0.6186), so both harvests were pooled for subsequent one-way ANOVA models. Fungal taxa richness was not significantly different across sections of the Elwha watershed (F$_{(5,42)}$ = 1.35, p = 0.2679; Figure 5A), but fungal diversity (Shannon's Diversity Index) differed significantly across sections (F$_{(5,42)}$ = 2.87, p = 0.0204). Litter incubated at the site of the former Mills Reservoir had the lowest fungal diversity and litter incubated in the Lower Elwha had the highest fungal diversity (Figure 5B).

Fungal taxa richness was negatively related to water temperature (Table 2; F$_{(1,46)}$ = 8.17, p = 0.0064), specific conductance (F$_{(1,46)}$ = 4.98, p = 0.0306), and algal biomass (chl-a: F$_{(1,46)}$ = 4.26, p = 0.0446) across the watershed. Fungal diversity was positively related to canopy cover (F$_{(1,46)}$ = 8.36, p = 0.0059), total P (F$_{(1,38)}$ = 6.48, p = 0.0151), total N (F$_{(1,38)}$ = 5.31, p = 0.0267), inorganic material at the site, both in the sediment (F$_{(1,38)}$ = 4.43, p = 0.0421) and in the seston (F$_{(1,46)}$ = 4.33, p = 0.0432). Several fungal taxa were differentially abundant in this study. Members of the order Helotiales (OTU 96) were significantly less abundant at the Aldwell Reservoir site than all other sites (ALDEx2 effect size = –1.21, p = 0.0159), and three OTUs, including members of the genus *Cladosporium* sp. (OTU 6; ALDEx2 effect size = 1.37, p = 0.0021) and two unidentified fungi (OTU 326; ALDEx2 effect size = 1.42, p = 0.0038; OTU 2; ALDEx2 effect size = 1.06, p = 0.0045) were significantly more abundant in Tributary sites.

Aquatic fungal communities that established on leaf litter were also significantly different across river sections (Figure 6; F$_{(5,36)}$ = 3.47, p = 0.0001, stress = 0.0914), but they did not differ between harvests (F$_{(1,36)}$ = 2.10, p = 0.0600) and were not influenced by the harvest*section interaction (F$_{(5,36)}$ = 1.49, p = 0.0709). Fungal taxa communities on leaf litter were similar to each other for Mills

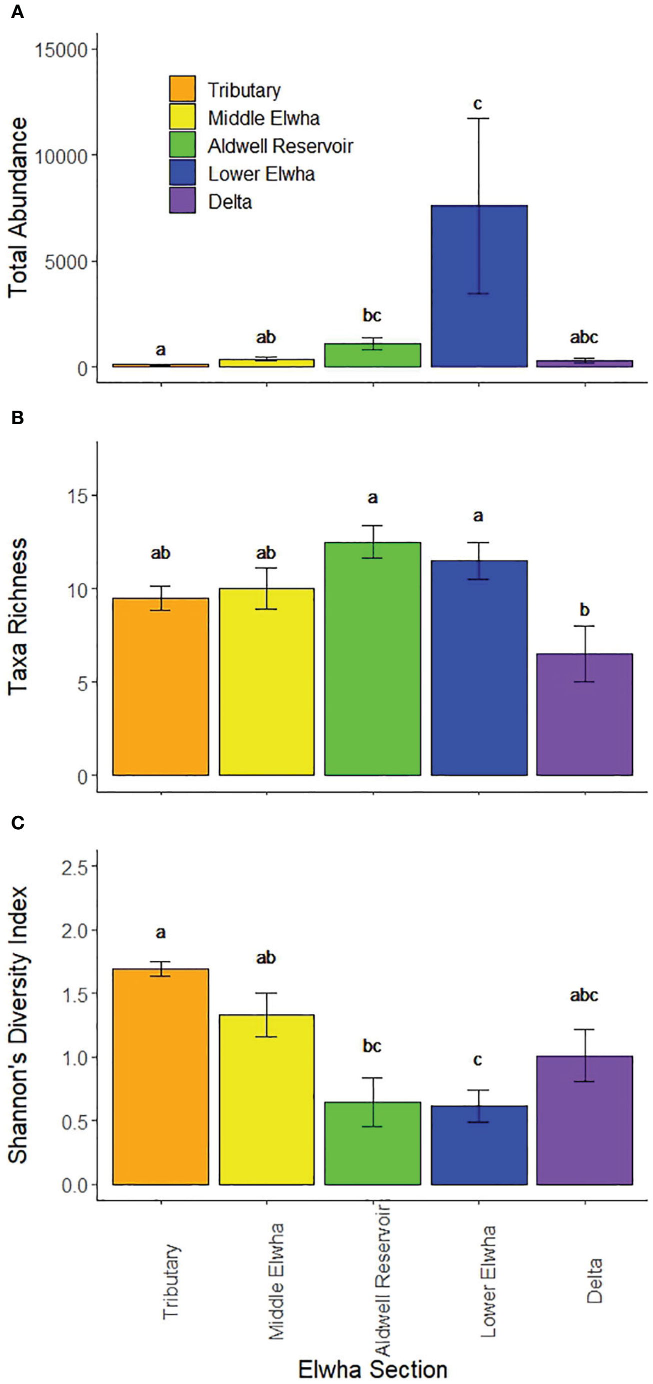

FIGURE 3
Aquatic macroinvertebrate patterns showing: **(A)** total invertebrate abundance (mean number of individuals per litterbag), **(B)** invertebrate taxa richness (mean number of species per litterbag), and **(C)** invertebrate taxa diversity (mean Shannon's H' per litterbag) across five Elwha watershed sections: 1) Orange bars: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 2) Yellow bars: four river sites downstream of the upper Glines Canyon Dam; 3) Green bars: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 4) Blue bars: four river sites downstream of the lower Elwha Dam; and 5) Purple bars: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). Bars represent means +/– 1 standard error and lower-case letters represent diversity values that differ significantly.

Reservoir, and those communities differed significantly from many other communities, except the Tributary and Delta sites. Surprisingly, the fungal communities at the Delta sites did not differ significantly from any other sites. These differences could have been driven by large differences in multivariate dispersion across sections of the Elwha ($F_{(5,42)} = 7.73$, $p = 0.001$). Environmental variables such as specific conductance, canopy cover, algal biomass (chl-a), total P, and larger sediment sizes (P7: proportion 9.5–13.2 mm; and P8: proportion 13.2–26.5 mm) were correlated with fungal communities found at Tributary sites

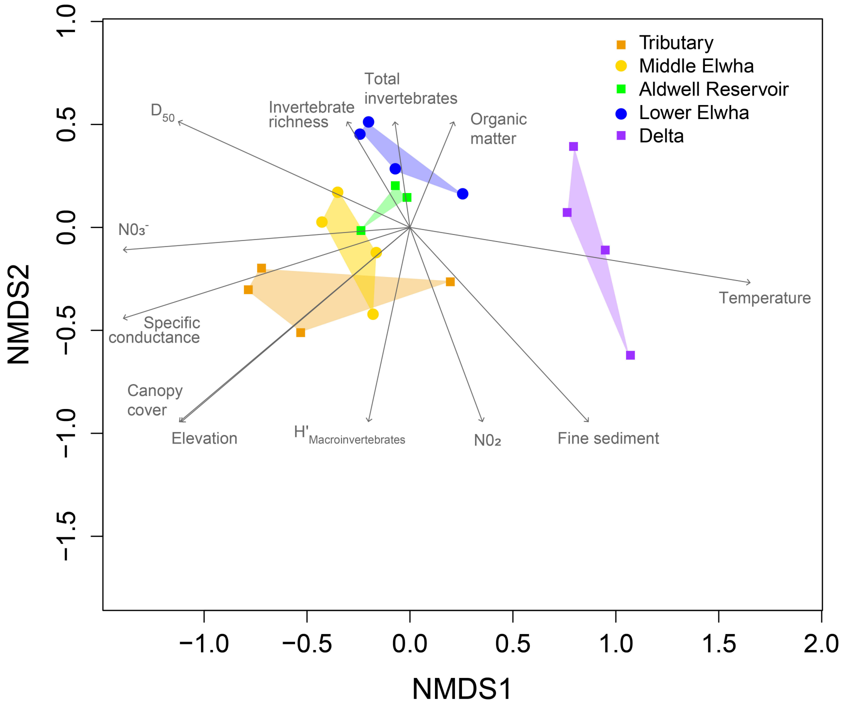

FIGURE 4
Non-metric multidimensional scaling (NMDS) ordination of aquatic macroinvertebrate communities. Symbols represent macroinvertebrate communities colonizing leaf litterbags in the Elwha River watershed following the removal of two major dams in 2014 placed at 20 study locations across five sections: 1) Orange squares: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 2) Yellow circles: four river sites downstream of the upper Glines Canyon Dam; 3) Green squares: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 4) Blue circles: four river sites downstream of the lower Elwha Dam; and 5) Purple squares: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). Vectors represent significant correlations through ordination space with environmental and biological factors. H', Shannon's diversity index; NO_3^-, nitrate concentration; NO_2, nitrite concentration; D_{50}, median sediment size.

(Table 2). Variables like SiO4 and the diversity of macroinvertebrate communities were correlated with fungal communities at some Middle Elwha sites, while fungal richness was correlated with fungal communities at the former Aldwell Reservoir, and smaller sediment sizes (P2: proportion 0.0106–0.106 mm) was correlated with fungal community structure at the former Mills Reservoir sites (Figure 6).

4 Discussion

This is the first study to examine leaf litter decomposition rates following the removal of large dams in a restored landscape. A few related studies have examined changes in leaf litter decomposition following small dam removal. One of these studies showed slower decomposition rates and much lower fungal biomass and macroinvertebrate diversity in leaf litter bags downstream of a diversion dam (Muehlbauer et al., 2009). Following six months of flow restoration, there was still slower decomposition at the site downstream of the dam, but both fungi and macroinvertebrates had recovered to upstream levels (Muehlbauer et al., 2009). In addition, aquatic macroinvertebrate communities began to converge following flow restoration, providing evidence that communities can recover within several years of flow restoration (Muehlbauer et al., 2009). One additional study examined reservoir drawdown during dam removal and found that organic matter decomposition was slower downstream of a dam before and during drawdown compared to nearby undammed reaches, but that all drawdown effects disappeared quickly (within one year), likely due to a long and slow drawdown process (Atristain et al., 2023). This study did not examine leaf litter decomposition, but instead used thin sheets of wood to examine organic matter processing. Reservoir drawdown negatively influenced biofilm metabolism and reduced autotrophic biofilm biomass (chlorophyll-a) on woody substrates, but both recovered quickly following drawdown (Atristain et al., 2023). In the present study, we found the slowest rates of decomposition in the new Elwha delta (as hypothesized), but contrary to our hypotheses the fastest decomposition rates were

TABLE 3 Macroinvertebrate taxa identified from leaf litter bags that indicate for specific sections of the Elwha watershed.

Section	Taxa	Indicator value	p-value
Elwha Middle	Ephemeroptera: *Baetis* sp.	0.3363	0.003
Lower Elwha	Annelida: Oligochaeta	0.4112	0.003
Lower Elwha	Plecoptera: *Zapada* sp.	0.3992	0.025
Lower Elwha	Diptera: Chironomidae	0.2936	0.005
Delta	Gastropoda: Physidae	1.0000	0.003

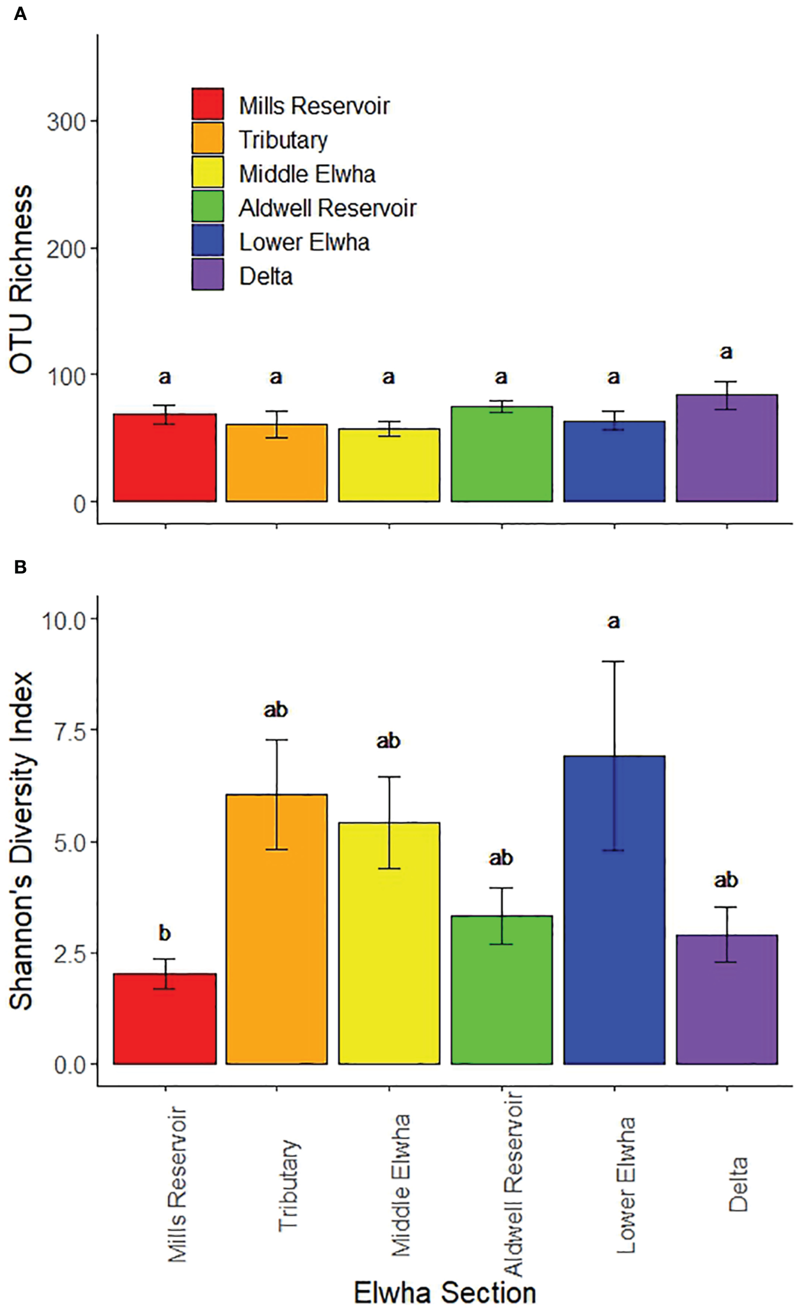

FIGURE 5
Aquatic fungal patterns showing: **(A)** fungal taxa richness (mean number of OTUs per litterbag), and **(B)** fungal taxa diversity (mean Shannon's H' per litterbag) across six different Elwha watershed sections: 1) Red bars: four rivers sites upstream of the Glines Canyon Dam in the former Mills reservoir footprint 2) Orange bars: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 3) Yellow bars: four river sites downstream of the upper Glines Canyon Dam; 4) Green bars: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 5) Blue bars: four river sites downstream of the lower Elwha Dam; and 6) Purple bars: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). Bars represent means +/– 1 standard error and lower-case letters represent diversity values that differ significantly ($p < 0.05$).

not in the tributaries, but in the Middle Elwha, possibly due to low deposition of fine sediment materials in this section (Peters et al., 2017). Decomposition rates did not decline longitudinally from upstream to downstream as has been hypothesized (Naiman et al., 1987; Sedell et al., 1989), but we may have seen more of a longitudinal pattern had we extended the study further upstream.

Although there are very few studies examining leaf litter decomposition following dam removals, there are several additional studies that have examined leaf litter decomposition above and below dams. In general, the type of dam can partially determine the influence of the dam on leaf litter decomposition because diversion dams result in downstream dewatered areas while

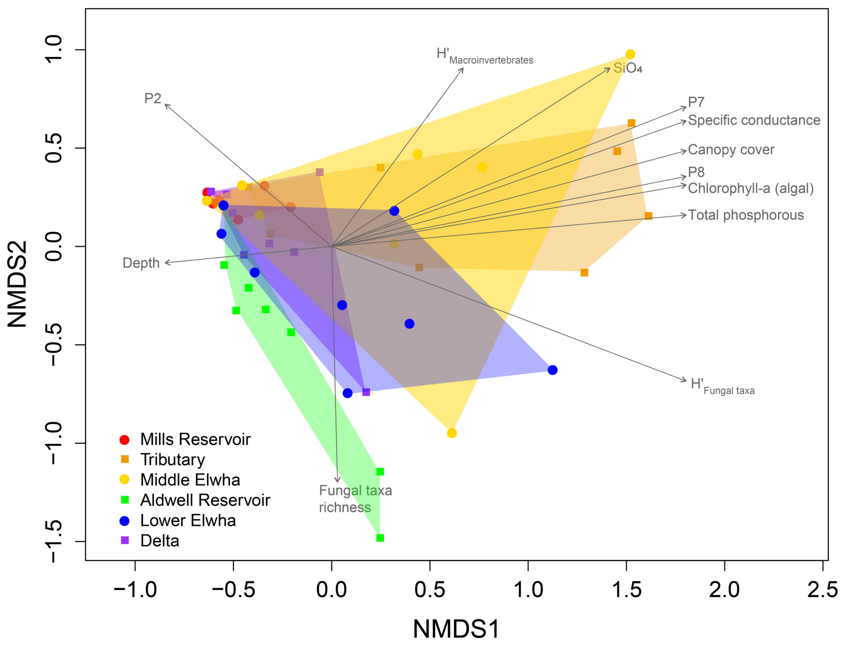

FIGURE 6
Non-metric multidimensional scaling (NMDS) ordination of aquatic fungal communities. Symbols represent fungal OTU (operational taxonomic unit) communities colonizing leaf litterbags in the Elwha River watershed following the removal of two major dams in 2014 and placed at 24 study locations across six sections: 1) Red circles: four rivers sites upstream of the Glines Canyon Dam in the former Mills reservoir footprint 2) Orange squares: four tributary sites not physically influenced by restoration activities (Griff Creek, Lower Little River, Indian Creek, and Madison Creek); 3) Yellow circles: four river sites downstream of the upper Glines Canyon Dam; 4) Green squares: four river sites within the footprint of the former Aldwell Reservoir upstream of the lower Elwha Dam; 5) Blue circles: four river sites downstream of the lower Elwha Dam; and 6) Purple squares: four lentic sites in the newly developing Elwha delta (freshwater sites, not brackish). Vectors represent significant correlations through ordination space with environmental and biological factors. H', Shannon's diversity index; SiO_4, silicate concentration; P8, P7, and P2 represent proportions of sediment of various sizes (P2 = proportion of sediment between 0.0106–0.106 mm; P7 = proportion of sediment between 9.5–13.2 mm; P8 = proportion of sediment between 13.2–26.5 mm).

hydropower dams result in high velocity, cold water releases below dams. Several studies report slower leaf litter decomposition rates below dams (Nelson and Roline, 2000; Tornwall, 2011; Mendoza–Lera et al., 2012; González et al., 2013), sometimes with significant reductions in shredders (Short and Ward, 1980; Tornwall, 2011; Mendoza–Lera et al., 2012) or fungal biomass below dams (Muehlbauer et al., 2009; Colas et al., 2016). However, at dam sites with high nutrient concentrations in tailwaters, the biomass of fungi and macroinvertebrates can be higher at downstream sites (Casas et al., 2000; Menéndez et al., 2012) and counteract the hydrological effects of dams, resulting in no difference in decomposition rates upstream and downstream of dams (Casas et al., 2000; Tabucanon et al., 2019), or occasionally, higher rates of leaf litter decomposition downstream of dams (Short and Ward, 1980; Menéndez et al., 2012; Russing, 2015).

The River Continuum Concept (RCC; Vannote et al., 1980) suggests that the importance of leaf litter inputs as carbon and energy sources to streams and rivers will decline in a downstream direction, with the greatest reliance on leaf litter in the headwaters and the least reliance in large-order rivers (Naiman et al., 1987; Sedell et al., 1989). The Riverine Productivity Model (RPM) modifies these predictions to argue that large rivers receive organic matter inputs laterally and from floodplains, and that decomposer communities can be important in large rivers, especially in littoral habitats (Thorp and Delong, 1994). Litter inputs to large rivers can still be important, as shown by one study which compared leaf decomposition in a low-order stream to a high-order river, and found slower decomposition rates in the high-order river, likely due to sediment deposition, but similar biological activity by invertebrates and fungi at both locations (Chauvet, 1997). Another study compared four locations within two river systems and found highest decomposition rates in headwaters with variation among lower reaches, but generally slower rates in high-order rivers (Minshall et al., 1983). Although not from a direct leaf litter decomposition study, one previous microbial study from throughout a river continuum found that microbial communities in sediments at headwater sites relied on allochthonous dissolved organic matter, with a shift to autochthonous dissolved organic matter downstream (Freixa et al., 2016). Newer visions of the River Continuum incorporate a more patchy dendritic network, and a less strict longitudinal system, incorporating ideas from landscape ecology and metacommunity ecology (Doretto et al., 2020). The newer RPM makes note of the importance of near-continuous inputs of coarse particulate organic matter in larger rivers (Thorp and Delong, 1994). There have been very few studies of leaf litter decomposition throughout watersheds to directly compare low-order and higher-order reaches of the same system, despite the ages of models like the RCC and RPM as well as more recent calls to do this research (Doretto et al., 2020).

Some of the patterns we observed in our data are similar to findings from an earlier study comparing benthic invertebrate and periphyton in dammed and undammed sections of the Elwha (Morley et al., 2008). In that study, the highest densities of periphyton were found in the lower river. Invertebrate communities in these areas of high autochthonous organic matter production may be less efficient at processing leaf litter, as reflected in the lower decomposition rates we observed in Lower Elwha and Delta. Morley et al. (2008) also found that benthic macroinvertebrate community structure differed between Upper, Middle, and Lower sections of the Elwha, with a higher proportion of non-insect taxa in the Lower Elwha compared to a dominance by mayfly in reaches between and above the dams. These pre-dam removal patterns still existed when this study was conducted after dam removal in 2016, with litterbag dwelling baetid mayflies associated with the Middle Elwha and chironomids and oligochaetes associated with the Lower Elwha. Other studies also show baetid mayflies to be abundant at sites just downstream of dams, especially those with high nutrient concentrations in the tailwaters (Brittain and Saltveit, 1989; Casas et al., 2000). In our study, we found that a Nemouridae stonefly (*Zapada* sp.) was also an indicator species for the Lower Elwha sites. Given that previous studies have shown Nemouridae stoneflies to be significantly less abundant downstream of dam sites (Mendoza–Lera et al., 2012), this finding could indicate potential post-dam recovery of in-stream litter dwelling macroinvertebrates.

Some of the most dramatic hydrological and habitat changes in the Elwha watershed after dam removal occurred downstream of both dams in the Lower Elwha (Locations 13, 14, 15, and 16) and the Delta (Locations 17, 18, 19, and 20). Predictive modeling expected that approximately 50–60% of the estimated 21 +/− 3×10^6 m^3 of fine and coarse-grained accumulated sediment behind the dams would erode from the reservoirs, and within the first two years after dam removal, the steep, high-energy Elwha River had transported a large fraction of sediments (mainly fine sediments; Warrick et al., 2015; Peters et al., 2017; Ritchie et al., 2018; Warrick et al., 2019), and water turbidity increased by three orders of magnitude (Foley et al., 2015). This study took place just after the period of greatest geomorphic change in the Elwha watershed, 5–6 years after the start of the dam removal process, and about two years after the removal process had been completed (East et al., 2018). The extreme redistribution and deposition of sediment pushed the river delta approximately 200 m offshore, reducing tidal influence in the pre-dam removal Elwha delta complex and transforming it into a river-driven freshwater system (Foley et al., 2015). This loss of estuarine habitat due to altered water flow, decreased salinity, and elevated turbidity is strongly predicted to alter Elwha food web structure and benthic nutrient cycling in the delta, and likely contributed to the slowest decomposition rates, low fungal diversity, and relatively low macroinvertebrate abundance and diversity at the Delta sites. Seaward of the Delta sites, in tidally regulated wetlands (Foley et al., 2017b), newly formed habitats are emerging where future studies could examine how primary and secondary succession proceed for decomposers in dynamic environments.

The macroinvertebrate and fungal decomposer communities we examined responded differently to the dam removal landscape of the Elwha River. Aquatic macroinvertebrate communities inhabiting leaf litter were structured differently at the Delta sites compared to the rest of the river. In contrast, fungal communities at the Delta sites were not different from any other communities in the river and the communities upstream of both dams (Mills Reservoir sites) were the most different from other sections of the river. Community structure within a section of the river was also more consistent for invertebrate communities, which did not differ in terms of multivariate dispersion among sections. In contrast, fungal communities were most similar to one another upstream of both dams (Mills Reservoir sites), and fungal community dispersion was much higher downstream in the watershed. Invertebrate diversity was highest at Tributary sites and decreased downstream (with a slight uptick at Delta sites), while fungal taxa diversity was actually highest at the Lower Elwha sites and lowest at the most upstream site (Mills Reservoir). Despite these community differences for invertebrates and fungi, two environmental variables, specific conductance and canopy cover influenced the community structure of both groups, with strong positive relationships with Tributary sites. The environmental variables that influenced macroinvertebrate diversity tended to be those associated with tributary conditions: greater canopy cover, higher elevations, and more upstream river distances. These patterns support the results shown by a large review of decomposer communities (Cummins and Klug, 1979; Cummins et al., 1989; Graça, 2001; Hayer et al., 2022). The environmental variables that influenced fungal diversity included greater canopy cover, but also higher nutrient contents (N and P) and greater proportions of inorganic material in the seston and sediment. There are fewer studies examining fungal communities across longitudinal gradients in river systems, but previous research in large rivers argues that fungal decomposers are major players even in high order river reaches (Baldy et al., 1995).

The Glines Canyon and Elwha dams were constructed without fish passage facilities, which prevented upstream migration of anadromous salmonids for over 90 years, as well as prevented extant resident salmonids above the dams from migrating downstream (Brenkman et al., 2008; Pess et al., 2008). The regulation of the river severely disrupted sediment transport and deposition, as well as the movement of woody debris, resulting in a loss of suitable spawning habitat in the reaches of the Lower Elwha (Pess et al., 2008). Pre-dam removal salmonid population declines likely contributed to decreased primary productivity in the Elwha River due to nutrient limitation, as marine-derived nutrient inputs from salmonids are important for freshwater food webs across trophic levels (Duda et al., 2011; Tonra et al., 2015; Kane et al., 2020). As anadromous salmonids return to the Elwha (Kane et al., 2020; Quinn et al., 2021), we expect increases in productivity at all trophic levels and continued alterations to other ecosystem processes like organic matter processing. For example, we found highest levels of fungal diversity at Lower Elwha sites, which could be related to greatest spawner densities.

Dam decommissioning and removal in the United States has increased in the last several decades as social and ecological risks have begun to outweigh benefits generated by dams (Duda et al., 2016). At the time of this study, the simultaneous removal of the Elwha and Glines Canyon dams on the Elwha River in northwestern Washington State was the largest dam removal in the world (Warrick et al., 2019). The two dam removals on the Elwha River offered a unique opportunity to evaluate the impact of watershed-wide ecological restoration within a relatively short timeframe on organic matter processing and decomposer communities. Information on fundamental ecological processes such as organic matter decomposition are essential to better understand the mechanisms underpinning restoration response.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/carrileroy/Elwha2016.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CL, SM, and JD conceived of this study. CL supervised all research and students, coordinated field trips, ensured quality control, created figures, analyzed data, coordinated microbial sequencing and processed sequencing data, and wrote major components of the manuscript. SM coordinated field trips, collected and summarized field data on environmental variables, supervised NOAA staff and field collections, and provided expert opinion on macroinvertebrate identification. JD coordinated field trips, collected and summarized field data on environmental variables, and supervised USGS staff and field work. MS sorted macroinvertebrate samples and provided preliminary identifications. AZ, PL, CP, AB, BK, SH, and CL updated macroinvertebrate identifications and organized final data. PL created the GIS map in ArcGIS Pro. RP provided sediment analysis at all study sites. RM and MF coordinated the placement and removal of litterbags and fungal samples at the Elwha Delta sites. RJ coordinated the placement of fungal samples across all river sections. JV prepared and processed fungal samples for DNA extraction. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research 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.2023.1231689/full#supplementary-material

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Persistent disconnect between flow restoration and restoration of river ecosystem functions after the removal of a large dam on the Sélune River

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The removal of the two dams on the Sélune River since 2019 has led to profound changes in the aquatic ecosystem. Lentic habitats bordered by forest had shifted to new conditions (running water and sparsely vegetated riverbanks) therefore shaping organisms' assemblies. We studied how the reestablishment of aquatic lotic habitats in interaction with riparian vegetation could mediate the restoration of important ecological functions in the new river. Six stations located along the river continuum were surveyed for 3 years after dam removal: two control stations upstream the former reservoir, three restored stations within the former reservoir, and one control station downstream. We monitored physico-chemical characteristics, phytobenthos biomass and the river's benthic metabolism, and assessed the functional composition of macroinvertebrate communities. We compared the recorded variables among upstream, downstream and restored sampling stations. We observed a rapid recolonization by invertebrates, but a still low phytobenthic primary production in restored stations. Such a low primary productivity was also reflected in the functional composition of invertebrate communities. Three years after dam removal, there was still a significant time lag between communities recovery and expected ecosystem functioning restoration. We observed a quick colonization by aquatic running-water invertebrate communities of new lotic reaches, but a slower recovery of important ecological functions rates such as those observed in control stations.

KEYWORDS

functional integrity, river restoration, phytobenthos, macroinvertebrate feeding groups, river metabolism, gas exchange, benthic chambers

1 Introduction

Dams and impoundments have been built for thousands of years for various purposes, including flood control, water supply, irrigation, recreation, navigation, and hydropower generation. However, the number of dams and reservoirs has increased markedly over the past decades, and they are potentially impacting up to 575,900 km of rivers worldwide (Lehner et al., 2011). Even if most of them are small, at least 50,000 of them are large dams higher than 15 m (Berga et al., 2006). Dams and reservoirs are among the main causes of freshwater biodiversity loss (Vörösmarty et al., 2010; Grill et al., 2019; Reid et al., 2019). Decades of research have highlighted the adverse effects of dams on the physical, chemical, and biological characteristics of rivers (Ward and Stanford, 1983; Poff et al., 1997; Rodríguez-Pérez et al., 2021). Consequently, the removal of dams has accelerated significantly in recent decades, and more than 2,000 have been removed in the United States and Europe, mainly low weirs and small dams considered obsolete or abandoned long ago (Bellmore et al., 2017; Habel et al., 2020).

Concomitantly, interest in dam removal as a means of river restoration has driven attention to important new challenges for watershed management and created opportunities for advancing the science of aquatic ecology (Hart et al., 2002; Bellmore et al., 2019). One of the main scientific challenges lies in determining the magnitude, timing, and range of the physical, chemical, and biological responses that can be expected following dam removal (Hart et al., 2002). Therefore, the removal of a dam is a tricky question, and the decision must be taken after careful examination of possible environmental consequences (Doyle et al., 2003; Noda et al., 2018; Habel et al., 2020). Given the relatively small number of studies on the effects of dam removal and the wide range of observed outcomes, the range, magnitude and trajectory of the expected ecological responses are highly uncertain. Environmental responses to dam removal depend on many factors not yet clearly addressed and are highly context dependent (Foley et al., 2017a; Bellmore et al., 2019). For example, improved understanding will require greater focus on how the responses to removal vary with the dam type, the river characteristics, and the watershed setting (Hart et al., 2002). The effects of small dam removal may be much smaller than those of large dam removal (Poff and Hart, 2002; Foley et al., 2017a), notably regarding the physical effects (Major et al., 2017) and their consequences on vegetation colonization and succession (Shafroth et al., 2016) and biological activities (Bellmore et al., 2019). Moreover, the sole responses of specific species (i.e., migratory fish) have been monitored in many studies, and the mechanisms underlying the restoration of the entire ecosystem are still poorly understood (Bellmore et al., 2017). The challenge is greater for the removal of large dams (>15 m high) presenting much larger impacted areas and bigger expected consequences and for which far fewer study cases are available than for small dams and weirs (Wieferich et al., 2021).

Current knowledge on the effects of large dam removal on sediment loss and channel morphology, fish, and riparian vegetation in the former reservoir or in the downstream section are rather limited (Wieferich et al., 2021). Upstream of the dam, a positive and rapid impact of dam removal on sediment storage and geomorphology has been showed (Wilcox et al., 2014; Randle et al., 2015) and also a positive and rapid effect on migratory fish (Bellmore et al., 2019; Duda et al., 2021), with potential indirect effects on non-migratory species (Tabor et al., 2022). The macroinvertebrate community also recovered quickly within 2 years following the removal of dams (Bellmore et al., 2019; Mahan et al., 2021). However, dam removal usually triggers the downstream movement of large amounts of sediment stored in the reservoir that typically increase turbidity, clog the substrate, decrease invertebrate density (Foley et al., 2017b; Mahan et al., 2021) and reduce autotrophic biofilm biomass and activity, at least over the short term (Bellmore et al., 2019; Atristain et al., 2023). In terms of temporal dynamics, most biological and physico-chemical components (Foley et al., 2015) respond much faster than geomorphological ones (Major et al., 2017). In large dam removal case studies, the subsequent responses of the fish and invertebrate communities take between a few months to 1–3 years after dam removal (Mahan et al., 2021; Dézerald et al., 2023), and the same is true for small dam removal (Carlson et al., 2018).

At the ecosystem level, the potential impacts on ecosystem functioning caused by the mobilization of stored sediment, nutrients, and organic matter from aquatic ecosystems and/or riparian vegetation changes are still poorly understood (Bellmore et al., 2019). This is especially true for large dams: no study had focused on the functional responses of their freshwater ecosystems, except the recent short-term study on Enobieta dam removal on biofilm in Spain (Atristain et al., 2023). Some of the potential impacts on ecosystem functioning can be deduced using known chemical, physical, and biological responses to dam removal. After the removal, the environmental conditions in the new channel shift from a lentic (lake) to a lotic (riverine) system that changes the types of organisms in the former impounded reach. Aquatic communities may also shift from pelagic-to benthic-dominated primary producers and invertebrate consumers (Bellmore et al., 2019). As a consequence, we should expect important changes of the river ecosystem functioning, notably its oxygen metabolism. The river metabolism is driven by two fundamental functional processes that regulate carbon and nutrient cycling in river systems (Tank et al., 2010): i) gross primary production (GPP) is the total fixation of inorganic C to organic C by all photoautotrophs, and ii) ecosystem respiration (ER) corresponds to the mineralization of organic C by all organisms in the ecosystem. The GPP/ER ratio can also be used to characterize heterotrophic streams (GPP/ER < 1) often supplied by external inputs of terrestrially derived organic C. Conversely, in autotrophic streams most of organic C is provided by the photosynthetic activity of primary producers. The river metabolism is highly correlated to the stream size (Vannote et al., 1980), turbidity or light (Dodds et al., 2013), or the presence of dams (Chowanski et al., 2020), so that it appears as a good indicator to follow ecosystem-level consequences of dam removal since all these parameters are affected by the removal.

To document the ecosystem responses to large dam removal, we assessed the consequences of the removal of one the Sélune River large dams (36 m high) over 3 years by following the trends in physico-chemical parameters, ecosystem functioning, and community structure shifts. We focused on benthic processes and communities—both producers and consumers—e.g., the benthos metabolism, the phytobenthos community composition, and the

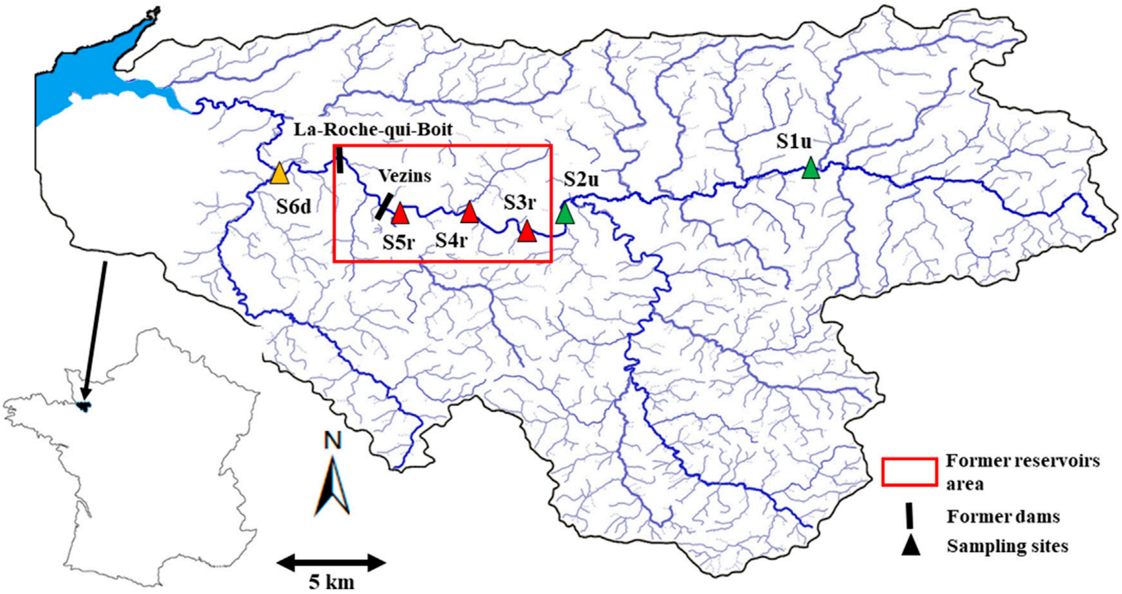

FIGURE 1
Spatial locations of sampling stations on the Sélune River.

macroinvertebrate community trophic structure. By comparing six lotic stations located upstream, downstream and in the new running-water reach that replaced the former reservoirs, we expected (hypothesis H1) a fast homogenization of physico-chemical conditions between the control stations upstream and the stations in the new channel following restoration of water flow, except for turbidity as sediments are exported and affect this parameters downstream. Conversely, the restoration of phytobenthos and of the river metabolism should take longer in the former reservoir and downstream (hypothesis H2) because of higher water turbidity and unstable sediment on the river bottom. Finally, the trophic structure of the macroinvertebrate community should reflect the changes in the availability of feeding resources such as the increase in benthos autochthonous primary production in comparison with a higher contribution of pelagic primary production in the former reservoirs and the decreased sedimentation of fine particles (hypothesis H3).

2 Materials and methods

2.1 Study site

The Sélune River is located in Normandy (France), in a temperate oceanic climate region (Rodríguez-Pérez et al., 2021). It is a 91 km-long coastal stream (mean slope 0.3% to 0.1% in its downstream part) flowing into the Mont Saint Michel Bay after draining a watershed of 1,106 km^2 mainly composed of schists and metamorphic rocks. The Sélune River basin lies in a patchy landscape made of forests, pastures, and traditional extensive livestock farming with very few crop areas. The watershed's climate is oceanic, with a low temperature amplitude and rainfall distributed throughout the year with highest precipitation in December and lowest in July. The Sélune River floods regularly in winter and spring (Fovet et al., 2023). Until recently, the water flow and chemistry of the Sélune River had been profoundly impacted over a 17 km-long section (Fovet et al., 2020; Rodríguez-Pérez et al., 2021) by two large hydropower dams built in 1919 and 1932, respectively and separated by a very short (<1 km) free-flowing section. The amount of fine sediments stored in the 2 dam reservoirs was estimated as 1,800,000 m^3 (IDRA, 2012). A small part of the reservoir was contaminated with heavy metals (Andrade et al., 2020), but these sediments were dredged and safely stored outside the riverbed before the removal. The most upstream dam—Vezins Dam (36 m height)—was removed in 2019 after 1 year of regular decrease of the water level in the reservoir, whereas the second dam—Roche-qui-Boit Dam (16 m height)—was completely removed in 2022 (see Dézerald et al., 2023 for details). To keep the massive amount of sediments stored in reservoirs from clogging the downstream section of the river, much of it was dredged and stored in ponds built with gabions and dykes made with local sediments (Berrée, 2019). After the sediments had dried, the gabions were removed.

Six sampling stations were chosen according to their relative positions to the dams (Figure 1). S1u (48°35′56.5″N 0°57′28.5″W) and S2u (48°34′18.0″N 1°06′58.4″W) were located upstream of the two reservoirs, had never been impacted by the dams except for the absence of migratory anadromous fishes, and were used as control stations. These two stations presented slightly anthropized conditions (pasture) but altogether natural river banks with typical riparian tree communities along the rivers of this region (Ravot et al., 2020). S3r (48° 33′ 53.9″N, 1° 09′ 2″W), S4r (48°34′22.1″N 1°10′51.9″W) and S5r (48°34′36.2″N 1°13′11.5″W) were located in the new channel after the recovery of the natural flow regime since 2019 (Figure 2). Finally, S6d was located 4 km downstream of the second dam (48° 35′ 44.9″N, 1° 17′ 35.9″W). The water depth was 80–100 cm maximum and the river was fully wadeable in all stations.

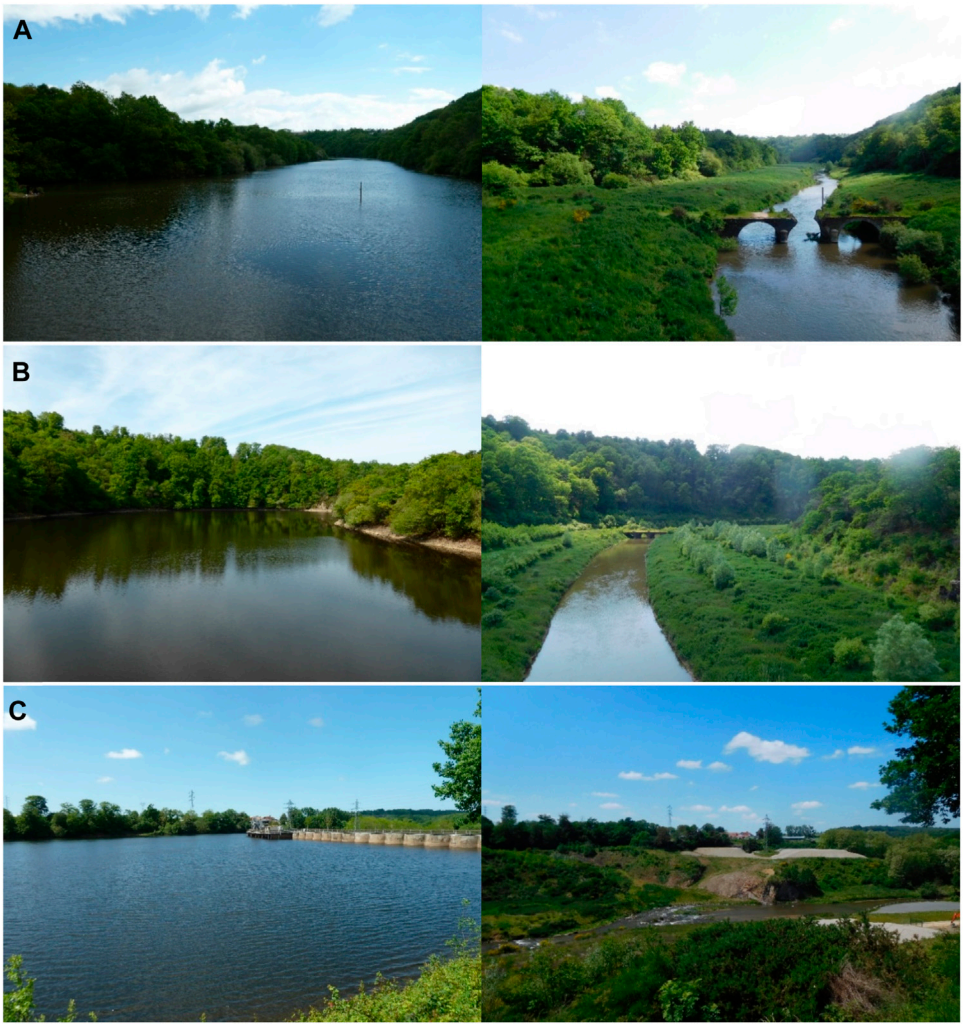

FIGURE 2
Pictures of the stations [**(A)**: S3r; **(B)** S4r; **(C)** S5r] in the Vezins Reservoir before (left side; May 2015) and after (right side; May 2023) the dam removal. Photograph credits of "Observatoire photographique des paysages de la Sélune—Université Paris Nanterre et SMBS".

2.2 Measurement of functional restoration

2.2.1 Physicochemical parameters

Water chemistry was recorded seasonally (four seasons per year) at each station from June 2020 to December 2022. Sampling frequency didn't allow to highlight short events (e.g., turbidity peak), but this monitoring programme was enough to compare the values between stations. Measurements were always carried out after stabilised water flows (i.e., at least 1 week) and almost simultaneously (time lag of more or less 2 h between S1u and S6d). Water temperature, conductivity, the pH, the dissolved oxygen content (WTW 3320, WTW, Weilheim, Germany) and turbidity (Turb 430T, WTW, Weilheim, Germany) were measured in the field. Filtered-water samples (Syringe filter 0.45 µm, Sarstedt, Nümbrecht, Germany) were analyzed by colorimetry methods for soluble reactive phosphorus, ammonium and nitrate using laboratory test kits for spectrophotometer (PhotoLab 7100 VIS WTW, Weilheim, Germany).

2.2.2 Phytobenthos composition and biomass

The biomass of chlorophyll a in the biofilm (i.e., green algae, diatoms and cyanobacteria), naturally growing on river's hard substrate, was estimated at each station by the end of June 2020, 2021 and 2022 using a BBE Benthotorch fluorescence probe (bbe moldaenke GmbH, Germany). Twenty-eight to thirty-four measurements were taken randomly at each station upon similarly sized pebbles and boulders.

2.2.3 Benthic metabolism

The benthic metabolism of the river bed was estimated in all stations in spring (mid-May) and summer (end of July) 2022, except at S5r and S6d where the use of equipment and measuring tools was not possible due to high turbidity and unstable sediment on the stream bottom in relation to the breaching of the second dam in June 2022. The metabolism was estimated using optically clear acrylic benthic chambers and dark benthic chambers for estimating benthic fluxes of CO_2 (pH values in this section of the river remained stable)

(Colas et al., 2021). The 20-cm diameter chambers were buried around 10 cm inside the sediment to reach a volume of around 3 L for the measurement of gas exchanges. The chambers were equipped at the top with a HOBO Temperature/Light sensor (UA-002) data logger, and a hand-held mixer inserted through cable glands. The mixer was used for water homogenization inside the chamber just before water sampling. A PVC tube (6 and 4 mm outer and inner diameters, respectively) with a valve inserted through a cable gland placed at the top of the chamber allowed the water to drain into the chamber during immersion and avoided air bubbles getting into the chamber. The PVC tube also allowed water to get inside the chamber during water sampling in the middle of the chamber at around 10 cm above the sediment. Deployments usually started between 10:30 and 11:00 a.m. by lowering the chamber into the sediment and fixing it using two threaded rod bars (12-mm diameter) sank 40 cm into the sediment and large wing nuts to maintain it in the sediment. Five pairs of dark and clear chambers were placed on soft gravel sediment at each station, at less than 1 m depth and 1-2 m from the bank to avoid shaded areas and vegetation patches. Incubation lasted around 5 h, during which temperature and light were recorded every 10 min to take into account frequent local variations in oceanic weather conditions. At the beginning and at the end of the incubation, 100-mL water samples were collected using 200-mL syringes with three-way stopcocks connected to the end of the PVC tubing equipped with a Luer-lock syringe valve. We created a 100-mL headspace in the syringes with ambient air for each water sample, and then the sample was shaken for 2 minutes to homogenize the concentration of dissolved and air gases. Then, the headspace was stored in Tedlar bags at room temperature (≅ 20°C) for less than 24 h. For each station, additional samples of air were taken at the beginning and at the end of the incubation. As photosynthetic activity was very low at the bottom of the river, the variation in dissolved O_2 was small and the probes were not sensitive enough to detect a small variation over only 5 h of incubation and our measurement protocol did not allow us to obtain robust values for O_2. Consequently, we preferred to use river metabolism using only dissolved CO_2 concentrations. The CO_2 concentrations were finally measured by GC-MS (microGC 3000, Agilent Technologies, Inc., Santa Clara, United States).

The CO_2 concentration (C, mmol) in the chamber was calculated as follows (Eq. 1):

$$C = \left(\beta + \frac{V_{atm}}{V_{water}}\right) \times (C_{water} - C_{atm}) \tag{1}$$

where V_{water} is the volume (mL) of the sample in the syringe and V_{atm} is the volume of the headspace, C_{atm} and C_{water} are the CO_2 concentrations (ppm) measured with the micro-GC in the atmosphere and in the water, and β is the Bunsen coefficient of dissolution (L/L_{atm}) computed as follows (Eq. 2):

$$\ln(\beta) = a_1 + a_2\left(\frac{100}{T}\right) + a_3 \ln\left(\frac{T}{100}\right) + S\left[b_1 + b_2\left(\frac{T}{100}\right) + b_3\left(\frac{T}{100}\right)^2\right] \tag{2}$$

where $a_1 = -58.0931$; $a_2 = 90.5069$; $a_3 = 22.294$ and $b_1 = 0.0278$; $b_2 = -0.02589$; $b_3 = 0.00506$ are constants for the Bunsen calculation (Weiss, 1970; 1974), T is temperature (K) and S salinity (‰).

The flux of CO_2 in chamber (F_{CO2}, mmol.m^2.day^{-1}) was calculated as follows (Eq. 3):

$$F_{CO2} = (C_t - C_0) \times \frac{24}{t_i} \times V_c \Big/ S_c \tag{3}$$

where C_0 is the CO_2 concentration at the beginning of incubation and C_t the concentration at the end, t_i is the duration of incubation (h), V_c the volume of the chamber (L) and S_c the surface area of the sediment enclosed in the chamber (m^2).

We used F_{CO2} in dark chambers as a proxy of the ER of the benthos, and the difference between F_{CO2} in the clear and dark chambers as a proxy of the Net Primary Production (NPP). Contrary to the classical approach of river metabolism with O_2, with F_{CO2} we could not measure the GPP as F_{CO2} is the result of the photosynthetic activity which consumed the CO_2 and the respiration of the benthos that produces CO_2. However we could use the NPP as a proxy of the intensity of the net ecosystem production of CO_2.

Finally, by using a YSI EXO2 multiparameter sonde (YSI, Yellow Springs, OH, United States) the following parameters were recorded every 10 s during the incubations: temperature (°C), electrical conductivity (µS.cm^{-1} corrected to 25°C), dissolved oxygen (% and mg.L^{-1}), turbidity (NTU), pH, total algae (chlorophyll + phycocyanin and phycoerythrin, RFU), fluorescent dissolved organic matter (fDOM, QSU), and water depth (m). These measures taken in the water surrounding chambers allowed to record any brief events occurring during the incubations.

2.2.4 Macroinvertebrate sampling

Benthic macroinvertebrates were sampled using a Surber net sampler (0.05 m^2, 0.5 mm mesh size) in May 2020 and 2022. Six stratified samples were collected at each date and station in order to cover a similar range of available habitats (cobble, sand-sediment, macrophytes, leaf litter and debris). The samples were immediately fixed with 96° ethanol and stored until sorting under a binocular microscope. Taxa were identified down to the species or genus levels (most crustaceans and Insect larvae), except Nematoda, Hydracarina (not identified further), and most of Diptera (identified down to the family/tribe levels).

We assigned trait values to each invertebrate taxon and each modality according to Tachet et al. (2010) and the freshwaterecology. info database (Schmidt-Kloiber and Hering, 2015). Whenever the taxonomic resolution of our list and that of the databases did not match, we used the next upper taxonomic resolution. Only the feeding habits were retained according to their potential sensitivity to changes in feeding resource availability (light, riparian vegetation) after dam removal. The percentage of each feeding group in the macroinvertebrate community was computed by multiplying the affinity scores of each invertebrate taxon for each feeding group by the abundance.

We also computed the abundances of scrapers/(shredders + collectors) ratio ($R_{a/h}$). This ratio highlights the balance between autotrophy and heterotrophy (Merritt et al., 2017). The ratio increases when invertebrates using autotrophic resources (i.e., scrapers) dominate the community in comparison with invertebrates using heterotrophic resources (shredders and collectors).

TABLE 1 Mean values (±SD) and results of the similarity percentage (SIMPER) analysis of water quality (normalized values) after the dam removal, and percent contribution to compositional dissimilarity between the control (C: S1u and S2u) and restored (R: S3r, S4r, and S5r) stations and between the restored and downstream (D: S6d) stations.

Parameter	Control stations	Restored stations	Downstream	Contrib. (%) C vs. R	Contrib. (%) R vs. D
Temperature (°C)	12.4 ± 4.4	13.5 ± 5.2	14.1 ± 5.8	11.6	19.1
pH	7.2 ± 0.2	7.5 ± 0.5	7.5 ± 0.4	14.2	16.9
Cond. ($\mu S.cm^{-2}$)	191 ± 41	225 ± 35	227 ± 31	16.1	11.0
Turbidity (NTU)	12.6 ± 4.3	15.1 ± 5.4	11.1 ± 4.4	14.2	16.0
NO_3^- ($mg.L^{-1}$)	28.5 ± 5.8	33.4 ± 4	35.0 ± 4	16.2	10.0
NH_4^+ ($mg.L^{-1}$)	0.09 ± 0.11	0.06 ± 0.02	0.07 ± 0.02	14.8	11.3
PO_4^{3-} ($mg.L^{-1}$)	0.10 ± 0.05	0.11 ± 0.03	0.10 ± 0.05	12.9	15.7

2.3 Statistical analysis

The seasonal physico-chemical datasets collected from 2020 to 2022 were used to test for differences in water quality between the control (S1u and S2u), restored (S3r, S4r, and S5r) and downstream (S6d) stations using PERMANOVA (Anderson and Walsh, 2013). The data were normalized before generating a similarity matrix (Euclidian distance similarities) to test the factors “station” and “date” with Monte-Carlo tests. We also conducted a similarity percentage analysis (SIMPER) to determine which water quality parameters changed according to the station type (control vs. restored and restored vs. downstream). PERMANOVA and SIMPER analyses were performed using PRIMER 7 software (PRIMER-E, Plymouth, United Kingdom).

Between-station differences in the phytobenthos biomass and benthic flux of CO_2 (F_{CO2}) were compared statistically using one-way ANOVAs *per* date and *per* type of chamber (dark vs. clear) with “station” as a fixed factor. For the macroinvertebrate feeding groups, we used two-way ANOVAs on square-rooted data for normalization, with “station” and “year” as fixed factors. For all tests, pairwise comparisons were performed using Tukey’s HSD tests. All analyses were carried out using Statistica 7 software (StatSoft).

3 Results

3.1 Physicochemical parameters

Physico-chemical parameters varied between stations along the upstream-downstream gradient and across years (see Supplementary File S1 for annual data). Briefly, we observed an increase in temperature up to 2.6°C and in a lower extend an increase in pH (up to 0.5 UI), conductivity (up to 72 $\mu S.cm^{-2}$) and NO3 (up to14.3 $mg.L^{-1}$), except for turbidity and PO_4^{3-} which increased from upstream to downstream but decreased at Sd6.

The PERMANOVA on the physico-chemical dataset showed a highly significant “station” effect (Pseudo-F = 2.84; $p = 0.001$) but a weak “sampling date” effect (Pseudo-F = 2.07; $p = 0.047$), and no interaction between “station” and “date” (Pseudo-F = 0.23; $p = 1.0$). Pairwise comparisons highlighted that the “station” effect only concerned S1u, which significantly differed from all other stations (p values <0.02), whereas the other stations did not differ significantly (p values >0.175). A marginal effect of “date” was found between 2021 and 2022 ($p = 0.042$). SIMPER analyses showed that multiple water quality parameters contributed to the change in overall conditions upstream and downstream (Table 1). Increases in turbidity, nitrate, conductivity, and pH accounted for 60.7% of the dissimilarity in water quality conditions between the two control and the three restored stations. In the downstream station, temperature increased but the pH, turbidity and reactive phosphorus decreased and accounted for 67.7% of the dissimilarity in water quality between the restored (S3r, S4r, and S5r) and the downstream (S6d) stations.

3.2 Phytobenthos composition and biomass

Whatever the station, the phytobenthos community was composed of a majority of diatoms (mean value 50.0% ± 15% of total biomass) and cyanobacteria (mean value 48.0% ± 16% of total biomass). Green algae represented only a very small share of the phytobenthos (1.0% ± 6% of total biomass). Green algae were detectable in only 4% of the samples, exclusively in summer. Consequently, this group was discarded for further analyses. The biomasses of cyanobacteria and diatoms strongly varied between years (Figures 3A, B; p-values <0.0001), but the overall trends among stations remained similar over time (Figure 3C), except for diatoms in S4r in 2020. S3r and S5r hosted a lower phytobenthic biomass than S1u and S2u (Figure 3C). However, the difference was greater in 2020, especially for diatoms, and was highly reduced in 2021 and 2022, except for in S6d where the biomass of both diatoms (Figure 3A) and cyanobacteria (Figure 3B) strongly declined in 2021 and 2022.

3.3 Benthic metabolism

Benthic gas fluxes of CO_2 were successfully estimated in the five stations in spring, and only in four stations in July because data from Sr5 were not reliable in summer (Figure 4). Fluxes ranged from −0.08–1.27 g CO_2. m^{-2}. d^{-1} for F_{CO2}. In most cases, a net benthic primary production was recorded in the clear chambers (CO_2 consumption), except at S2u in spring and at S4r in summer

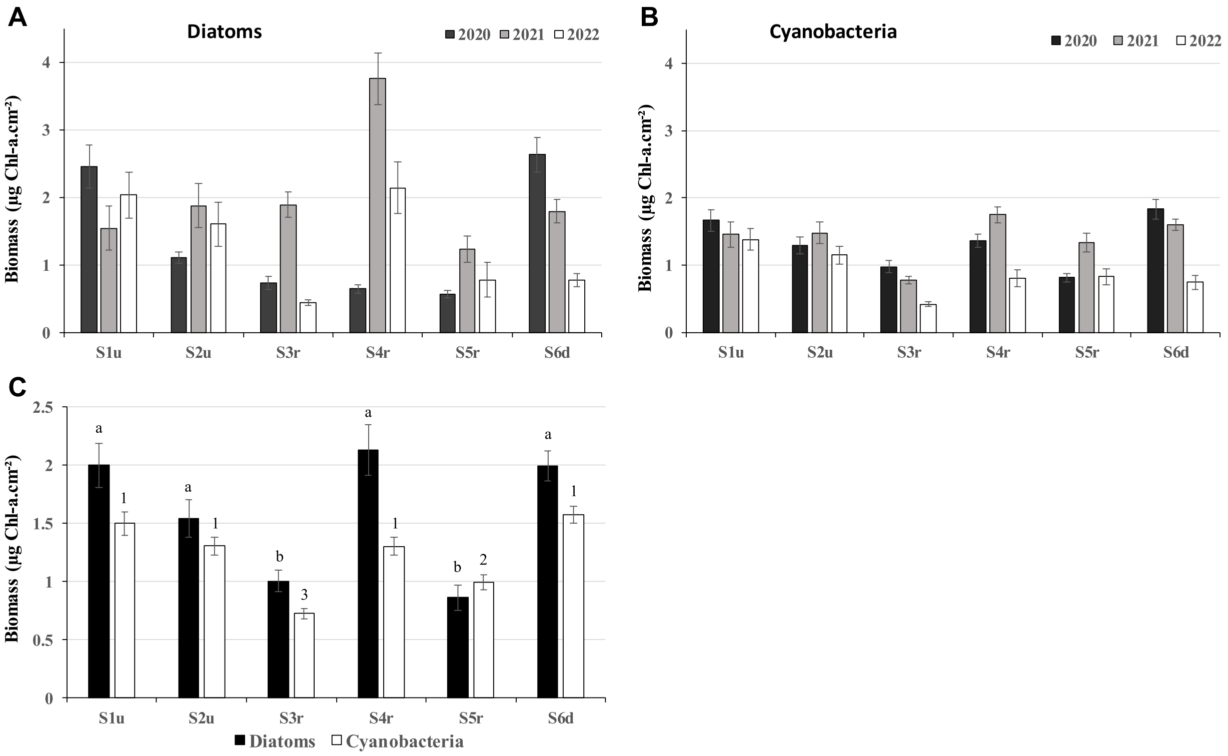

FIGURE 3
Mean chlorophyll biomass values ± SD measured in the summer 2020, 2021 and 2022 at each station for diatoms **(A)** and cyanobacteria **(B)** and mean values ± SD per station **(C)**. Small letters (for diatoms) and numbers (for cyanobacteria) indicate significant differences between stations.

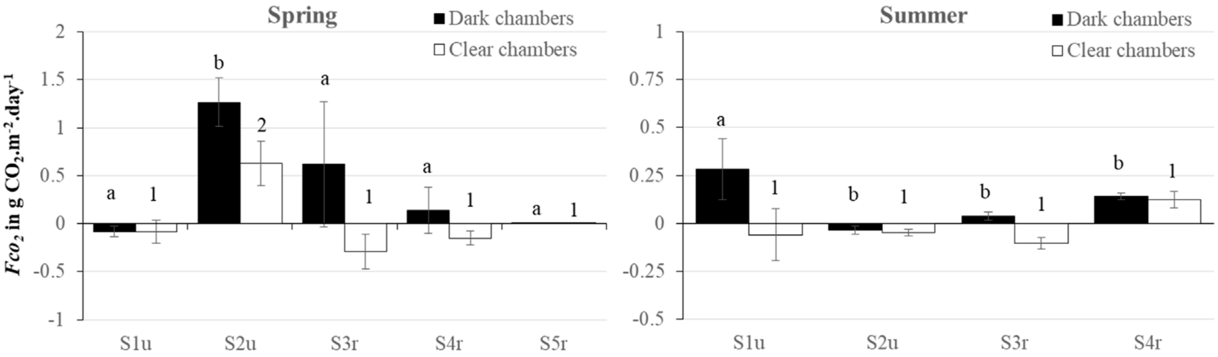

FIGURE 4
Mean values ± SE of benthic flux of CO_2 measured in dark chambers (black bars) and clear chambers (white bars) in spring and summer 2022. Small letters (for dark chambers) and numbers (for white bars) indicate significant differences between stations.

that exhibited benthic fluxes suggesting a higher sediment respiration.

The ER of the benthos tended to be lower in the restored stations in spring and in control and restored stations in summer, but the difference were not significant (Fisher exact *t*-test, *p* values >0.210). Conversely, GPP was similar in all stations in spring ($p = 0.392$), but decreased significantly in the restored stations in summer (Table 2, $p = 0.029$). The GPP/ER ratio (Table 2) increased significantly in restored stations compared with control stations in spring ($p = 0.026$) and tended to be higher also in summer, even if the difference was not significant in summer ($p = 0.472$).

3.4 Macroinvertebrate feeding groups

The proportion of most of the different feeding groups (Figure 5) varied significantly across stations (*p* values <0.049) and years (*p* values <0.006), except for deposit feeders that were similar among stations ($p = 0.093$), and shredders that remained

TABLE 2 Mean values (±SE) of ecosystem respiration (ER) and gross primary production (GPP) in the control (S1u and S2u) and restored (S3r, S4r, and S5r) stations in spring and summer 2022. Small letters indicate results of Fisher exact t-tests between stations and seasons for each indicator.

Parameter	Stations	Spring	Summer
ER (g CO_2.m^{-2}.d^{-1})	Control	0.59 ± 0.67^a	0.12 ± 0.16^a
	Restored	0.25 ± 0.19^a	0.09 ± 0.05^a
GPP	Control	0.32 ± 0.32^a	0.18 ± 0.16^a
(g CO_2.m^{-2}.d^{-1})	Restored	0.40 ± 0.27^a	0.08 ± 0.6^a
GPP/ER	Control	0.24 ± 0.27^a	0.81 ± 0.39^a
	Restored	1.49 ± 0.36^b	1.99 ± 1.86^a

stable across stations and years (Figure 5B, $p = 0.283$ and $p = 0.490$, respectively).

As for the feeding groups, the $R_{a/h}$ ratio also varied spatially and temporally (p values <0.001). There was not significant interaction between "station" and "year" for the feeding groups (p values >0.077), except for scrapers ($p < 0.001$) and the $R_{a/h}$ ($p < 0.001$) ratio. The proportion of scrapers increased toward the downstream station to become the dominant feeding group (Figure 5A), whereas deposit-feeders (Figure 5C) and predators (Figure 5E) decreased toward the downstream station. The proportion of filter-feeders (Figure 5D) remained stable across stations and years except in D where they significantly dropped down in 2022. As for scrapers, their $R_{a/h}$ ratio also increased in the restored (S3r, S4r, and S5r) and downstream (S6d) stations (Figure 5F).

4 Discussion

The ecosystem of the Sélune River was strongly modified by the erection of two successive large dams between 1919 and 1932. For almost one century, deep changes occurred in this ecosystem and shaped plankton and macroinvertebrate communities along half of

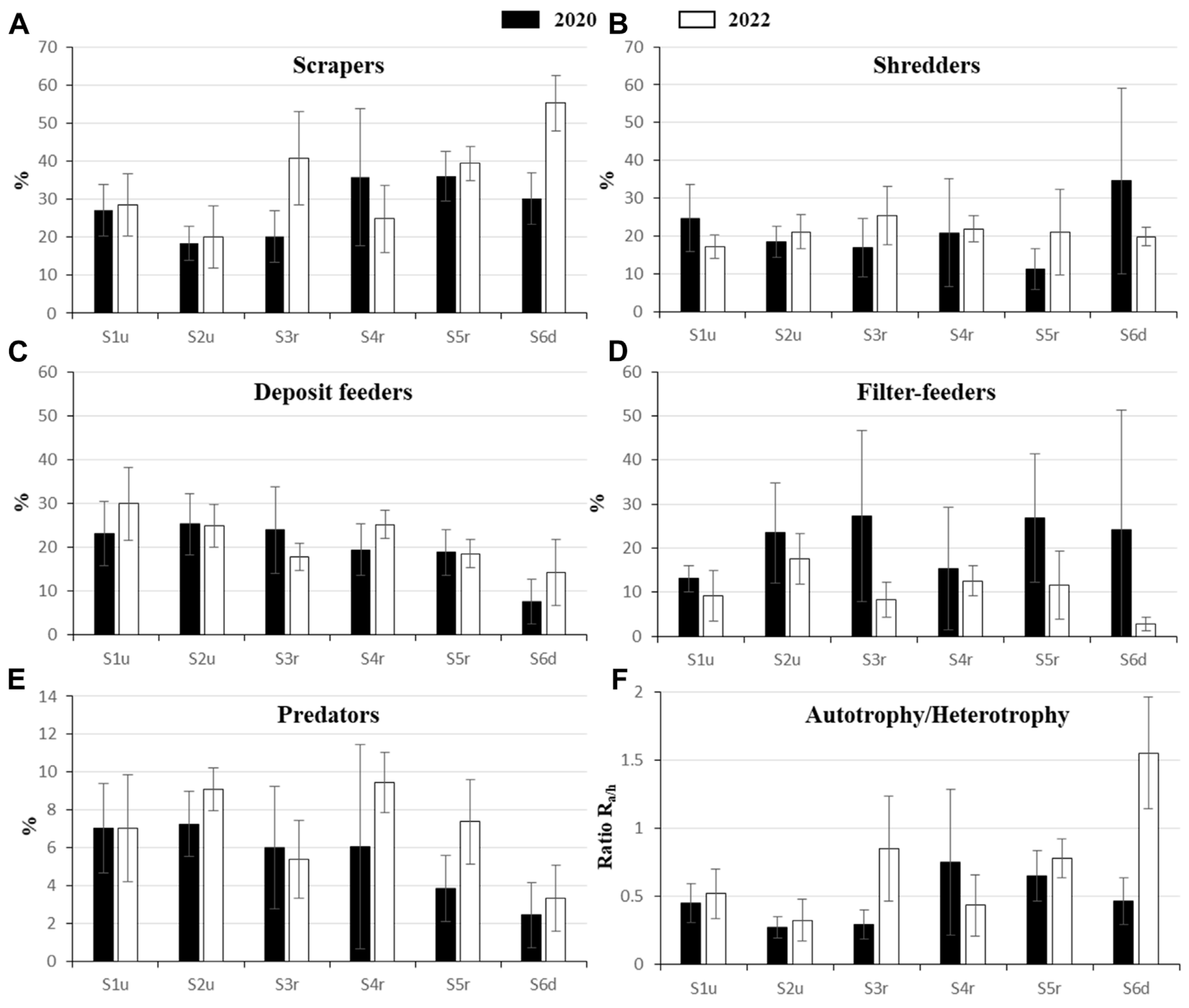

FIGURE 5
Mean percentage values (±SD) of the main feeding groups in the macroinvertebrate community in 2020 (dark bars) and 2022 (white bars): **(A)**, scrapers; **(B)**, shredders; **(C)**, deposit feeders; **(D)**, filter feeders; **(E)**, predators; **(F)**, $R_{a/h}$ ratio.

the main stem (Rodríguez-Pérez et al., 2021) and also induced a major discontinuity in the natural process of C flow in aquatic food webs along the river by promoting carbon sequestration (Roussel et al., 2024). The two dams strongly altered the physical, chemical and biological continuity of the river, but their vicinity was not sufficient to create differential impacts: their impact is as that of a single artificial water mass (Rodríguez-Pérez et al., 2021). Overall, our results show that the removal of dams leads to a relatively fast homogenization of habitats and environmental conditions within the former reservoirs, but also important changes downstream since the removal.

4.1 Consequences of dam removal on physico-chemical conditions

In 2021, only 1 year after the removal of Vezins Dam and the decommissioning of Roche-qui-Boit Dam (i.e., the reservoir has been emptied in 2021 before its removal in 2022), only subtle changes in water quality were noticed downstream between the control, restored and downstream stations. This result confirms a very fast restoration of water flows and homogenization of chemical factors following geomorphological restoration, except for turbidity (Fovet et al., 2023) and temperature (hypothesis H1), as observed in previous restorations of large dams (Foley et al., 2015; Atristain et al., 2023) and as expected in conceptual models (Bellmore et al., 2019). Before the dam on the Sélune River was removed, reservoirs were characterized by higher temperature, higher conductivity, a higher total nitrogen concentration but a lower turbidity and lower phosphorus concentrations than in running-water reaches (Rodríguez-Pérez et al., 2021). These differences disappeared for most of the parameters, except temperature and turbidity. Turbidity tended to increase in the restored stations in comparison with the control (S3r, S4r, and S5r) and downstream (S6d) stations, likely explained by the destocking of fine sediment (Wilcox et al., 2014; Bellmore et al., 2019) that was partly deposited downstream in the second reservoir of the decommissioning dam in 2021 and before reaching the downstream station and subsequently the ocean after the removal of the second dam in 2022. This result is corroborated by the continuous monitoring of physico-chemical parameters and sediment transfer from 2017 to 2022 between the upstream part of the reservoir of the former Vezins Dam (between S2u and S3r) and the downstream station S6d (Fovet et al., 2023). Temperature slightly increased between the upstream control stations and downstream stations, probably as a consequence of the lack of riparian vegetation and the reduced the canopy cover in the restored stations (Figure 1) that added heat to the river reach (Webb and Zhang, 2004).

4.2 Phytobenthos and river metabolism restoration

The characteristics of the geomorphic and aquatic habitats changed rapidly after sediments started eroding from the former reservoirs (Fovet et al., 2023). One year after the reservoir emptying (in 2020), the proportion between the two dominant groups in phytobenthos, diatoms and cyanobacteria, remained similar across all stations. However, their biomass was twice as low at the restored sites, especially for diatoms, and had only partly recovered after 2 years (as expected in hypothesis H2). Contrary to restored stations, the biomass of phytobenthos decreased in 2021 and 2022 in the downstream station S6d. The reduction of phytobenthos biomass is likely related to an increase in turbidity and fine sediment concentration following the release of fine sediments into the water column after the dam removal (Fovet et al., 2023). Reduced light associated with increased turbidity is indeed a well-known consequence of dam removal (Bellmore et al., 2019). Sediment release can be very fast in large dams, and most of the stored sediment can be removed only a few months after dam removal (Wilcox et al., 2014; Foley et al., 2015). However, this process occurred throughout the whole study period in the Sélune River, even if it decreased since 2021 (Fovet et al., 2023). This result is mainly due to a long emptying process in several steps, consisting in a high reduction of the water level in the reservoir since 2018 by opening the bottom gates for operations on sediments and bank stabilization before breaching the dam in 2019. The method was selected to avoid a high amount of sediment release in the water downstream in order to protect the Mont St Michel Bay since the Sélune River is one of its main tributaries. This methodological choice diluted the sediment release over time and may explain the lower extent of the increase in turbidity and its persistence over time in the restored stations. The removal process also explains the response in the downstream station S6d since part of the sediment is being retained in the river before reaching the station S6d. The similar phytobenthos biomass observed in control and downstream stations in 2020 and 2021 may be explained by the presence of the Roche-qui-Boit dam, which trapped the sediment released after the Vezins dam breaching. These trapped sediments were then progressively released into the Mont St Michel Bay over time. The quantity of sediments released to the station downstream the former reservoirs was lower in 2020 and 2021, hence lower turbidity and the low impact of dam removal on the phytobenthos during the first 2 years after removal of Vezins Dam. However, the complete removal of the second dam in June 2022 (after its decommissioning in 2021) released a lot of sediment downstream (Fovet et al., 2023), which could have had a significant impact on sediment colonization by phytobenthos this year.

Sediment release does not only affect turbidity, but also sediment stability—a key parameter to allow the colonization by photosynthetic biofilm (Biggs, 1996). Sediment instability in the restored stations likely explains the specific response of station S4r (shows ER = NPP in spring and ER > NPP in summer suggesting biofilms are lacking photosynthetic organisms and likely dominated by non-photosynthetic organisms. S4r was indeed located in a 300-m linear and homogenous stretch with a laminar flow (personal observation) providing more stable conditions for phytobenthos growth (Hondzo and Wang, 2002).

The metabolism of the Sélune River was still weakly but significantly altered in the restored stations as regards phytobenthic biomass 2 years after dam removal (hypothesis H2). The change was mainly driven by ER, which decreased in the restored and control stations both in spring and in summer whereas NPP remained more stable. The spring increase in ER in restored station when discharge was highest suggests that the overall metabolism of the Sélune River may be mainly driven by the seasonal availability of allochthonous C and to a lesser extent by autochthonous processes and light attenuation in the water column (Dodds et al., 2013). The lower ER rates in the restored stations compared with the control stations suggest that a significant proportion of the carbon stored in the fine sediments of the former reservoir may be removed by sediment leaching and may not contribute significantly to sediment respiration. The low contribution of primary producers measured in our study is also partly explained by the location of benthic chambers outside macrophyte beds to avoid their potential impact on the river metabolism (Kupilas et al., 2016) and to focus only on the effect of dam removal on sediment metabolism. The contribution of autotrophy to the river metabolism tends to increase slightly in the restored stations but only in spring. However, the GPP/ER ratio recorded during our short-term incubations increase highly in restored stations both in spring and in summer. The difference observed in the restored stations could result from the increase in available light and a warmer temperature due to the lack of riparian vegetation in the restored stations (Webb and Zhang, 2004).

4.3 Functional composition of the macroinvertebrate community

Dam removal strongly modified the availability of the algal primary feeding resources of macroinvertebrates with strong consequences on the relative contribution of the functional feeding groups in the restored (S3r, S4r, S5r) and downstream (S6r) stations since it is the main primary resources available for macroinvertebrates at this part of the Sélune River (personal observation). These effects were still observed 3 years after removal. As for the river metabolism, the contribution of autotrophy increased in the restored stations, mainly driven by the increased abundance of scrapers whereas the abundance of shredders remained stable and the abundance of deposit feeders tended to decrease in the station downstream of the former reservoirs. This result is congruent with our third hypothesis (H3), i.e., a change in the trophic structure of the macroinvertebrate community is expected following changes in the availability of feeding resources. Dam removal, especially for large dams, deeply changes the interactions between riparian and aquatic ecosystems by reducing the abundance of riparian trees (Ravot et al., 2020). As a consequence, we suspect reduced terrestrial inputs into the Sélune River and a higher contribution of autotrophy in the system. An increased percentage of scrapers was observed in restored channels during the first 2 years after the removal of a small dam (Pollard and Reed, 2004; Poulos et al., 2019), but also in woodland harvesting with clear-cutting of riparian trees (Thompson et al., 2009) or agricultural practices (Piscart et al., 2009; 2011). Moreover, Tonin et al. (2017) suggested that variability in decomposition rates between stream reaches was primarily explained by variation in local canopy cover rather than environmental conditions at the catchment scale, indicating the importance of local leaf inputs. Contrary to the percentage of scrapers, the percentage of deposit feeders tended to decrease in the restored channel. Previous studies on small dam removal have highlighted this kind of change (Sullivan and Manning, 2017; Sullivan et al., 2018; Poulos et al., 2019). For large dam removal, the result of the only study available was opposite (Mahan et al., 2021). However, in that case, the increased percentage of deposit feeders was mainly explained by the greater abundance of Chironomidae larvae in the restored channel than in the control reaches, and the percentage of predators declined downstream of the control stations, as the percentage of deposit feeders did. Previous studies have highlighted more idiosyncratic responses with contradictory results making the pattern of predators less predictable and likely site-dependent. In our study, the decreased percentage of predators could be related to an increase in size of predators since predators are mainly represented by small dipterans in control stations and by larger *Rhyacophyla* sp. larvae in restored and downstream stations. The percentage of shredders remained stable across all stations, whereas the absence of riparian trees in the restored stations might lead to a decreased percentage of shredders in the community. However and surprisingly, the percentage of shredders often remains stable following small or large dam removal (Sullivan et al., 2018; Mahan et al., 2021). This suggests a site effect: for instance, Amphipoda are the dominant shredders in the Sélune River and they are indeed omnivores (Macneil et al., 1997) with opportunistic feeding behavior (Maazouzi et al., 2009; Pellan et al., 2016). A complementary hypothesis, could be the availability of leaf litter material transported longitudinally over a few kilometres from the upstream part of the river and/or laterally over 30–50 m from older riparian trees.

The other parameters (phytobenthos, physico-chemistry) showed that the macroinvertebrate community in the downstream station responded more or less in the same way as in the restored stations, with a higher contribution of autotrophy associated to an increased percentage of scrapers and a decreased percentage of deposit-feeders and predators. Sediment release downstream seems to have had a limited impact on the functional feeding groups even 1 year after removal in 2020. In 2022, the downstream station reacted differently than the other stations, with a very strong increase in the percentage of scrapers and a strong decline in the percentage of filter-feeders, hence a high increase of the autotrophy/heterotrophy ratio. The change in trajectory observed in 2022 may likely be linked to lower turbidity in the station that year.

4.4 Conclusion

Our study shows that, although macroinvertebrate biodiversity recovered rapidly, the ongoing restoration of ecosystem functional responses to the removal of a large dam is still detectable 3 years after the removal. Even if physico-chemical variables reacted quickly, the continuous release of fine sediment and the instability of habitats lead to unfavorable conditions for primary producers. The modification of terrestrial/aquatic linkage inputs of terrestrial carbon and the increase in water temperature in restored stations devoid of riparian trees may also have altered the metabolism of the Sélune River by promoting photoautotrophs. Changes in feeding resources both in the benthic (biofilm, fine sediment) and pelagic (suspended organic matter) areas also impacted the functional groups of macroinvertebrates even after 3 years. These impacts are congruent with impacts observed in small dam removal studies. However, the impact of large dam removal on the riparian area and the huge quantity of sediment trapped in rivers may have functional impacts in the former reservoir and downstream over decades, the time required for trees to grow and stabilize the geomorphology of the river. Finally, our study highlights potential site-specific responses (size of the river, geomorphology, land cover). Delays in restoring the productivity of the restored ecosystems should not affect the recolonization of migratory fishes, since they only have an impact on the restored station of the former reservoirs and the station located downstream. Further studies and long-term monitoring are required to fully understand the functional consequences of large dam removal at the ecosystem level.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CP: Writing–original draft, Writing–review and editing. OD: Writing–review and editing. LP: Writing–review and editing. NL: Writing–review and editing. HR-P: Writing–review and editing. TB: Writing–review and editing. DH: Writing–review and editing. J-MR: Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2024.1250810/full#supplementary-material

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Fast but transient recovery of aquatic and terrestrial communities after a large dam removal

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Introduction: Ecological restoration through dam removals receives increasing attention from scientists, environmental managers and policy makers. However, most dam removal projects focus on small structures (< 10 m in height) and on few ecosystem compartments at a time (e.g. river morphology, reservoir sedimentation, aquatic invertebrates, terrestrial vegetation), but rarely aquatic and riparian ecosystems simultaneously.

Methods: We explored the joint taxonomic recovery (temporal patterns in α- and β-diversity) of three communities after the removal of the Vezins dam (36 m in height; Sélune River, France): aquatic benthic invertebrates, riparian invertebrates, and the riparian vegetation. These communities were monitored yearly, during three years after the dam removal, on sites located within (n = 3; restored sites) and outside (n = 3; two upstream and one downstream; non-impounded sites) the former reservoir.

Results: Results showed a fast recovery of the three ecological communities, as patterns in α-diversity between restored and non-impounded sites were not necessarily different from each other 1.5 years after complete reservoir dewatering. The mean number of species or morphospecies (± standard deviation) reached up to 28.2 ± 5.2, 17.0 ± 2.3 and 77.5 ± 11.2 for the aquatic invertebrates, and the riparian vegetation and invertebrates, respectively. Relative to the sampled area, the riparian invertebrates were the most diversified of all ecological communities with > 500 taxa (i.e., pooling all sites and years). In addition, in some restored sites, α-diversity kept increasing over time while species turnover (β-diversity) remained high after three years for all ecological communities suggesting a transient recovery (i.e., still facing temporal changes in species diversity and composition). This recovery was mediated by the identity of the ecological community as inter-annual changes in α- and β-diversity of the riparian vegetation were less pronounced compared to those of aquatic and terrestrial invertebrates. This recovery depended also on site-specific features as the most distant restored site from the former dam had more time for recovery following the slow reservoir dewatering and through increased sedimentation in the downstream site.

Discussion: Differential patterns of recovery in α- and β-diversity found in this study are discussed in light of species functional traits and ecosystem functioning.

KEYWORDS

ecological restoration, metacommunity, riparian vegetation, macroinvertebrate, habitat fragmentation and modification, river continuum

Introduction

Increasing societal concerns towards biodiversity and water has shed new light on a widespread but overlooked driver of rivers' ecosystem functioning: the barriers to free flow. Barriers to free flow have played an important role in modern human history to control water for irrigating crops, drinking water, generating hydropower and preventing floods. Recent estimates, most likely far below reality, point to at least 1.6 million instream barriers in Europe (Belletti et al., 2020), and only a few remaining very long and free-flowing rivers worldwide (Grill et al., 2019). In addition, although most of those barriers are less than a couple of centuries old, many began to be outdated with unsafe structures and low benefit-cost ratios. Consequently, those barriers, mainly dams, are frequently dismantled, thus drawing attention from the scientific community (Hart et al., 2002; O'Connor et al., 2015; Ryan Bellmore et al., 2017; Habel et al., 2020) and leading to the emergence of a new field in restoration ecology: "the science of dam removal" (Poff and Hart, 2002).

Dam removal projects offer unique opportunities to explore the ecological mechanisms underlying the recovery of rivers after the long-term press disturbances induced by dams. The ecological consequences of dam removals on habitat fragmentation through longitudinal processes are well-documented, with particular emphasis on fish and aquatic macroinvertebrate communities. For instance, fish communities rapidly recolonize upstream areas following small dam removals (Hogg et al., 2015; Kornis et al., 2015; Bubb et al., 2021), although communities may not necessarily recover immediately after the removal (< 3 years; Catalano et al., 2007; Stanley et al., 2007; Poulos and Chernoff, 2017). Long-term trends also agree on overall positive effects of river restoration on fish populations (Birnie-Gauvin et al., 2017) and fish communities (Whittum et al., 2023). Aquatic macroinvertebrate communities show more mitigated responses to dam removal compared to fish with first decreases in diversity, most likely due to high downstream sedimentation (Chiu et al., 2013; Renöfält et al., 2013; Rubin et al., 2017), followed by increases in diversity over time (Orr et al., 2008; Kil and Bae, 2012; Mahan et al., 2021). Yet, macroinvertebrate communities may not recover completely even after three years following dam removals (Hansen and Hayes, 2012; Renöfält et al., 2013; Poulos et al., 2019; Mahan et al., 2021). In addition, increasing evidence supports strong influence of taxa identity (Sethi et al., 2004; Tszydel et al., 2009), seasonality (Sullivan and Manning, 2017), geomorphic features (Tullos et al., 2014) and habitat characteristics (Pollard and Reed, 2004; Claeson and Coffin, 2016; Poulos et al., 2019) on patterns of macroinvertebrate recovery in stream following dam removal.

Removing dams not only affect aquatic habitats longitudinally but also terrestrial habitats through both longitudinal and lateral processes. For instance, recent evidence supports strong longitudinal patterns in riparian vegetation communities following dam removals (Brown et al., 2022) with pioneer plant species tracking changes in geomorphic and hydrologic features in downstream new coastal habitats (Foley et al., 2017) and in newly dewatered habitats closest to the river channel (Lisius et al., 2018; Ravot et al., 2020). A study on an exposed reservoir due to dam maintenance confirms an important shift in species composition from mesic to xeric plant communities within less than four years (Auble et al., 2007). In restored sites, plant recovery was usually fast (Laslier et al., 2019) and was positively affected by mycorrhizal and ectomycorrhizal fungi (Cortese and Bunn, 2017) while being threatened by non-native and competitive plant species (Orr and Stanley, 2006; Tullos et al., 2016). In turn, only few studies have investigated the effects of dam removals on the terrestrial fauna (e.g., megafauna, birds; Stephens, 2017; McCaffery et al., 2018; McCaffery et al., 2020). Concerning macroinvertebrates, some evidence suggest strong declines in spiders within four years post-removal (Sullivan et al., 2018). Altogether, the primary literature on dam removal highlights three important limitations to our understanding of mechanisms at play during community recovery. First, most studies focus on local processes following the removal of small dams (< 10 m in height; but see Foley et al., 2017). More specifically, compared to small dams, tall dams may have stronger impacts on the hydromorphological features (e.g., increased sediment load in impounded sites, large spatial extent of influence) of rivers, and thus may trigger lagged responses and longer recovery of ecological communities. Second, most studies focus on one ecological community (e.g. aquatic invertebrates, terrestrial vegetation), mainly aquatic ones (Doyle et al., 2005; Carlson et al., 2018), while investigating multiple ecological communities should provide more accurate responses of ecosystems to dam removals (Thomson et al., 2005; Chang et al., 2017; Cook and Sullivan, 2018; Atristain et al., 2023). Third, we lack an integrated view of spatial (longitudinal and lateral processes) and temporal (inter-annual processes) patterns of recovery. It is particularly difficult to find appropriate control sites when comparing restoration processes due to high historical contingencies and ecological idiosyncrasies. In addition, very often we lack information on the state of ecosystems before removals. We therefore advocate to move further away from restored *vs*. control and before *vs*. after treatment designs.

Changes in α- and β-diversity, i.e., the spatial variations in local and regional species composition (Whittaker, 1965), offers unparalleled insights into the mechanisms (i.e., species sorting, species competition, dispersal limitation) supporting meta-community dynamics (López-Delgado et al., 2020). These changes can also inform biodiversity-based conservation decisions by identifying sink and source populations of colonizers for enhanced recovery (Socolar et al., 2016). Therefore, exploring temporal changes in α- and β-diversity of multiple ecological communities following a dam removal may then help dissecting spatial-temporal patterns of recovery. In the present study, we aimed to address all three above-mentioned limitations from dam removal studies. We explored temporal changes in patterns of α- and β-diversity in both terrestrial and aquatic environments by monitoring multiple ecological communities (i.e., aquatic benthic invertebrates, riparian invertebrates, and the riparian vegetation) from one to three years after the removal of the tall Vezins dam (36 m in height; Sélune river, France). The sampling sites, both within and outside the former reservoir, were selected to reflect a longitudinal upstream-to-downstream gradient along the river thus moving further away from the common restored *vs.* control study design. In addition, since some study sites were previously under water (i.e., precluding meaningful before *vs.* after comparisons), we started the monitoring right after the dam removal thus moving away from a before *vs.* after study design. Based on knowledge gained from previous studies, we specifically tested two main hypotheses. Our first hypothesis (H1) states that taxonomic recovery is driven by rapid inter-annual increase in α-diversity in restored sites. Indeed, evidence shows that the diversity of invertebrate and plant communities can increase in just a few month up to less than four years even though transient decreases can be observed right after the dam removal or dewatering (Auble et al., 2007; Foley et al., 2017; Carlson et al., 2018). Our second hypothesis (H2) stipulates that β-diversity remain high between distant sites with gradual changes in species composition from upstream to downstream sites and across years of sampling. This second hypothesis follows a pattern found in a companion study using the same ecosystems but occurring before the dams were removed (Rodríguez-Pérez et al., 2021). Last, we briefly discussed how spatial-temporal patterns in α- and β-diversity can be community-dependent (e.g., invertebrates vs. vegetation, aquatic vs. terrestrial) due to their conspicuous differences in life history traits, which integrate environmental changes over different time scales (Southwood, 1977; Townsend and Hildrew, 1994; Doyle et al., 2005).

Materials and methods

The Sélune River, dams and sampling sites

The Sélune is a 91 km-long river located in northwest France, it drains a watershed of 1,106 km^2, and flows into the Mont Saint Michel bay (Figure 1A; Rodríguez-Pérez et al., 2021). The climate is temperate oceanic with a mean annual precipitation of 800 mm and a mean annual temperature of 10°C. The Sélune river flows across a patchy landscape, mainly composed of crops, pastures and livestock farming, with the presence of a few forested and urbanized areas. Two hydropower dams, the Roche-qui-Boit (built in 1919; 16 m in height) and the Vezins (built in 1932; 36 m in height) were located at 26 km and 30 km from the Sélune's mouth, respectively (Figure 1). The emptying of the Vezins' reservoir started in May 2017 and was complete in May 2019 (Figures 1B–E). Note that the reservoir was filled again in October/November 2018 after decisions related to water and sediment management issues during the winter period (Figure 1F). The dismantling of the Vezins dam started in 2019 and ended in late 2020 while the Roche-Qui-Boit dam was completely removed in 2023 after gradual decreases in water levels (i.e., free flowing water since June 2022; Figure 1F).

Six sampling sites were selected and monitored once a year in late spring/beginning of Summer for three years (i.e., 2020, 2021, and 2022) after the end of the reservoir emptying (spring 2019). This sampling period was chosen, assuming that it maximizes peaks of species richness and abundances of all studied ecological communities (i.e., plants and animals, aquatic and terrestrial; Sullivan and Manning, 2017). Two sites were located upstream the former Vezins' reservoir: S1u (latitude: 48.599043; longitude: -0.958010083) and S2u (latitude: 48.57171721; longitude: -1.116205727; Figure 1). Three restored sites were located within the former dam reservoir: S3r (latitude: 48.56789852; longitude: -1.146223939), S4r (latitude: 48.57532161; longitude: -1.178982545), and S5r (latitude: 48.57576597; longitude: -1.221868824). The last site was located downstream all dams: S6d (latitude: 48.59570284; longitude: -1.2938635). The sites S3r and S5r were located in the shallowest and deepest part of the former reservoir, while S4r was at intermediate depth. Beside constraints in sampling efforts, those sites were selected to reflect potential upstream-downstream patterns in species richness in aquatic communities that could influence the recovery of communities within the former dam reservoir (S3r-S5r). In addition, they were selected because the terrestrial habitats in those sites reflect the typical landscape in the Sélune basin with S1u, S2u and S6d being close to crops, pastures and livestock farms (i.e., intermediate human activities between forest and urban patches) while S3r, S4r and S5r being located in a relatively more steep-sided river valley (i.e., typical of the former dam reservoir) also located nearby crops, pastures and livestock farms. Note, that it may be challenging to select sampling sites in dam removal projects in an attempt to optimize the trade-off between statistical robustness and processing time and costs. This is particularly important as funding opportunities and successes fluctuate over time, while dam removal projects may last for decades (Birnie-Gauvin et al., 2017). We therefore initiated a simple sampling

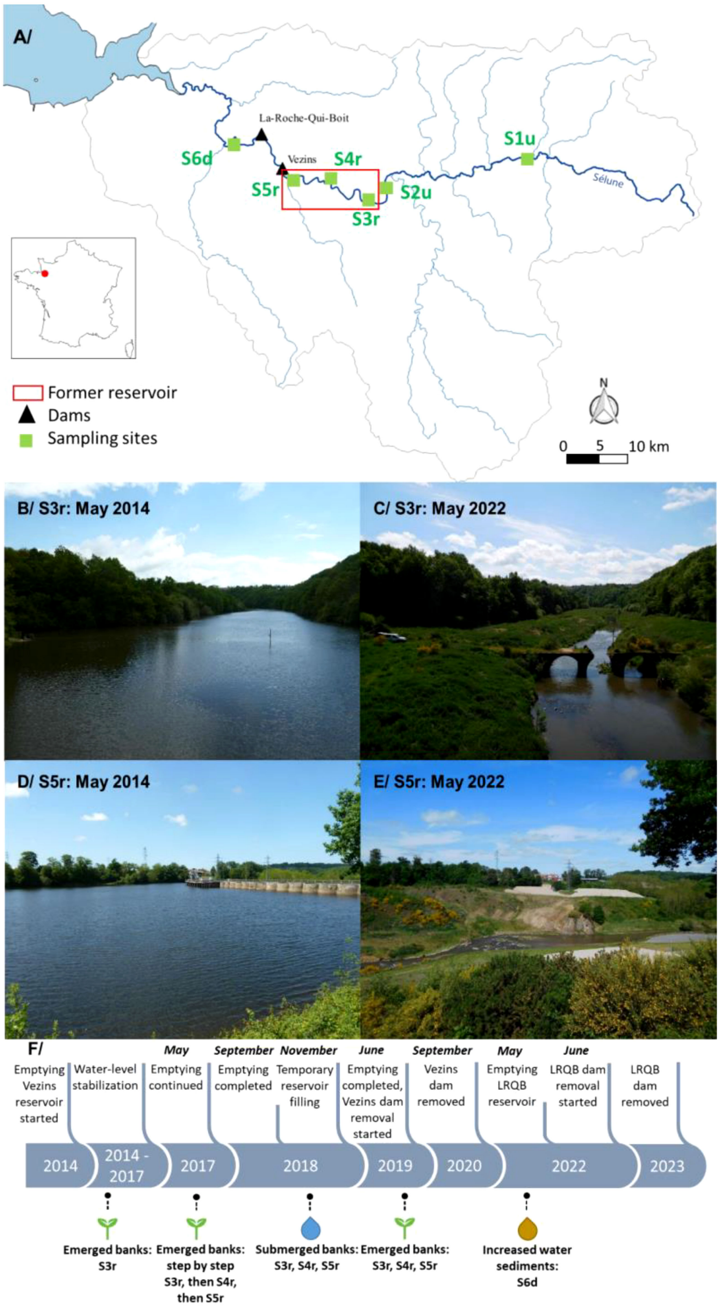

FIGURE 1
Environmental context of the Sélune river. **(A)** spatial locations of sampling sites. Pictures displaying the effect of the dam removal in S3r **(B**, **C)** and S5r **(D**, **E)** between 2014 **(B**, **D)** and 2022 **(C**, **E)**. **(F)** Timeline of events related to the removal of the Vezins and La-Roche-Qui-Boit (LRQB) dams. Photos credits: Observatoire photographique des paysages de la Sélune - Université Paris Nanterre et SMBS.

procedure (i.e., six sites sampled once a year at the same period) that could easily be maintained in the long run, especially in cases of funding shortages.

Aquatic and terrestrial macroinvertebrates

Benthic macroinvertebrates, hereafter 'aquatic invertebrates', were sampled using a Surber net sampler (collecting area: 0.05 m^2; mesh size: 500 μm). Terrestrial macroinvertebrates, hereafter 'riparian invertebrates', were sampled using a suction sampler (13 cm in diameter; mesh size: 500 μm). To mimic the collecting area of the aquatic invertebrates (0.05 m^2), four suctions were performed over 10 seconds to constitute one sample of riparian invertebrates. Then six samples of aquatic and riparian invertebrates per site and date were collected to reflect dominant habitats occurring at the sites. Samples were preserved in the field with 96° ethanol and stored until processed in the laboratory. Samples were sorted under binoculars and identified to the lowest taxonomic resolution (i.e., species or morphospecies level), except for some taxa (e.g., nematods, water mites, midges, flies), which were identified at the family or order level. We will hereafter use the terms 'taxa' or 'richness' or 'taxonomic richness', in reference to this diversity of taxonomic resolutions in our database. The sampling of aquatic invertebrates in S1u, S2u and S3r was not done in 2021.

Riparian vegetation

The riparian vegetation was characterized at each site using 18 quadrats (1 x 1 m). For each quadrat, the species' identities and relative percent cover were determined, *in situ*, by the same person across all three years of sampling. Quadrats were located either close to (n = 9) or further away from (n = 9; > 15 m depending on field topography) the stream to integrate local heterogeneities in site conditions. Note that terrestrial communities, the riparian vegetation and invertebrates, were all sampled within 20 m from the river channel. The information from 12 quadrats in S1u 2020 were lost while nine quadrats from S6d were not done in 2021. The exact location of quadrats (i.e., riparian vegetation) and collecting areas (i.e., aquatic and terrestrial invertebrates) could vary by just a few meters at most from year to year.

Statistical analyses

To test for changes in α-diversity across years and sites, we used generalized linear models (GLMs; *stats*-package) with the taxonomic richness as response variable fit with either *Poisson* or *Negative Binomial* families. The year and site identities and two-way interactions were used as predictors. Pairwise comparisons were evaluated using Tukey method (*emmeans*-package). One model was built for each ecological community (i.e., aquatic invertebrates, riparian invertebrates, riparian vegetation). Models were checked for overdispersion (*performance*-package), and model fit was graphically evaluated. The normality of residuals was assessed using a Shapiro test (*stats*-package).

To explore changes in β-diversity across years and sites, we used a permutational multivariate analysis of variance (PERMANOVA; *RVAideMemoire*-package; Hervé, 2020). The Jaccard dissimilarity index (*vegan*-package; Oksanen et al., 2019) was calculated on a matrix with the presence/absence of species across years and sites (rows). The year and site identities, and two-way interactions were used as predictors. Since PERMANOVA may fail to appropriately identify potential intra-group variability (e.g., year and site), we performed the analysis of homogeneity of multivariate group dispersions (PERMDISP; *vegan*-package) with similar model construction as the PERMANOVA. Results from both PERMANOVA and PERMDISP were graphically displayed using Principal COordinates analysis (PCO; *ecodist*-package; Goslee and Urban, 2007). Since our study design follows a longitudinal upstream-to-downstream gradient rather than a restored *vs.* control design, the influence of dam removal on α- and β-diversity can be highlighted by significant 'site:year' interactions and by further exploring significant pairwise differences across sites (i.e., upstream, restored, downstream) and within restored sites across years following GLM, PERMANOVA, and PERMDISPs analyses. All statistical analyses were done with the R software (R Core Team, 2020).

Results

Ecological communities along the Sélune river

After three years of sampling and across the six sites, i.e., pooling all years and sites, the riparian invertebrates were the most diversified of all ecological communities with 530 species distributed into 92 families and 29 orders. The riparian vegetation displayed the second highest number of species (n = 158) distributed into 41 families and 23 orders. Last, we found 110 species within aquatic invertebrates with 70 families and 19 orders. Regardless of the year of sampling, any given sampling site displayed between 53 and 69 aquatic species, between 37 and 93 species of plants, and between 236 and 350 species of riparian invertebrates. In the different sites, the number of families varied from 39 to 52, from 17 to 35, and from 64 to 77, aquatic invertebrates, riparian vegetation and riparian invertebrates, respectively. Similarly, the number of orders were in the range 13-17, 11-20 and 20-25 for the aquatic invertebrates, riparian vegetation and riparian invertebrates, respectively. Overall, we collected between one (i.e., multiple taxa) and 13,145 (i.e., Simuliidae spp) aquatic invertebrate specimens (mean ± SD: 455 ± 1,709) and between one (i.e., multiple taxa) and 5,236 (i.e., Entomobryomorpha sp2) terrestrial invertebrate specimens (mean ± SD: 64 ± 294). The number of specimens for the riparian vegetation could not be estimated.

Changes in α-diversity across sites and years

Overall, the mean richness varied (± standard deviation) from 14.2 (± 3.66) to 28.2 (± 5.23), from 3.9 (± 1.41) to 17.0 (± 2.35) and from 23.5 (± 13.8) to 77.5 (± 11.2) for the aquatic invertebrates, and riparian vegetation and invertebrates, respectively (Figure 2). The richness was significantly influenced by the interaction between site and year of sampling for the aquatic and riparian invertebrates ($p < 0.0001$ and $p < 0.0001$, respectively; Table 1) but not for the riparian vegetation ($p = 0.16$; Table 1; Figure 2). However, when the interaction is not included in the riparian vegetation model, the site and year effects became significant (Chi2 = 117.5, $p < 0.0001$ and Chi2 = 18.4, $p < 0.0001$, respectively; results not shown).

In 2020, approximately 1.5 years after the beginning of the reservoir dewatering, levels of taxonomic richness of all

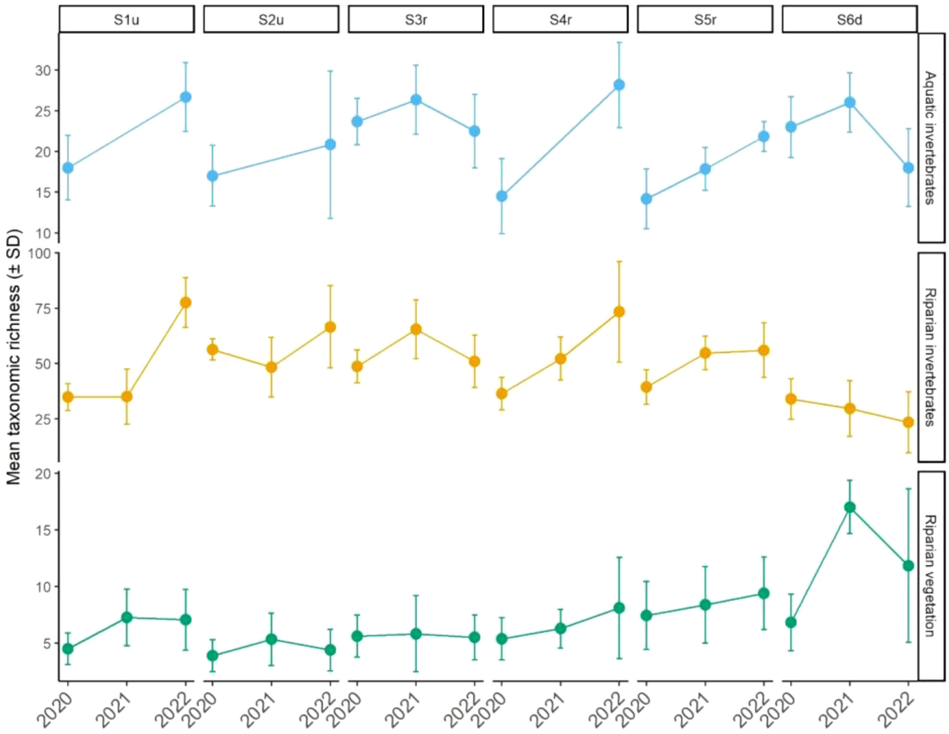

FIGURE 2
Changes in mean taxonomic richness of the aquatic invertebrates, the riparian vegetation and the riparian invertebrates from upstream to downstream sites and over time (see Table 2 for slope significance).

communities in restored sites (i.e., S3r-S5r) were not significantly different from that of sites located outside the former reservoir (i.e., S1u, S2u, S6d; Table S1). The richness of all ecological communities increased significantly over time in the restored site S4r (Table 2; Figure 2). Similar patterns were found in S5r for the aquatic and riparian invertebrates but the relationship was not significant for the riparian vegetation (Table 2; Figure 2). In the upstream of all restored sites (S3r), none of the communities showed significant changes in richness over time (Table 2; Figure 2). We also found a significant increase in taxonomic richness over time in S1u for the aquatic and riparian invertebrates and in S6d for the riparian vegetation (Table 2). Last, a significant decrease in richness of the riparian invertebrates was found in S6d (Table 2; Figure 2).

Changes in β-diversity across sites and years

All three ecological communities (i.e., riparian vegetation, aquatic and riparian invertebrates) showed significant differences

TABLE 1 Results of GLMs evaluating the effects of the sampling sites, years and two-way interactions on the taxonomic richness.

Models (R^2)	Effects	Chi2	df	*P*
Aquatic invertebrates (0.47)	**Site**	**34.52**	**5**	**1.9e-06**
	Year	**10.15**	**1**	**1.4e-03**
	Site : Year	**34.51**	**5**	**1.9e-06**
Riparian vegetation (0.34)	Site	7.93	5	1.6e-01*
	Year	1.92	1	1.7e-01*
	Site : Year	7.95	5	1.6e-01
Riparian invertebrates (0.53)	**Site**	**39.02**	**5**	**2.4e-07**
	Year	**31.2**	**1**	**2.3e-08**
	Site : Year	**39.04**	**5**	**2.3e-07**

*becomes significant when removing the Site : Year interaction from the model.
Bold font indicates significant relationships.

TABLE 2 Contrasts of GLMs evaluating the effects of the sampling sites, years and two-way interactions on the taxonomic richness of three ecological communities (see Table 1 for associated models and Figure 2 for visualizations).

Models	Estimates	SE	Z	*P*
Aquatic invertebrates				
S1u	**0.197**	**0.062**	**3.156**	**1.6e-03**
S2u	0.102	0.067	1.524	1.3e-01
S3r	-0.024	0.059	-0.411	6.8e-01
S4r	**0.332**	**0.066**	**5.032**	**4.9e-07**
S5r	**0.215**	**0.069**	**3.123**	**1.8e-03**
S6d	-0.112	0.061	-1.831	6.7e-02
Riparian vegetation				
S1u	0.14	0.1	1.395	1.6e-01
S2u	0.056	0.087	0.645	5.2e-01
S3r	-0.01	0.08	-0.124	9.0e-01
S4r	**0.207**	**0.076**	**2.73**	**6.3e-03**
S5r	0.116	0.069	1.68	9.3e-02
S6d	**0.246**	**0.064**	**3.84**	**1.2e-04**
Riparian invertebrates				
S1u	**0.414**	**0.077**	**5.346**	**9.0e-08**
S2u	0.085	0.074	1.136	2.6e-01
S3r	0.023	0.075	0.305	7.6e-01
S4r	**0.351**	**0.076**	**4.622**	**3.8e-06**
S5r	**0.174**	**0.076**	**2.288**	**2.2e-02**
S6d	**-0.183**	**0.084**	**-2.191**	**2.8e-02**

Estimates display the slope estimates between taxonomic richness and years of sampling. Bold font indicates significant relationships.

TABLE 3 Results of PERMANOVAs evaluating the effects of the sampling sites, years and two-way interactions on the pairwise taxonomic dissimilarities (Jaccard's index on presence/absence matrices).

Models	Effects	Sum of Squares	F	Df	P
Aquatic invertebrates	**Site**	**3.13**	**4.34**	**5**	**1.0e-03**
	Year	**1.38**	**4.81**	**2**	**1.0e-03**
	Site : Year	**2.67**	**2.65**	**7**	**1.0e-03**
	Residuals	10.80	–	75	–
Riparian vegetation	**Site**	**24.77**	**17.28**	**5**	**1.0e-03**
	Year	**4.47**	**7.80**	**2**	**1.0e-03**
	Site : Year	**12.93**	**4.51**	**10**	**1.0e-03**
	Residuals	81.71	–	285	–
Riparian invertebrates	**Site**	**4.56**	**3.13**	**5**	**1.0e-03**
	Year	**5.70**	**9.76**	**2**	**1.0e-03**
	Site : Year	**5.66**	**1.94**	**10**	**1.0e-03**
	Residuals	26.28	–	90	–

Bold font indicates significant relationships.

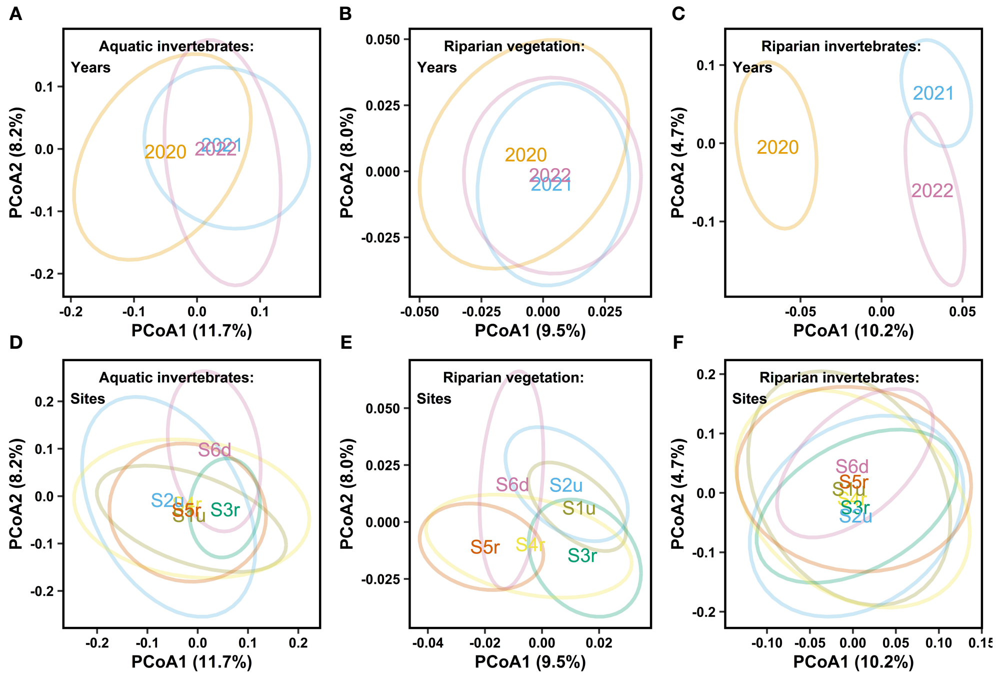

FIGURE 3
Principal coordinate analyses displaying the centroids (position of labels) and dispersions around centroids (ellipses) of two sources of variation (i.e., years: **A–C**; sites: **D–F**) of three ecological communities (i.e., aquatic invertebrates: **A, D**; riparian vegetation: **B, E**; riparian invertebrates: **C, F**) within the Jaccard's dissimilarity space. For the sack of visual clarity, results of pairwise comparisons across sites and years are not shown (significant year: site interaction in PERMANOVA and PERMDISP but see Tables S2 and S5, respectively).

in taxonomic turnover (Jaccard's dissimilarity index on presence/absence data) across sites and years ($p < 0.0001$; Table 3; Figure 3). Posthoc tests after the PERMANOVA indicates that the taxonomic turnover of each community varied significantly across all years (Figures 3A–C; Table S2) and sites (Figures 3D–F; Table S2), except for the turnover in taxa identity between S2u and S4r of the aquatic invertebrates, which was not significant (Figure 3D; see more details about pairwise comparisons across years and sites in Table S3). The temporal turnover in taxa of all ecological communities indicated that the year 2020 differed from 2021 and 2022 (Figures 3A–C). For the aquatic invertebrates, the average intra-site and intra-year Jaccard dissimilarity in restored sites decreased by 0.053 ± 0.10 between 2020 and 2022 (e.g., pairwise comparisons of all samples within S3r in 2020), while it increased by 0.010 ± 0.12 and 0.17 ± 0.04 for the riparian vegetation and riparian invertebrates respectively (Table S4). In 2022, the average intra-site dissimilarity between three restored sites remained high for all ecological communities: the aquatic invertebrates (0.49 ± 0.06), the riparian vegetation (0.74 ± 0.07), and the riparian invertebrates (0.79 ± 0.05). The average intra-site and inter-year dissimilarity in restored sites (e.g., pairwise comparisons of all samples between S3r - 2020 and S3r - 2022) were the highest and lowest for the riparian (0.88 ± 0.01) and aquatic invertebrates (0.63 ± 0.05), respectively (intermediate values for the riparian vegetation: 0.86 ± 0.10; Table S4). In addition, the first PCoA axis of the riparian vegetation was positively correlated with upstream sites (S1u, S2u and S3r) and negatively with downstream ones (S4r to S6d) suggesting some signal of the river continuum (Figure 3E). The second PCoA axis of the riparian vegetation discriminates the communities found in restored sites (S3r-S5r; negatively correlated with PCoA2) from those found in other sites (S1u, S2u and S6d; positively correlated with PCoA2; Figure 3E).

The overall variability in taxonomic turnover of aquatic invertebrates across sampling years and sites were not significantly different (posthoc tests after PERMDISP; Table S5; ellipses in Figure 3). In turn, the variability was significantly different between most years (except between 2021 and 2022) and sites (except for S1u-S3r, S2u-S5r, S4r-S6d) for the riparian vegetation (Table S5). Last, the variability in taxonomic turnover of riparian invertebrates was significantly different across all years, and only between S1u-S6d, S2u-S6d, S3r-S6d, S4r-S6d, S5r-S6d (Table S5; see more details pairwise comparisons across years and sites in Table S6).

Although previous analyses on β-diversity were done at the species or morphospecies level (i.e., very rich information; n = 798 taxa in total), we here start exploring main trends in taxonomic turnover using the order level (n = 71 orders in total; Figure 4). Similar exploration of taxonomic turnover can be done at the family (Figure S1) and species/morphospecies levels (Figure S2). Across all six sites, Diptera were amongst the most dominant orders of aquatic organisms, along with Ephemeroptera and Amphipoda (Figure 4). Spatial patterns in plant orders were slightly more complex with more turnover in the most dominant orders from S1u to S6d compared to the aquatic invertebrates. Overall, Poales followed by Rosales were the most dominant orders in S1u, S2u, S3r, S6d, while Asterales and Poales dominated communities in S4r and S5r

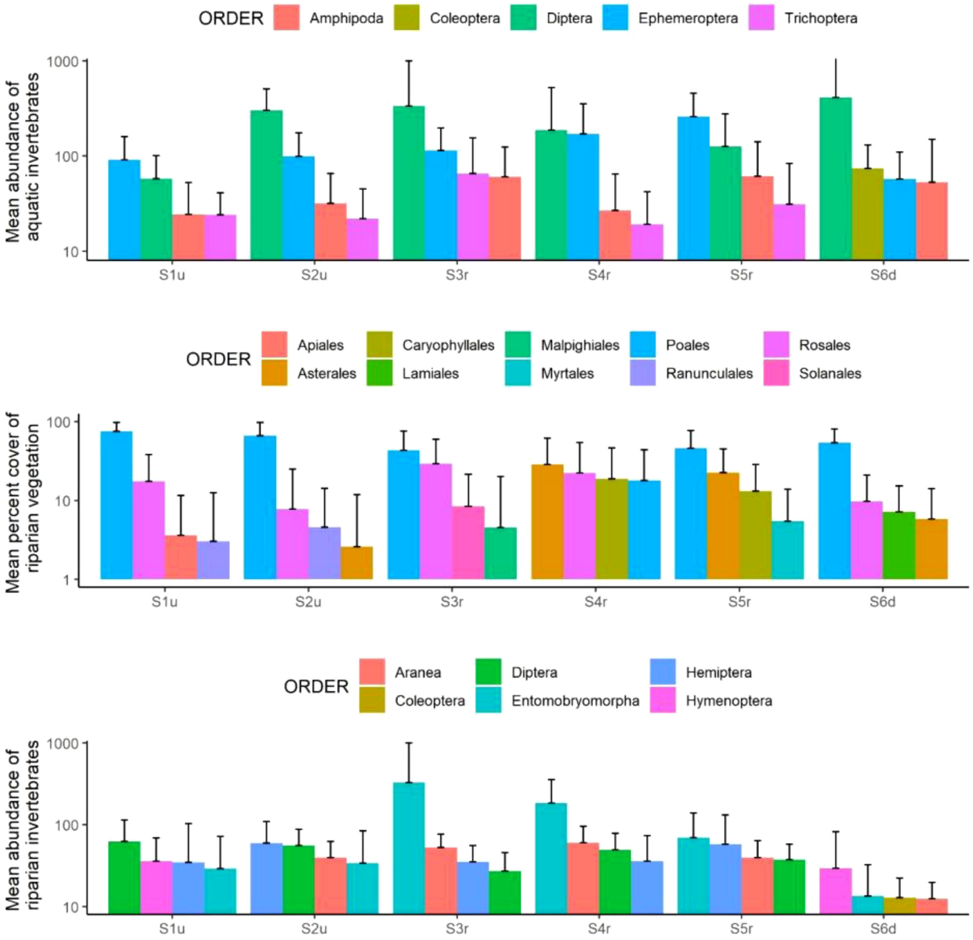

FIGURE 4
Distribution of the four most abundant orders of aquatic invertebrates, riparian vegetation and riparian invertebrates within each sampling site. Note that y-axes are displayed in the log10 scale.

(Figure 4). Non-impounded sites (S1u, S2u, S6d) can be distinguished from other sites by the presence of Apiales, Ranunculales and Lamiales in the four most abundant orders. The riparian invertebrates showed the highest turnover in the ranks of dominant orders compared to the aquatic invertebrates and the riparian vegetation (Figure 4). Entomobryomorpha dominated communities within restored sites (S3r to S5r), but were also present in the most abundant orders in other sites (S1u, S2u and S6d). Araneae were among the most abundant orders in the restored sites: S3r and S4r.

Discussion

Fast taxonomic recovery in restored sites (α-diversity)

In less than 1.5 years after the complete dewatering of the Vezins' reservoir, the mean taxonomic richness of riparian vegetation, riparian invertebrates and aquatic invertebrates found in restored sites was similar to that of non-impounded sites. This suggests a fast recovery as expected (H1), in line with results from previous studies (Claeson and Coffin, 2016; Lisius et al., 2018; Poulos et al., 2019; Mahan et al., 2021). It contrasts, however, with other studies on macroinvertebrate recovery, which found either null or negative effects of dam removal on taxonomic diversity followed by an increase in diversity in subsequent years (Stanley et al., 2002; Kil and Bae, 2012). We found a negative but nonsignificant effect of the dam removal on the taxonomic richness of the aquatic invertebrates in the downstream site S6d, possibly impacted by increased downstream sedimentation after the removal of the second dam (La-Roche-Qui-Boit; Figure 1F; Mahan et al., 2021). Indeed, the presence of the La-Roche-Qui-Boit dam between the Vezins dam and S6d may have downplayed the adverse effects of increased sediments on aquatic communities in S6r by filtering the sediments coming from the removal of the Vezins dam. Overall, changes in the geomorphic (Tullos et al., 2014), and habitat features (Pollard and Reed, 2004; Claeson and Coffin, 2016) following dam removal should impose strong constraints on local communities, but the intensity of these constraints may depend on the spatial locations of study sites relative to the removed dam.

Contrary to our first hypothesis (H1), the α-diversity of all communities did not continue rising after one year post-removal in S3r, which rather hosted communities with near constant mean taxonomic richness over time. Two interrelated explanations could support this result. First, ecological communities in S3r had more time to colonize the new riverbanks and channel compared to other restored sites because of the slow dewatering (i.e. over several months) of the Vezins' reservoir. Second, S3r is also the closest of all restored sites to the two upstream non-impounded sites (i.e., S1u and S2u), which may be important sources of colonizers (e.g., hydrochory, active dispersal of winged organisms). Therefore, community recovery may have been enhanced by a rapid organismal colonization at S3r from nearby upstream sites (i.e., upstream non-impounded sites, river tributaries) and *in situ* seed banks or dormant forms. For instance, the riparian vegetation in S3r displayed the characteristics of a fast colonizing and competitive post-pioneer assemblages, which were dominated by *Urtica urtica* (stinging nettle) and *Phalaris arundinacea* (reed canary grass; Figure S2). To help understand ecological recovery, future dam removal studies could identify nearby and *in situ* pools of colonizers (Ravot et al., 2021), for instance, within the 100 m from river channel (< 20 m in the present study; enhancing lateral recovery; Auble et al., 2007) or by increasing the sampling effort along the river and its tributaries (enhancing longitudinal recovery).

Patterns of recovery depended on ecological community, which is in accordance with our expectations. At the most downstream of the three sites in restoration (S5r), the riparian vegetation displayed no increase in mean taxonomic richness after one year compared to significant increases for both aquatic and riparian invertebrates. This site had a shorter restoration time than S4r and S3r (Figure 1F), and hosted, for instance, more pioneer plant taxa in communities, which then have either been replaced by more persistent taxa or prevented the establishment of additional taxa due to strong competition for limiting space and resources (Foley et al., 2017; Laslier et al., 2019).

In turn, all ecological communities showed significant increases in mean taxonomic richness across all three years of sampling in S4r. Studies on dam removals found similar temporal patterns for macroinvertebrate (Hansen and Hayes, 2012; Renöfält et al., 2013; Poulos et al., 2019; Mahan et al., 2021) and riparian vegetation (Foley et al., 2017; Lisius et al., 2018; Brown et al., 2022). The literature is far less abundant regarding responses of riparian invertebrate communities to dam removal, but some reports suggest strong declines in spiders within four years post-removal (Sullivan et al., 2018). Our results indicate that spiders (Figures 4, S1, S2) were among the most abundant taxa in restored sites. The extent to which taxonomic richness will continue to rise in S4r for all communities and in S5r for aquatic and riparian invertebrates beyond three years is unknown. Altogether these results suggest that the ecological recovery although fast is transient over three years for some communities and restored sites (i.e., context-dependent).

Spatial-temporal turnover in taxonomic composition (β-diversity)

We originally assumed that the upstream-to-downstream gradient would leave an imprint on the recovery of ecological communities in the form of gradual changes in taxonomic composition (β-diversity) from upstream to downstream sites (S1u to S6d; H2; Rodríguez-Pérez et al., 2021). This assumption was supported by the riparian vegetation (supporting H2), displaying an upstream-to-downstream pattern in β-diversity. To a lesser extent, this spatial signal was also found in aquatic communities (i.e., upstream-to-downstream changes correlated with PCoA2 except for S1u; Figure 3F). This upstream-to-downstream pattern in β-diversity suggests that the longitudinal dispersal of communities along the river may play an important role in community recovery to dam removals.

Last, we expected the taxonomic recovery to vary according to the identity of the ecological community. This assumption was also partially supported as we found that all studied communities displayed high compositional differences in 2020 compared to 2021 and 2022 (including restored and non-impounded sites). This result may find an explanation when considering unmeasured but large-scale processes. For instance, Sullivan and Manning (2017) found that seasonality was as much important as local drivers (e.g., daily discharge, water depth and velocity, stream width) in macroinvertebrate responses to a dam removal. In addition, as for α-diversity, we found a strongly significant interaction between sites and years of sampling driving patterns in β-diversity of all ecological communities, suggesting a strong temporal and context-dependence of community recovery. Interestingly, the temporal turnover in taxonomic composition was higher in riparian organisms (i.e., invertebrates and plants) than in aquatic invertebrates. This difference between realms may arise because riparian organisms are influenced by *in situ*, lateral and longitudinal colonization processes while aquatic organisms are mainly driven by *in situ* and longitudinal processes. These finding add to the growing evidence of the spatial, temporal and ecological complexity of river recovery following dam removals. This recovery may result from direct and indirect interactions between local and regional deterministic processes along with dispersal limitations of organisms.

Functional recovery and implications for species interactions within and across ecosystem boundaries

Functional ecology offers a powerful framework to better understand the causes and consequences of species-environment relationships (Southwood, 1977; Townsend and Hildrew, 1994; Violle et al., 2007) with countless implications in conservation biology and restoration ecology. It is a common practice in dam removal projects to investigate changes in the functional characteristics of fish communities (Shaffer et al., 2018; Jones et al., 2023), aquatic macroinvertebrate communities (Pollard and Reed, 2004; Hansen and Hayes, 2012; Kil and Bae, 2012; Poulos et al., 2019; Mahan et al., 2021), and riparian vegetation (Foley et al., 2017). In the present study, we explored taxonomic changes of these three communities as a first step to report ecosystem recovery after dam removal. Yet, rapid evaluations of taxonomic lists in our study (Figures 4, S1, S2) corroborate some evidence found in previous studies. For instance, collector-gatherers, represented by Chironomidae (Diptera) and Baetidae (Ephemeroptera), were among the most dominant taxa in newly restored channels (S3r to S5r; Mahan et al., 2021). In addition, pioneer plant taxa rapidly colonized the newly emerged riverbanks (e.g., Salicaceae, Polygonaceae, Asteraceae; Foley et al., 2017). A non-exhaustive review of the literature on the use of functional traits in dam removal studies highlighted, however, three main trends: most studies evaluate trophic-related traits (but see Tullos et al., 2014; Sullivan and Manning, 2017) excluding potentially important traits related to community recovery (e.g., dispersal capacities, flood-resistant seeds, dormant forms, reproduction type, life history traits), and functional information is scarce regarding many ecological communities (e.g., riparian vegetation, riparian invertebrates) thus preventing from a more integrated vision of ecosystem functioning under recovery. Exploring trophic relationships or food webs among organisms provides such an integrated picture of ecosystem functioning. Injecting food-web perspectives into the science of dam removal is, however, a daunting challenge. Only very few attempts explored how dam removal may affect cross-ecosystem trophic interactions (Sullivan et al., 2018). We therefore push future dam removal studies to further investigating the joint recovery of multiple ecological communities from both aquatic and terrestrial realms through the lens of trait-based and food-web ecology.

Conclusion

In between spring 2018 and 2019, the emptying of the one-century old, large-dam reservoir of Vezins offered new habitats to aquatic and terrestrial organisms on the Sélune River catchment. One year later, in spring 2020, we found that plants and invertebrates communities, reached levels of taxonomic diversity (α-diversity) similar to what is observed elsewhere on the river and its banksides suggesting a fast recovery. However, after three years post-removal, the α-diversity kept increasing and dissimilarity in taxonomic composition (β-diversity) remained high in some sites, suggesting a fast but transient ecological recovery. These patterns of recovery were strongly influenced by the identity of the ecological community, as well as spatial (e.g., lateral, longitudinal) and temporal (e.g., slow dewatering of former reservoirs) processes. These findings are in line with recent evidence of the strong context-dependent responses of ecological communities to large dam removals. This study initiates a first step within a larger goal to further understanding long-term and ecosystem-wide consequences of large dam removals.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

OD: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. JMR: Conceptualization, Methodology, Funding acquisition, Project administration, Writing – review & editing. EL: Writing – review & editing. TB: Writing – review & editing. AB: Writing – review & editing. HR-P: Writing – review & editing. SD: Conceptualization, Funding acquisition, Project administration, Writing – review & editing. IB: Conceptualization, Funding acquisition, Project administration, Writing – review & editing. CP: Conceptualization, Methodology, Funding acquisition, Project administration, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1254462/full#supplementary-material

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Nearshore subtidal community response during and after sediment disturbance associated with dam removal

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Dam removal is used increasingly to restore aquatic ecosystems and remove unnecessary or high-risk infrastructure. As the number of removals increases, there is a growing understanding about the hydrologic, geomorphic, and ecological responses to these removals. Most dam removal studies, however, focus on river and watershed responses to dam removal. The removal of two dams on the Elwha River provided a unique opportunity to characterize the response of nearshore (coastal) ecosystems. We conducted SCUBA surveys between 2011 and 2022 to quantify trajectories of change in a nearshore ecosystem during and after dam removal. We focused on the degree to which the abundances of kelp, benthic invertebrates, and fish changed in response to patterns of sediment fluxes during and after dam removal. Our findings point to two pathways of response depending on the disturbance mechanism and species type. Sites with persistent sediment deposition were characterized by wholesale community changes that did not recover to a before dam removal condition. Instead, the sites were colonized by new species that were largely absent prior to dam removal. Sites that experienced high turbidity but lacked persistent seafloor deposition were primarily characterized by a reduction in the abundance of kelp and other algae during dam removal and a rapid recovery after sediment flux to the nearshore declined. Dam removal influences on invertebrates and fish at these sites were more variable, benefiting some species and disadvantaging others. In addition to dam removal, sea star wasting syndrome and a marine heatwave exerted distinct controls on subtidal communities during the same period. The loss of the predatory sea star *Pycnopodia helianthoides* was associated with gains in some of its prey species, and kelp community changes reflected regional trends in ocean temperature and kelp abundance. The results presented here have important implications for understanding the response of marine ecosystems to future dam removals and similar sediment perturbation events.

KEYWORDS

dam removal, nearshore, Elwha, sediment, disturbance, recovery

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1 Introduction

In marine ecosystems, sediment plays an important role in determining community composition in time and space (Hall, 1993; Airoldi, 1998; Lohrer et al., 2004; Erftemeijer et al., 2012). Large disturbance events that alter sediment dynamics in marine systems—such as storms and debris flows—can result in high turbidity, bed scour, and burial of benthic communities. Studies from disturbance events in a wide range of ecosystem types tend to point to two pathways of response for both the physical and ecological aspects of the system. The first is the stable state response, whereby the system is “resilient” and returns to the pre-disturbance state over time (Holling, 1973; Gunderson, 2000; Fuller et al., 2019). The second is the alternative state response, wherein the system resets to a state different from the pre-disturbance condition (Beisner et al., 2003; Knowlton, 2004; Schröder et al., 2005; Phillips and Van Dyke, 2016). Disturbance events such as these are natural laboratories that can provide insights about effects, recovery, and resilience, including the magnitude of impact, types of species affected, and the duration and trajectory of the recovery (Paine and Levin, 1981; Sousa, 1984; Palumbi et al., 2008).

Dam removal is a relatively new sediment disturbance in aquatic and marine ecosystems as dam removal activities in the United States and elsewhere have increased, particularly in the last three decades (O’Connor et al., 2015). As such, there is a growing body of literature that describes the physical, hydraulic, geomorphic, and ecological changes that occur following dam removals of all sizes in a range of watershed types (Foley et al., 2017b). For small dam removals, the effect on freshwater benthic communities is often undetectable or short lived (Doyle et al., 2005; Tullos et al., 2014), while larger dam removals can result in benthic effects that can be detected multiple years after dam removal (Morley et al., 2020). Because many of the dam removals to date have been small and/or far upstream, there are few studies describing the ecological response in marine ecosystems following dam removal. Many of those that have been published in the last ten years (Rubin et al., 2017; Shaffer et al., 2017; Glover et al., 2019) are associated with dam removal on a single river, the Elwha, which is the subject of the study described in this paper.

In this paper we describe observations of change for kelp (brown algae in the order Laminariales), benthic invertebrates, and fish over a twelve-year period, between 2011-2022, in the nearshore ecosystem during and after the removal of two dams on the Elwha River. The analysis presented here builds on the observed changes to the nearshore system presented in Rubin et al. (2017) by following kelp, benthic invertebrate, and fish communities for an additional eight years after dam removal was complete. This paper focuses on the following dam-removal related hypotheses for kelp, benthic invertebrate, and fish communities: 1) fine suspended sediment load in the Elwha nearshore will decrease after the completion of dam removal and algal communities at unburied sites will return to conditions similar to those that existed before dam removal; 2) kelp, benthic invertebrate, and fish community composition at the buried sites will not return to those that existed before dam removal due to persistent changes in habitat characteristics; 3) decreased suspended sediment and (or) recovery of kelp communities at the unburied sites will benefit kelp-dependent benthic invertebrates that decreased during dam removal and hinder invertebrates that increased during dam removal due to increased food supply or relaxed competition for space with algae.

During the 2011-2022 period, additional regional phenomena occurred that likely affected the trajectory of ecological recovery. In 2013, sea star wasting syndrome (SSWS) decimated populations of a major predatory sea star, *Pycnopodia helianthoides* (hereafter referred to as *Pycnopodia*), coast-wide during our study period (Montecino-Latorre et al., 2016). In addition, a marine heatwave affected the eastern Pacific from 2014-2016 (Tolimieri et al., 2023). While the focus of the paper is on dam removal effects, we also tested the effects of SSWS and compared kelp recovery trajectories to regional kelp data, specifically focusing on two additional hypotheses: 4) SSWS will negatively impact sea star density and positively impact other benthic invertebrates, particularly those released from predation; and 5) kelp abundance at unburied and control sites will show similar patterns of loss during the marine heatwave compared to regional kelp surveys.

1.1 Background and study area

The Elwha River is a relatively short (72-km long), high gradient river flowing north out of the Olympic Mountains into the Strait of Juan de Fuca (Figure 1). Two dams constructed on the Elwha River, Washington State, USA (Figure 1B), in the early 1900s trapped approximately 30 million tonnes (Mt) of sediment by 2011 (Ritchie et al., 2018). The staged removal of the 32-m tall Elwha Dam (at river kilometer 8) and the 64-m tall Glines Canyon Dam (at river kilometer 21), began in September 2011 and was completed by 2014. Sediment flux through the lower river and to the coast increased dramatically in response to dam removal, starting in March 2012, during the deconstruction of the lower Elwha Dam (Ritchie et al., 2018). The reservoir upstream of the Glines Canyon Dam, Lake Mills, started spilling sediment past the dam site in October of 2012. During the first two years of dam removal, between September 2011 and September 2013, over 10 Mt of sediment were eroded from the two reservoirs. Turbidity in the river downstream of the dams increased nearly three orders of magnitude above background levels during the same period (Magirl et al., 2015). In the subsequent three-year period (September 2013 to September 2016), an additional ~9 Mt of sediment eroded from the reservoirs, thereby resulting in almost 20 Mt of sediment eroded since the beginning of the project (Ritchie et al., 2018).

Roughly 90% of the sediment eroded from the reservoirs during dam removal was transported rapidly through the river to the dynamic coastal environment of the Strait of Juan de Fuca. The diurnal tidal range, the difference between mean lower low and mean higher high water is 2.1 meters, and the exchange of tides through the Strait of Juan de Fuca generates large tidal currents that regularly exceed 1 m/s near the Elwha River delta (Warrick and Stevens, 2011). Wave energy in the Strait of Juan de Fuca near the Elwha River delta is a mix of locally forced wind waves and swell waves propagating from the Pacific Ocean, with a mean annual

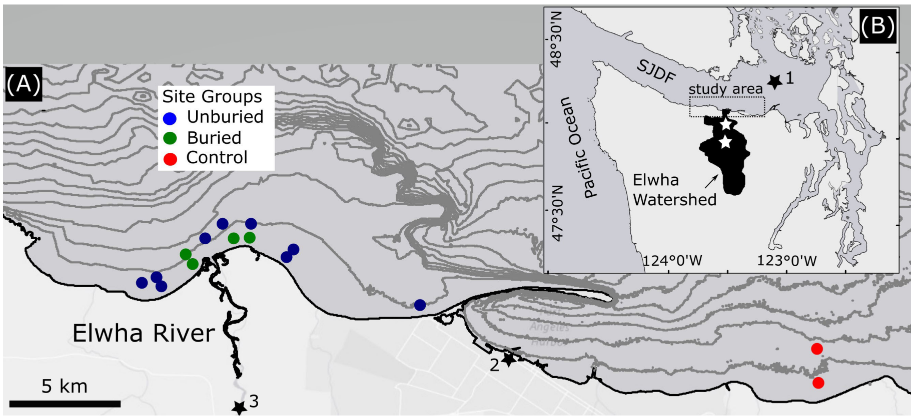

FIGURE 1
Study area **(A)** and regional context **(B)**. The location of the two former dams on the Elwha River are shown with white stars in **(B)** Analysis of marine community response was based on three groups of subtidal survey sites (colored circles in **A**). Black stars mark the locations of environmental data discussed in the paper, including wave data from NDBC 46088 (1), water level data from NOAA 9444090 (2) and river flux and turbidity data from USGS 12046260 (3). Contour intervals in **(A)** are 10m and derived from pre-dam removal bathymetry.

significant wave height of ~0.4 m and a bimodal distribution of dominant period, with peaks at 4 and 10 seconds (Miller et al., 2011).

The large increase in sediment supply associated with the dam removals resulted in dramatic physical changes in the nearshore, including: 1) growth of the river mouth delta landform and modification of a variety of coastal habitats (Foley et al., 2017c; Warrick et al., 2012; Gelfenbaum et al., 2015; Warrick et al., 2019), 2) increased turbidity in coastal waters near the river mouth (Foley and Warrick, 2017; Glover et al., 2019), and 3) persistent and intermittent sedimentation on the seafloor offshore of the delta (Eidam et al., 2016; Foley and Warrick, 2017; Glover et al., 2019). These dam removal-mediated habitat alterations had a variety of implications. Rubin et al. (2017) documented > 75% decrease in brown algal density and decreased benthic invertebrate species diversity at sites near the Elwha River mouth during dam removal compared to before dam removal surveys. Changes in algal abundance during dam removal were associated with the deposition of sediment and reductions in light driven by increased turbidity (Rubin et al., 2017; Glover et al., 2019).

2 Materials and methods

A suite of approaches for monitoring and tracking the influence of dam removal were developed prior to dam removal. Methods are briefly described below and in greater detail in previously published papers, including Magirl et al. (2015) for fluvial sediment fluxes, Gelfenbaum et al. (2015) for coastal morphology, and Rubin et al. (2017) for nearshore subtidal communities.

2.1 Grain size, bathymetry and sediment flux measures

Seafloor grain size and topographic and bathymetric measurements were collected annually on and around the Elwha River delta, typically over 3-4 days during the summer (Gelfenbaum et al., 2015; Stevens et al., 2017). Intertidal topographic measurements were collected with differentially corrected GNSS systems, mounted on backpacks, and walked by surveyors along the beach and the backshore during low tides. The GNSS system records positions and elevations in an auto-by-interval mode, in which observations were collected automatically as the surveyors moved over the beach and backshore. Measurements were concentrated on cross-shore oriented transects with approximately 50-m alongshore spacing, but surveyors also collected observations along slope breaks and irregular features.

Bathymetric observations were made during the same surveys using personal watercraft equipped with GNSS systems coupled with depths measured using single beam echosounders. Vessel operators collected bathymetric data at high tide along the same set of cross-shore oriented transects used by walking surveyors at low tide, and generally collect observations between mean lower low water (0.12 m NAVD88 at Elwha) and offshore depths of 15-20 m. The combined topographic and bathymetric data are interpolated onto a uniform grid with a resolution of 5 m. The resulting digital elevation model (DEM) has an estimated vertical uncertainty of 12 cm (Stevens et al., 2017).

Surface sediment samples were collected with a petite ponar grab sampler (Gelfenbaum et al., 2015). Samples were obtained along a series of cross-shore transects at sites that, prior to dam removal, were subtidal (elevations between -1 and -12 m, NAVD88). As the bathymetry of the Elwha River delta changed during and after dam removal (Ritchie et al., 2018), the sampling locations stayed the same, such that some sites sampled from a boat in 2012 were sampled by hand from the beach in subsequent years. For samples collected with the grab sampler, up to three attempts were made to collect a sample with adequate mass (approximately 50 g) from the seafloor; if no sample could be collected the site was assumed to be coarse-grained. Suitable samples were transported to a U.S. Geological Survey (USGS) laboratory in Santa Cruz, California, USA, and analyzed to determine the disaggregated grain size distributions using a combination of sieves and a Beckman Coulter LS 13 320 particle size analyzer (Stevens et al., 2017).

Sediment fluxes in the Elwha River for the period between September 2011 and September 2016 were estimated using the methods of Magirl et al. (2015) as calculated and tabulated by Ritchie et al. (2018) for the USGS gaging station 12046260 on the Elwha River (Figure 1), which captures the sediment inputs from both reservoirs upstream. Suspended sediment concentrations (SSC) were derived from a combination of standard flow-weighted suspended sediment samples, automated point-sampler daily composite samples, and three sediment-surrogate instruments—two optical turbidimeters and one acoustic Doppler velocity meter (ADVM)—to generate 15-min interval records of SSC during the 2012 to 2016 water years. These estimates include the proportions of the suspended sediment discharge within sand grain sizes (0.063 to 2 mm) and silt and clay grain sizes (less than 0.063 mm), which we termed fine suspended sediment load (FSSL). Sediment discharge was calculated by the product of SSC and measured river discharge, which were summarized into daily and annual sediment discharge values.

Turbidity measurements in the Elwha River were discontinued after the 2016 water year, so sediment fluxes after that time were estimated using a rating curve derived from measurements of 2016 water year average daily river discharge (Q, m3/s) and daily suspended-sediment discharge (Qs, t/d) using power-law formulations. Sediment rating curves were generated from least-squares regression for both sand grain-size fractions ($Q_s = 0.000188$ $Q^{3.3181}$; $r^{2\,=}$ 0.77) and silt-to-clay grain size fractions ($Q_s = 0.000786$ $Q^{3.1366}$; $r^{2\,=}$ 0.76) and applied to daily average discharge records (Warrick et al., 2012). Our computations assume that the sediment supply rates to the river continued to be dictated by river flow and that the sediment availability stayed relatively constant with time. These assumptions likely result in overestimates of sediment discharge because they do account for the observed decreased sediment availability over time after dam removal ended (Ritchie et al., 2018).

2.2 Subtidal SCUBA surveys

Subtidal marine community surveys were conducted annually between mid-July and early September at 13 sites near the Elwha River delta, and at two additional control sites at Green Point, approximately 20 km east in the Strait of Juan de Fuca (Figure 1). Before dam removal, each site was surveyed at least once between 2008 and 2011 (Rubin et al., 2017). Since 2012 all sites have been surveyed annually except the two control sites, which were not surveyed in 2018. Sites vary in depth between 5 and 17 m, and (excepting the control sites) are distributed up to 7.5 km east and 2.5 km west of the Elwha River mouth. Substrate type at sites is a mix of sand, gravel, cobbles, and boulders (Rubin et al., 2017) and has not changed measurably except where persistent deposition occurred.

Each site was marked on the seafloor with a stainless steel post, which identifies the center of two 50-m long transects, one trending east and one trending west, marked on either end by a cement block. Along each transect, divers enumerated benthic invertebrates greater than 2.5 cm along any dimension and kelp and acid kelp (*Desmarestia* sp) greater than 24 cm in length, within a 30-m long and 1-m wide swath. Divers also enumerated fish of any size within a 30-m long by 2-m wide by 2-m high tube. Additionally, a modified uniform point contact methodology was used to characterize the substrate type and algal cover at 0.5 m intervals along the transect (Rubin et al., 2017).

2.3 Data analysis

Kelp, invertebrates, and fish were analyzed separately. Species were grouped to the lowest taxonomic level practicable for consistency among observers and across years. Many fish were small, cryptic, and mobile, and are generally aggregated to taxonomic levels higher than those for kelp or invertebrates. Common rather that scientific names were used for fish. Data were averaged over transects within each site-year before analysis. All data collected between 2008 and 2011, before the start of dam removal, were consolidated and are presented here as belonging to 2011 (see Rubin et al., 2017 for full details). All data used in analyses are publicly available (Rubin et al., 2023).

Sites were categorized into three “site groups” prior to analysis: buried (4 sites), unburied (9 sites), and control (2 sites; Figure 1). Buried and unburied site groups were separated because previous analyses (Rubin et al., 2017) indicated fundamental differences in biological response between sites buried under persistent sediment deposits and unburied sites. We classified a site as buried if it experienced deposition greater than 15 cm based on analysis of bathymetry survey data or measurements of a post installed at each site that allowed divers to estimate changes in elevation unless the depth of deposition exceeded post height (Rubin et al., 2017). Sites classified as buried first became buried in 2013 or 2014 and remained buried for the duration of our study; unburied sites did not experience persistent burial.

2.4 Community analysis

Community analyses compared trajectories of change among communities at buried, unburied, and control sites. A difference in trajectory for the control sites compared to the other two site groups would suggest that change at the buried and unburied sites was due to dam removal. A trajectory difference between buried and unburied sites would suggest that communities were differentially affected by dam removal at buried compared to unburied sites. Community analyses addressed hypotheses 1, 2, and 3.

Multivariate community analyses were conducted using species that were present in at least five site-years. Analyses were performed on Bray-Curtis similarity matrices computed from square root-transformed species densities (Clarke et al., 2014). Analyses were conducted in Primer 7 (Clarke and Gorley, 2015).

Two-way analysis of similarity (ANOSIM) with factors survey year and site was used to investigate which major taxon (kelp, invertebrates, or fish)-by-site group combinations showed significant community change across years (Clarke et al., 2014). Site was included as a factor to account for (i.e., factor out) variation due to spatial differences among sites. Taxon-by-site group combinations that did not exhibit significant community change across years were not included in subsequent analyses, except for testing the effect of the density of the sea star *Pycnopodia* on community composition within the control and unburied site groups.

Two-way analysis of similarity percentages (SIMPER) with factors survey year and site was used to investigate which species contributed most to community change across years within each site group (Clarke et al., 2014). SIMPER generated percent contribution of species contributing most to the difference between each year pair, up to a cumulative contribution of 70%. We computed a weighted average of a species' contribution to each year pair difference where the weights were the average community dissimilarity between each year pair. This gave a single mean percent contribution to community differences among years for each species. Species contributing most to differences over time were highlighted in subsequent analyses.

Nonmetric multidimensional scaling (NMDS) analysis was conducted on densities averaged across sites within site groups and was used to investigate when community change occurred and the trajectory of change (e.g., unidirectional with different start and end states, circular with similar start and end states). Species vectors, indicating the strength and direction of correlations between species densities and each NMDS axis were superimposed on NMDS plots (Clarke et al., 2014; Clarke and Gorley, 2015).

Species analyses (Somerfield and Clarke, 2013) were used to identify groups of species that changed similarly across years. Analyses were conducted on densities averaged over sites within site groups. Densities were standardized by total within species (density from each year was divided by total density across years). Then cluster analysis was performed on Bray-Curtis similarity matrices computed from standardized densities (no square root transformation). Species that did not contribute to community change between at least one pair of years according to SIMPER analysis were excluded. Species that did contribute to community change but only occurred in one year were also excluded.

2.5 Mechanisms driving change

Analyses of mechanisms driving change addressed whether communities or individual species were affected by variables directly or indirectly related to dam removal or other stressors. Variables considered were fine suspended sediment load (FSSL), algal cover, and *Pycnopodia* density. Mechanism analyses primarily addressed hypotheses 3 and 4.

We used regression approaches to test the three mechanisms, with FSSL, percent algal cover, and *Pycnopodia* density as independent variables. We chose FSSL in the river as the independent variable representing suspended sediment because suspended sediment in the nearshore was linked to FSSL in the river (Glover et al., 2019). We used cumulative FSSL between February 1 and July 31 because our observations of the system suggest that elevated suspended sediment during that period could suppress algal recruitment and growth in our study area.

Distance-based redundancy analysis (dbRDA) was used to investigate whether community change was related to FSSL, percent algal cover, or *Pycnopodia* density (McArdle and Anderson, 2001). dbRDA is akin to multivariate regression and is appropriate when the dependent variables, in our case densities of species, are represented by a Bray-Curtis similarity matrix as ours were. Site was included in dbRDAs as an independent variable (as a fixed effect because dbRDAs do not allow random effects) to account for spatial effects. dbRDAs were conducted in Permanova + (Anderson et al., 2008).

Univariate regression analysis was used to investigate whether densities of single species were related to FSSL, algal cover, or *Pycnopodia* density. Species identified by SIMPER as contributing most to community change across years at Elwha unburied sites were chosen for this analysis. Species density was log-transformed before analysis to increase normality and decrease heteroskedasticity. Sites where the species did not occur in any year were excluded. Analyses were conducted in R (R Core Team, 2022). We used General Additive Models (GAM) to test which shape of a curved relationship fit best, or whether a linear relationship fit better than any curve, and also to test which of four error structures fit best: 1) including site as a random effect, 2) including an auto-correlation term (AR1) to account for any non-independence due to consecutive years of data, 3) including both site as a random effect and an auto-correlation term, and 4) including neither site nor an auto-correlation term (R package mgcv; calls gam or gamm; Wood, 2017). The model with the lowest AIC value was selected as the best fit. A final step was to test whether adding to the best fitting model a term allowing residual spread to vary as a function of the independent variable (VarExp variance structure; Zuur et al., 2009) improved model fit further (Pinheiro et al., 2023).

3 Results

3.1 Sediment flux and coastal turbidity

Between water years 2011 and 2015 the Elwha River discharged roughly 14 Mt of suspended sediment to the coastal waters, composed of ~58% silt and clay, and ~42% sand, and roughly 5 Mt of sand and gravel bedload. After dam removal ended in 2014 sediment discharge declined rapidly: A total of ~3 Mt of suspended sediment were discharged between water years 2016 and 2022, composed of ~62% silt and clay and 38% sand (Figure 2A). The seasonality of suspended discharge also changed during and after dam removal. Most of the suspended-sediment discharge occurred during winter high flow events both during and after dam removal. Suspended sediment fluxes during the lower flows of summer, though, decreased rapidly after dam removal ended as the

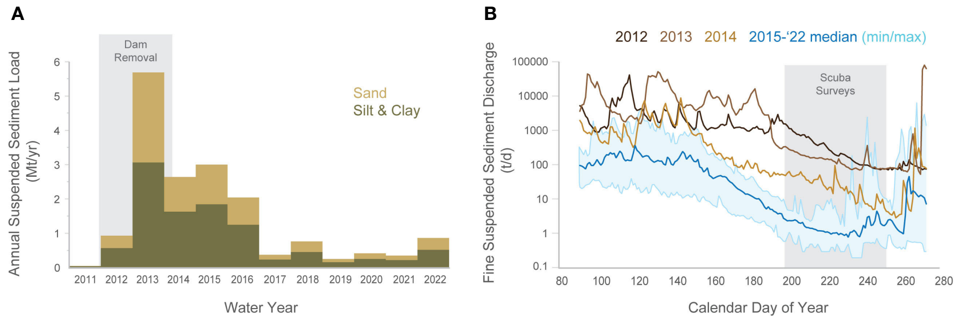

FIGURE 2
Annual suspended sediment **(A)** discharge from the Elwha River for the period 2011-2022, and daily fine suspended sediment **(B)** discharge during the estimated biologically relevant "growing season" (mid-March to October) for the years during dam removal (2012, 2013 and 2014) and after dam removal (2015-2022). Data for water years 2012-2016 are from Ritchie et al. (2018); and water years 2017-2022 from rating curves derived from WY2016 data.

availability of erodible sediment decreased (Figure 2B). These summer season decreases in sediment discharge were especially apparent after dam removal was completed (WY2015-2022; Figure 2B), whereas during dam removal (WY2012-2014), the suspended-sediment discharge during the summer was several orders of magnitude higher. For example, by early August (day of year 200) when many of the scuba surveys were conducted, the Elwha River was discharging 20 to 400 t/d during active dam removal (WY2012-2014) but only ~1 t/d following the completion of dam removal (WY2015-2022; Figure 2B). Thus, dam removal resulted in three distinct intervals of time with respect to river sediment and turbidity: 1) during dam removal (WY2012-2014), when suspended sediment discharge was high during both winter and summer seasons, 2) immediately following dam removal (WY2015-2016), when annual suspended-sediment discharge was high, but with lower turbidity and sediment discharge during the summer, and 3) several years following dam removal (WY2017-WY2022) when river sediment loads were relatively low in both winter and summer.

3.2 Sea-floor morphology changes

Morphologic changes to the seafloor occurred near the Elwha River mouth during dam removal (Gelfenbaum et al., 2015), resulting in vertical sediment deposition exceeding 5 m in some locations (Figure 3E). Sediment deposits to the west of the river mouth were composed primarily of mud, and to the east of the river mouth of fine sand (Figure 3H). As sediment flux to the nearshore declined after dam removal ended (Figure 2A) these new sub-tidal deposits were eroded and re-worked in response to hydrodynamic forces (Figures 3C, F, I). Notably, the sand deposit on the east side of the delta eroded, and deposits at all points around the delta coarsened (Figures 3F, I). The four sites in the buried site group include those nearest to the river mouth, and at shallower depths. Two sites were in an area of mud deposition to the west of the river mouth, and two sites were in an area of fine sand deposition to the east of the river mouth (Figures 3E, F).

3.3 Change in density and richness of kelp, invertebrates, and fish

The earliest and most pronounced change during dam removal was the decrease of kelp density and species richness at both buried and unburied site groups beginning in 2012 (Figures 4A, B). This change is consistent with the timing of an increase in suspended sediment flux from the river following the breach of the Elwha Dam (Figure 2A; Rubin et al., 2017), increasing the turbidity of coastal waters (Foley and Warrick, 2017) and reducing the availability of light in the water column (Glover et al., 2019). The trajectory of change following the initial response of kelp to dam removal, however, was different for the buried and unburied site groups. Within the buried site group, density and species richness of kelp did not recover to pre-removal levels by 2022 (Figures 4A, B) despite a substantial reduction in suspended sediment flux between 2017 and 2022 (Figure 2).

At the unburied sites, kelp density and richness decreased immediately following dam removal when suspended sediment flux was highest (Figures 2, 4A, B). Unlike the buried sites, the density of kelp at unburied sites started to rebound in 2015 (Figure 4A), coinciding with reduced sediment flux from the river, especially during the spring and summer months (Figure 2B). The rate of kelp recovery was rapid at unburied sites, largely returning to pre-removal levels by 2015 for richness and 2017 for density, although variability among sites was considerable within the unburied group (Figures 4A, B). Density of *Desmarestia* sp., the other main group of brown algae in the study area besides kelp, total percent cover of algae, and percent cover of red algae, the other main algal group besides brown, showed trends across time generally like kelp at buried and unburied sites (Figures S1B, C, E, F).

For invertebrates and fish at sites within the buried group, density and species richness also decreased during dam removal and had not recovered to pre-removal levels by 2022 (Figures 4C–F). The decrease in invertebrate and fish density and species richness were most pronounced in 2013 (fish) and 2014 (invertebrates), which coincided with the period of sediment deposition in the buried site

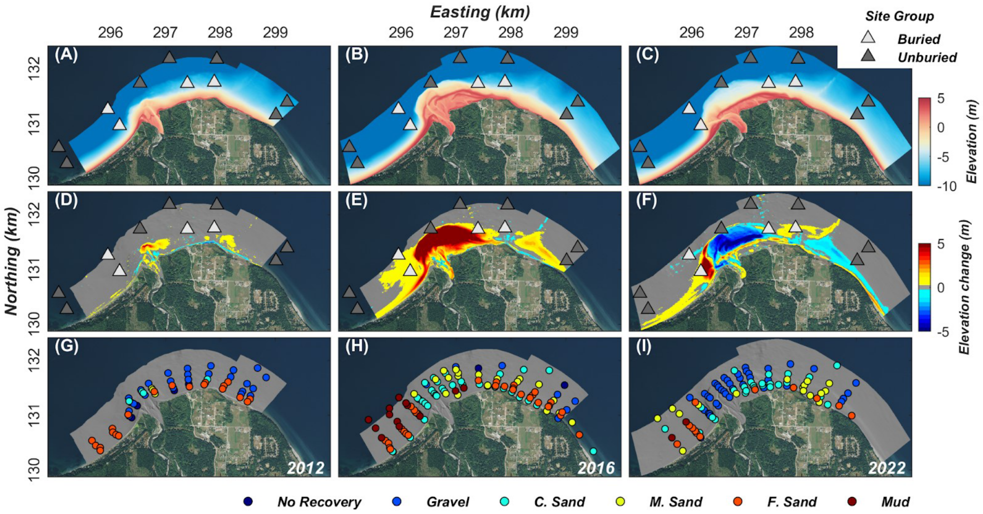

FIGURE 3
Bathymetry **(A–C)**, elevation change **(D–F)**, and mean surface sediment grain size **(G–I)** of the Elwha River delta in 2012 (left column), 2016 (middle column), and 2022 (right column). Elevation changes are calculated between 2012-2011 **(D)**, 2016-2012 **(E)**, and 2022-2016 **(F)**. Sites where no sediment sample was recovered were interpreted to represent hard ground or a substrate so coarse that a sample could not be collected, and are marked on the map as "No Recovery". Bathymetry and grain size data are from Stevens et al. (2017). The dive sites shown in Figure 1 are added in panels **(A–F)** for context, and shaded according to their site group (i.e., buried vs. unburied).

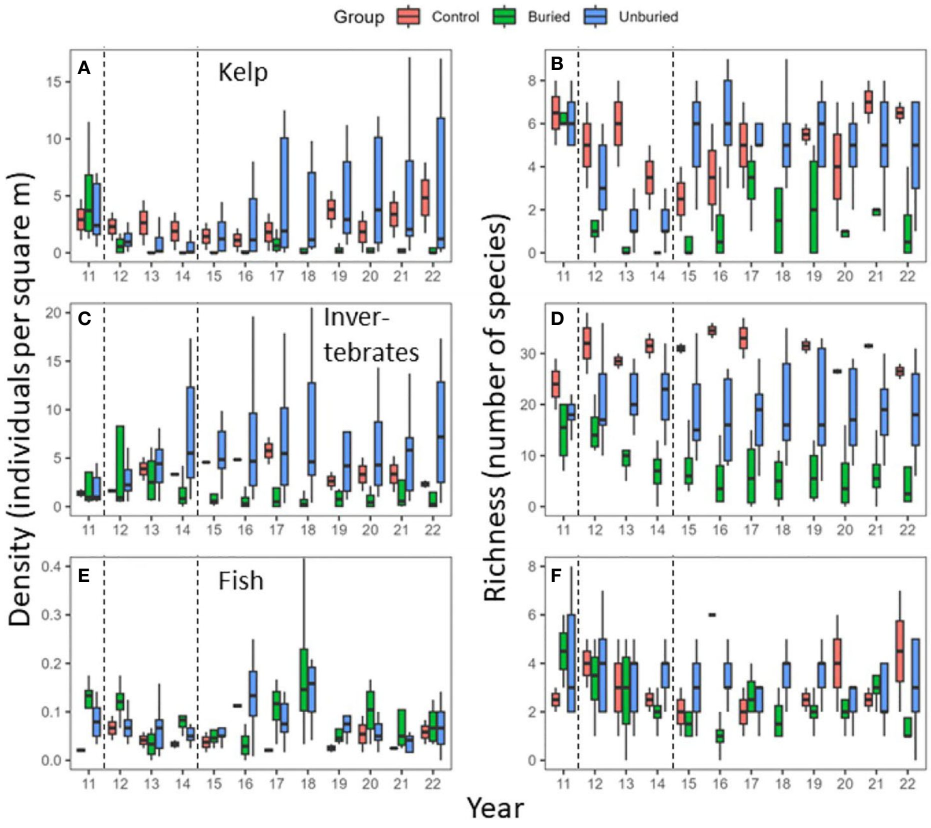

FIGURE 4
Box and whisker plots of density (left panels) and species richness (right panels) for kelp **(A, B)**, invertebrates **(C, D)**, and fish **(E, F)** by year and site group. Boxes were constructed from data for each site-year. The top and bottom of boxes are the upper and lower quartiles and the line is the median. The whiskers extend from the upper (or lower) quartile to the largest (or smallest) value no farther than 1.5 times the inter-quartile range. Outliers are not shown. Dotted lines indicate the start and end of dam removal.

group (Figure 3; Gelfenbaum et al., 2015; Rubin et al., 2017). At buried sites, fish density increased briefly in 2017 and 2018, decreased in 2019, and then remained low through 2022 (Figure 4).

Invertebrate and fish density and species richness did not decrease within the unburied site group during dam removal (Figure 4; Rubin et al., 2017). Invertebrate density at unburied sites increased in 2014 and remained high through the end of the time series. Fish density within the unburied site group briefly increased from 2016-2018, but otherwise remained at a similar level throughout the time series. Invertebrate and fish density and species richness were highly variable within site groups between 2011-2022 without any clear trend over time.

At the control sites, density and species richness of kelp, invertebrates, and fish, and density for *Desmarestia* sp. and percent cover for red algae, varied annually between 2011 and 2022, but with no clear trend over time (Figures 4, S1A, D). The decrease in kelp richness at control sites in 2014-2016 is consistent with regional patterns of kelp decline due to a marine heatwave affecting the eastern Pacific (Tolimieri et al., 2023).

3.4 Community composition during and after dam removal

3.4.1 Kelp

Kelp community composition changed significantly from 2011-2022 at all site groups (Table 1; Figure 5A). For the buried site group, the loss of all kelp species drove the change in community composition between years (Figures 5B, 6A; Tables S1, S2). Community composition measured at the buried sites was most different between 2011 (before dam removal) and 2014 (end of dam removal; points on the NMDS plot that are closer together are more like each other than points farther apart). Community composition did move closer to starting conditions after 2014, mainly due to modest increases in *Pterygophora californica* and *Nereocystis luetkeana* (Figure 6A; Table S1), but did not return to before dam removal composition by 2022 within the buried group. Between-year variability became less pronounced between 2018 and 2022 (Figure 5B) when sediment flux from the river was lower than previous years (Figure 2A).

For the unburied site group, the loss of all kelp species during dam removal drove the change in composition across years, particularly from 2012-2015 (Figure 6B). Consistent with the recovery of density and species richness (Figures 4A, B), kelp community composition returned to a state similar to that before dam removal by 2018 (Figure 5C). Individual species density was highly variable across years (Figure 6B), but most species started to increase in 2015.

Within the control group, changes in kelp community composition across years (Figure 5D), which was least variable over time of the three site groups (Figure 5A), was driven by the annually variable densities of kelp species (Figure 6C) rather than a complete loss of species as in the buried and unburied site groups. Note that there was little change in kelp community composition from 2011-2013 within the control group, which is when drastic changes occurred at the buried and unburied site groups (Figures 4–6), suggesting the effects of dam removal did not affect the control group.

3.4.2 Benthic invertebrates

For the invertebrate community, composition change across years was significant for the buried and unburied site groups but not for the control (Table 1; Figure 7A). Within the buried site group, species composition changed substantially following dam removal, driven by the loss of multiple species, including anemones (*Halcampa* spp. and *Epiactis* spp.), sabellid tubeworms (*Schizobranchia* spp., *Chone aurantiaca*, *Eudystylia vancouveri*), and an increase in crabs (*Metacarcinus magister*), geoduck (*Panopea abrupta*), and polychaete worms (*Pista* sp., *Diopatra ornata*) (Figures 7B, 8A, B; Tables S1, S2). Community composition did not return conditions like those before dam removal by 2022, but composition was similar in 2021 and 2022.

TABLE 1 Results of two-way crossed ANOSIM results for community differences among years and sites for kelp, invertebrates, and fish at buried, unburied, and control site groups.

		Year		Site	
Taxon	Site Group	R	p	R	p
Kelp	*Buried*	*0.198*	***0.014***	*0.145*	***0.011***
	Unburied	*0.460*	***0.000***	*0.536*	***0.000***
	Control	*0.617*	***0.000***		
Invertebrates	*Buried*	*0.488*	***0.000***	*0.610*	***0.000***
	Unburied	*0.408*	***0.000***	*0.599*	***0.000***
	Control	*-0.011*	*0.500*		
Fish	*Buried*	*0.269*	***0.001***	*0.083*	*0.083*
	Unburied	*0.033*	*0.112*	*0.228*	***0.000***
	Control	*0.142*	*0.182*		

Site was included in the analysis to account for high variability between sites within each group. R ranges from -1 to 1, with 0 indicating no difference among groups (in this case years or sites) and 1 indicating maximum difference among groups. Bold text represents significant effects.

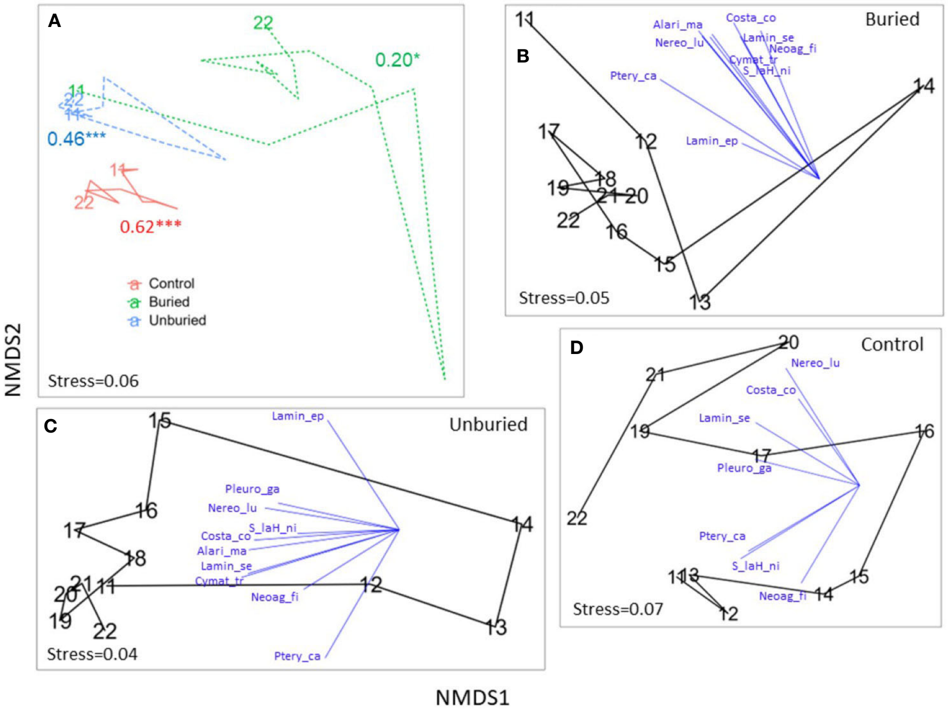

FIGURE 5
NMDS plots showing trajectories of kelp community change across years by site group. The communities—in terms of species composition and density—in the closer together points are more similar than farther away points. **(A)** Site groups are shown together with ANOSIM R and p-values (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for each site group included (see Table 1) and the first and last years labeled. **(B–D)** Buried, unburied, and control site groups, respectively, are shown separately with blue vectors indicating the direction and strength (vector length) of correlations between density of kelp species and NMDS axes included for species contributing most to community change (see Table S1), and all years labeled. See Table 2 for full species names. Note that points in **(A)** were plotted with the goal of showing similarities (differences) among all year-by-site group combinations, whereas points in **(B–D)** were replotted to show similarities between years within a particular site group, so trajectories in A do not exactly match trajectories in **(B–D)**.

TABLE 2 Full names and abbreviations assigned to species, or lowest identified taxonomic level, in figures and tables.

Taxon	Full name	Abbreviated name
Kelp	*Alaria marginata*	Alari_ma
	Costaria costata	Costa_co
	Cymathere triplicata	Cymat_tr
	Laminaria ephemera	Lamin_ep
	Laminaria setchellii	Lamin_se
	Neoagarum fimbriatum	Neoag_fi
	Nereocystis luetkeana	Nereo_lu
	Pleurophycus gardneri	Pleur_ga
	Pterygophora californica	Ptery_ca
	Saccharina latissima_Hedophylum nigripes	S_laH_ni
Invertebrates		
Anemone	*Epiactis sp*	An_Epi
	Halcampa sp	An_Hal
	Other	An_oth
Bivalve	*Clinocardium nuttallii*	BV_Cli_nu
	Mya truncata	BV_Mya_tr
	Other	BV_oth
	Panopea generosa	BV_Pan_ge
	Saxidomus gigantea	BV_Sax_gi
	Tresus capax	BV_Tre_ca
Chiton	*Mopalia sp*	Ch_Mop
	Tonicella sp	Ch_Ton
Crab	*Cancer productus*	Cr_Can_pr
	Metacarcinus magister	Cr_Met_ma
	Metacarcinus magister juvenile	Cr_Met_mj
	Pugettia gracilis	Cr_Pug_gr
Hermit crab	Other	HC_oth
	Pagurus beringanus	HC_Pag_be
Sea pen	*Ptilosarcus gurneyi*	Pe_Pti_gu

(Continued)

TABLE 2 Continued

Taxon	Full name	Abbreviated name
Polychaete worm	*Diopatra ornata*	PW_Dio_or
	Pista sp	PW_Pis
Shrimp	*Crangon sp*	Sh_Cra
	Pandalus sp	Sh_Pan
Snail	*Calliostoma sp*	Sn_Cal
	Nucella sp	Sn_Nuc
Sea star	*Henricia sp*	St_Hen
	Pycnopodia helianthoides	St_Pyc_he
Sabellid worm	*Chone aurantiaca*	SW_Cho_au
	Eudystylia polymorpha	SW_Eud_po
	Eudystylia vancouveri	SW_Eud_va
	Myxicola sp	SW_Myx
	Schizobranchia sp	SW_Sch
Urchin	*Mesocentrotus franciscanus*	Ur_Mes_fr
Fish	Flatfish other (Pleuronectiformes)	FF_Other
	Starry flounder (*Platichthys stellatus*)	FF_Starr
	Gunnel sp (Pholidae)	Gunnel
	Poacher sp (Agonidae)	Poacher
	Ratfish (*Hydrolagus colliei*)	Ratfish
	Pacific sand lance (*Ammodytes hexapterus*)	Sandlanc
	Buffalo sculpin (*Enophrys bison*)	Sc_Buffa
	Sculpin other (Cottoidei)	Sc_Other
	Snailfish unknown (Liparidae)	Snailfis

Mean density and percent occurrence over all site-years are given in Table S3.

Invertebrate community composition was comparatively less variable over time for the unburied site group than the buried site group and was driven by increases and decreases of a range of species (Figures 7C, 8C, D; Tables S1, S2). This response was fundamentally different from the response of the kelp community, which had the same trajectory for all species. There was a marked increase in two sabellid worms (*Schizobranchia* spp., *Eudystylia vancouveri*) and bivalves (*Saxidomus gigantea*, *Tresus capax*), and a decrease in anemones (*Halcampa* sp.), bivalves (*Mya truncata*, other), and two other sabellid worms (*Chone aurantiaca*, *Myxicola* sp.). The dissimilarity between invertebrate community composition across years in the unburied site group was much smaller than in the buried site group (Figure 7A), which was also the case for kelp (Figure 5A). However, invertebrate community composition in the unburied site group did not return to before dam removal conditions by 2022, but composition was relatively stable from 2019-2022 (Figure 7C).

In the unburied site group, there was also a marked decrease in sea star abundance, particularly *Pycnopodia* (Figure 8C). While negative effects from dam removal cannot be completely ruled out, the disappearance of this species and *Henricia* sp. was likely most attributable to sea star wasting syndrome (SSWS) that decimated sea star populations in the eastern Pacific beginning in 2014 (Montecino-Latorre et al., 2016). Note that Pycnopodia also decreased at buried sites but the decrease mainly occurred in 2013 (Figure 8A) when sites became buried but before SSWS started. The red urchin, *Mesocentrotus franciscanus*, only occurred at one unburied site, but at that site its abundance started to increase in 2014 concurrently with the loss of sea stars, reaching a peak in 2015 and continuing to be higher than before SSWS occurred (Figure 8D). Algae had not recovered at the site by 2014.

3.4.3 Fish

Fish community composition in the buried site group changed significantly between years (Table 1; Figure 9A). Like invertebrates in the buried site group, the density of many fish species—including gunnel (Pholidae), ratfish (*Hydrolagus colliei*), and sculpins (Cottoidei)—decreased when vast amounts of sediment were deposited near the river mouth in 2013-2014 and did not return to previous densities (Figure 10B). Some fish species, however, were able to take advantage of the newly created habitat at the buried sites near the river mouth, including flat fish (Pleuronectiformes), snailfish (Liparidae), and poacher (Agonidae), and increased in density after dam removal (Figure 10A). Similar to kelp and invertebrates, fish community composition did not return to a state similar to that prior to dam removal by 2022 but was relatively similar from 2020-2022 (Figure 9B).

Pacific sand lance (*Ammodytes hexapterus*) were difficult to accurately count because they were either darting in and out of the sediment or schooling in the water column, so we only recorded them as present or absent. When sand lance were present there were usually many of them. We rarely encountered sand lance at unburied sites (4 occurrences in 108 site-years) or control sites (4 occurrences in 22 site-years).

3.5 Mechanisms driving change in the buried and unburied site groups

The major physical changes in the nearshore during dam removal included increased suspended sediment flux (Figure 2) and sediment deposition (Figure 3). For the buried site group, the dominant mechanism driving community change was burial and an accompanying change in grain size (Figures 3G–I). The change in grain size, however, was not the same at all buried sites. At the sites to the west of the river mouth, sand was buried by mud; to the east, gravel was buried by sand (Figures 3G–I).

This change in grain size resulted in changes in invertebrate and fish species present within the buried group (Figure 11). For invertebrates, the bivalves *Clinocardium nuttallii* (cockles) and *Panopea generosa* (geoduck clams) and the polychaete worms

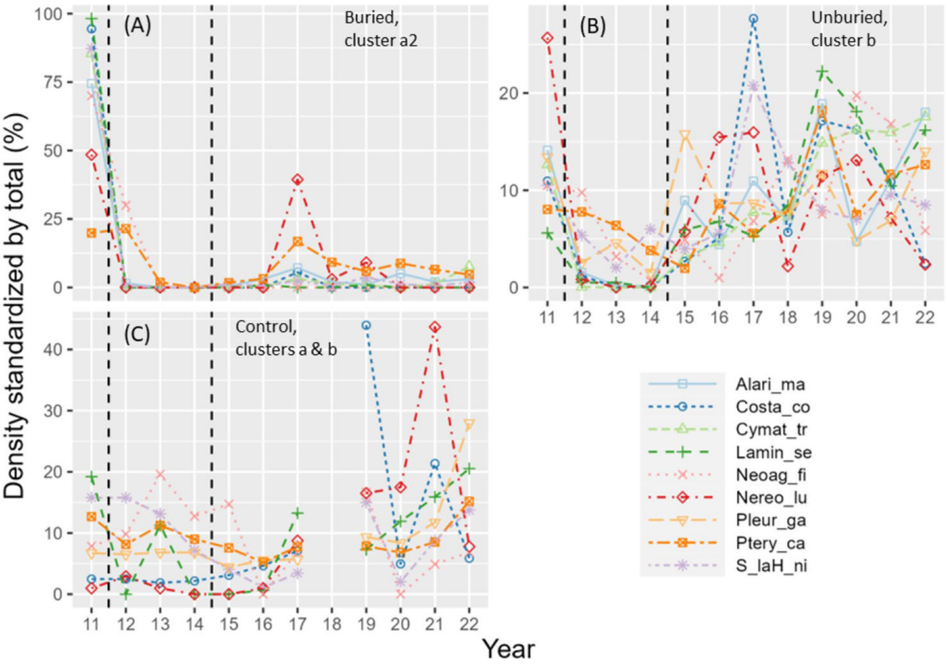

FIGURE 6
Standardized density (density in each year divided by total density across all years) versus year for kelp species that changed similarly across years according to cluster analyses (see Table S2 for clusters) for buried **(A)**, unburied **(B)**, and control **(C)** site groups. Vertical dashed lines show start and end of dam removal. See Table 2 for full species names.

Diopatra ornata and *Pista* sp. were more abundant at the western buried sites (mud) following dam removal than before (Figure 11B). For fish, flatfish and snailfish became more abundant at the western sites when the habitat changed from sand to mud after burial. Poacher decreased after the western sites were buried but were still occasionally present.

For the buried sites on the eastern side of the delta where the habitat changed from gravel to sand, *Metacarcinus magister* (Dungeness crab) were recorded during our surveys after the sites were buried and had not been observed at those sites before. Sand lance were present during every survey in the new sand habitat at the eastern sites despite not being observed there before deposition (Figure 11A). Flatfish (other and starry flounder *Platichthys stellatus*) also became more abundant following burial at the east sites than before.

The mechanisms driving change in the unburied site group varied depending on taxonomic group. The only dam removal-related physical change at unburied sites was elevated suspended sediment. Kelp community composition was strongly related to FSSL in the river, which was correlated with suspended sediment in the nearshore (Glover et al., 2019), and total kelp density and percent algal cover were strongly negatively correlated with FSSL (Tables 3, 4; Figure S2A), suggesting that algal trajectories of change during and after dam removal were primarily driven by high suspended sediment levels during dam removal followed by water column clearing following dam removal (Figures 2, 4–6, S1). Kelp community composition was also related to *Pycnopodia* density at unburied sites ($p < 0.05$; Table 3). Kelp community composition (Table 3), kelp density, and algal cover were unrelated to FSSL within the control site group ($p > 0.05$).

Invertebrates in the unburied site group were affected by changes in suspended sediment and (or) algal cover, and by changes in *Pycnopodia* density. Invertebrate community composition change within the unburied site group was significantly related to FSSL, algal cover, and the density of *Pycnopodia* ($p < 0.001$ for all three terms; Table 3). For invertebrates within the control site group, community change was not significantly related to FSSL or algal cover ($p > 0.05$) but was related to *Pycnopodia* density ($p < 0.05$; Table 3) even though the ANOSIM test did not detect significant community change across years at control sites (Table 1).

For individual invertebrate species that contributed most to community composition change within the unburied site group (Table S1; vectors in Figure 8C), the significance of associations with FSSL, algal cover, and the density of *Pycnopodia* varied widely based on the univariate regressions (Table 4). Except for the seastar *Henricia* sp., all species that were positively correlated with FSSL (Figure S2) were filter feeders (bivalves and sabellid worms). Most of those species also had a significant negative correlation with algal cover (Figure S3). Comparatively, *Cancer productus* (crab) density was negatively correlated with FSSL and positively correlated with algal cover. Multiple invertebrate species were negatively correlated with *Pycnopodia* density, including two species of bivalves, one snail, two sabellid worms, and one urchin (Figure S4). This correlation suggests that the loss of *Pycnopodia* from our sites between 2013 and 2014 could be driving the increase

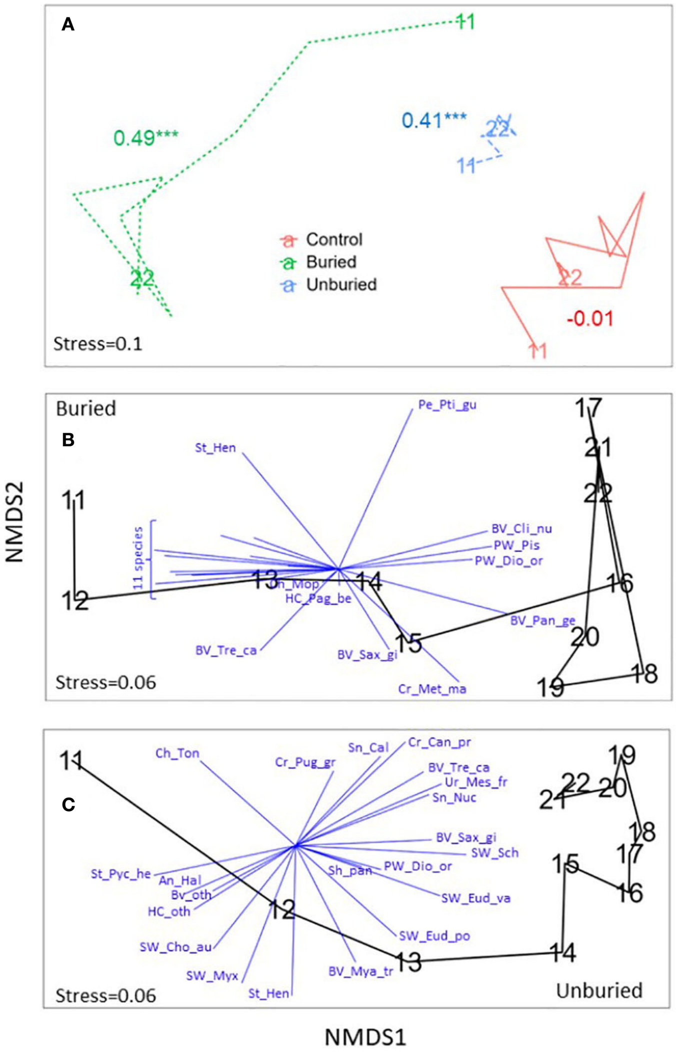

FIGURE 7
NMDS plots showing trajectories of invertebrate community change across years by site group. **(A)** Site groups are shown together with ANOSIM R and p-values (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for each site group included (see Table 1) and the first and last years labeled. **(B)** and **(C)** Buried and unburied site groups, respectively, are shown separately with blue vectors indicating the direction and strength (vector length) of correlations between density of invertebrate species and NMDS axes included for species contributing most to community change (see Table S1), and all years labeled. The 11 bracketed species in **(B)** are: An_Epi, An_Hal, An_oth, Cr_Can_pr, Cr_Met_mj, Hc_oth, Sh_Cra, St_Pyc_he, SW_chone, Tw_Eud_va, and SW_Sch. See Table 2 for full species names.

in abundance of those species (Figure 8D), particularly for species that were not correlated with FSSL or algal cover (bivalves, sabellid worm *Eudistylia polymorpha*, and red urchin *Mesocentrotus franciscanus*). Mean *Pycnopodia* density (averaged over site years) was higher at control than at unburied sites, and community composition change was significantly related to the density of *Pycnopodia* within the control and unburied site groups. However, different species were affected by *Pycnopodia* within those two site groups. All invertebrate species that were negatively correlated with the density of *Pycnopodia* within the unburied site group had no relationship with *Pycnopodia* density within the control site group, possibly because the density of these species was lower in the control than in the unburied site group (< 0.75 times as high).

4 Discussion

Sediment flux and deposition associated with dam removal can drive both short-lived and persistent changes to aquatic ecosystems (Foley et al., 2017b; Bellmore et al., 2019; Stanley and Doyle, 2003; O'Connor et al., 2015). During and immediately following dam removal on the Elwha River (2012-2016), nearly 90% of the 20 Mt of sediment eroded from behind the two dams was transported to the Strait of Juan de Fuca, resulting in significant deposition at the mouth of the river (Figure 3) and three orders of magnitude increase in suspended sediment concentration above background levels in the river. The physical changes associated with this sediment flux—deposition, changes in seabed substrate, and increased turbidity—were the dominant drivers of the multiple

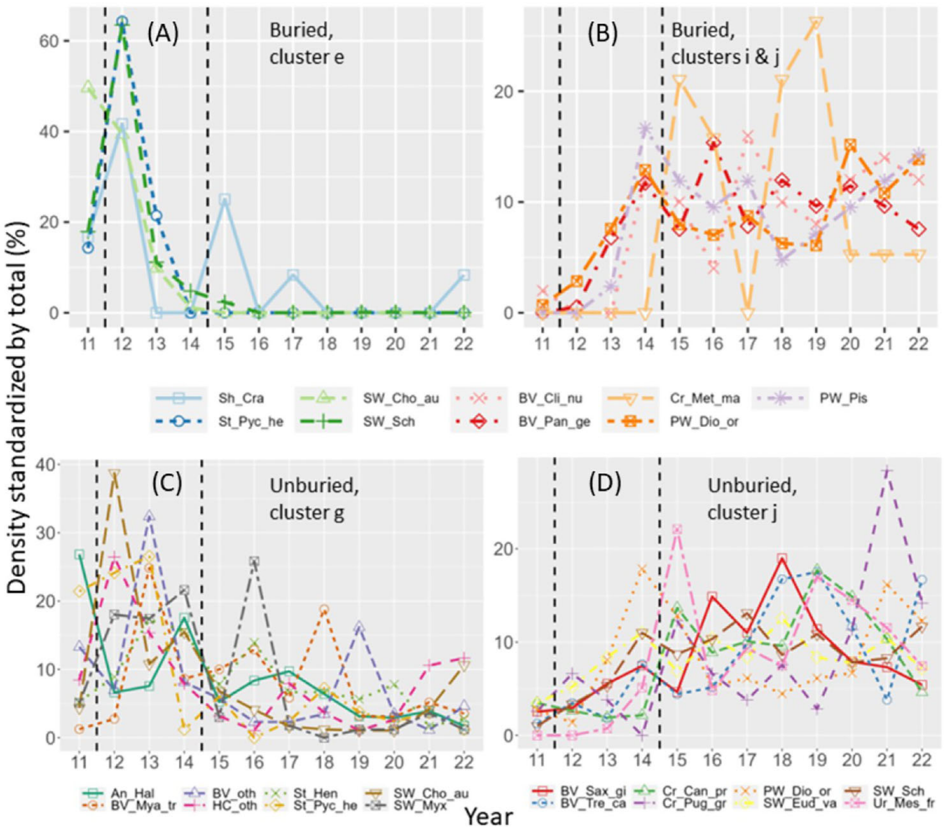

FIGURE 8

Standardized density (density in each year divided by total density across all years) versus year for invertebrate species that changed similarly across years according to cluster analyses (see Table S2 for clusters). **(A)** Species that decreased at buried sites. **(B)** Species that increased at buried sites. **(C)** Species that decreased at unburied sites. **(D)** Species that increased at unburied sites. See Table 2 for full species names. Vertical dashed lines show start and end of dam removal.

direct and indirect pathways that drove changes in algal, benthic invertebrate, and fish communities in the Elwha nearshore.

4.1 Two response trajectories: buried vs. unburied

Following disturbance events, systems can have a range of trajectories. In most cases, systems tend to either return to a condition closely resembling the pre-disturbance state or reset to a different state (Palumbi et al., 2008; Fryirs and Brierley, 2016). In the Elwha, Ritchie et al. (2018) described evidence for both models in the geomorphic system. Similarly, we found evidence for two trajectories of species and community change in the Elwha nearshore depending on the location of a site and whether a site was exposed to the joint stressors of increased turbidity and sediment deposition (buried site group, close to the river mouth) or only increased turbidity (unburied site group, farther away from the river mouth). Within each of these groups, we also found that different taxonomic groups responded differently to burial and increased turbidity, including differences in timing of response.

The geomorphic response in the coastal environment can explain, in part, the response trajectory of the marine community. Within the unburied site group, kelp responded directly to the increased flux of fine suspended sediment as soon as dam removal began (2012; Table 4) and started to rebound quickly once turbidity decreased shortly after dam removal was complete (Figures 4A, B, 5C). Increased suspended sediment decreased light availability at the unburied site group (Rubin et al., 2017), but may have also resulted in increased scour and temporary deposition, which is known to negatively affect algal recruitment and survival of juvenile sporophytes (Traiger and Konar, 2018; Picard et al., 2022). Kelp density and species richness at the unburied site group responded rapidly (Figure 4)—within a year—to the attenuation of FSSL after dam removal was complete. Overall kelp community composition at the unburied site group took longer—closer to ten years—to re-establish a state equivalent to the initial condition (Figure 5C). The close similarity between the initial kelp community and the community present at the end of our study, after a major disturbance, is notable. Watson and Estes (2011) followed recovery of kelp after sea otters reoccupied areas and removed red urchins, and found considerable variation in the re-established communities attributable to propagule availability, succession, and demography.

The invertebrate response within the unburied site group was not as universal across species as it was for kelp, nor was it directly

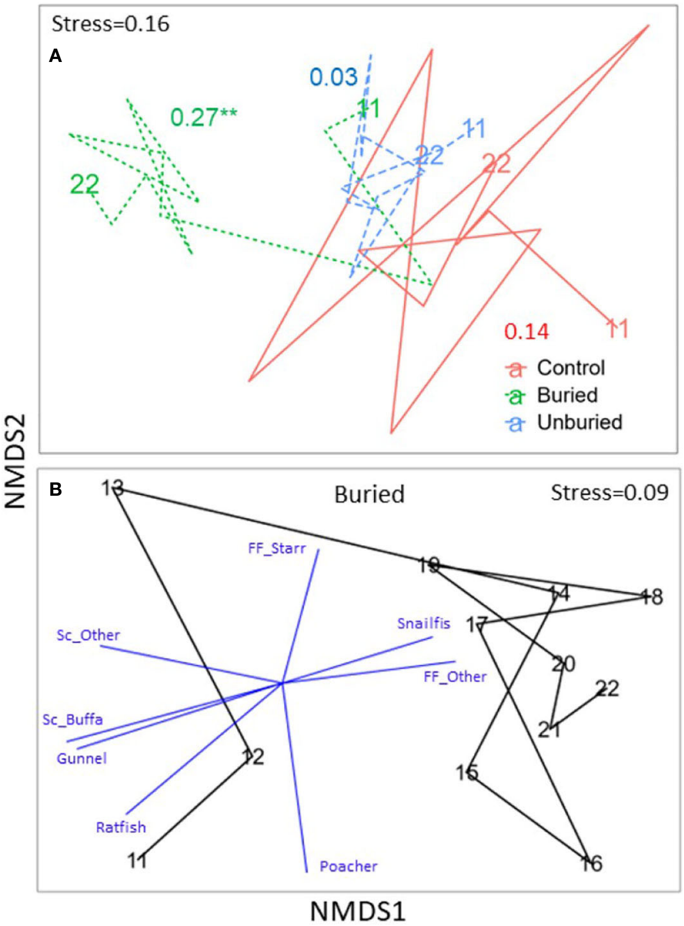

FIGURE 9
NMDS plots showing trajectories of fish community change across years by site group. **(A)** Site groups are shown together with ANOSIM R and p-values (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for each site group included (see Table 1) and the first and last years labeled. **(B)** The buried site group is shown separately with blue vectors indicating the direction and strength (vector length) of correlations between density of fish species and NMDS axes included for species contributing most to community change (see Table S1), and all years labeled. See Table 2 for full species names.

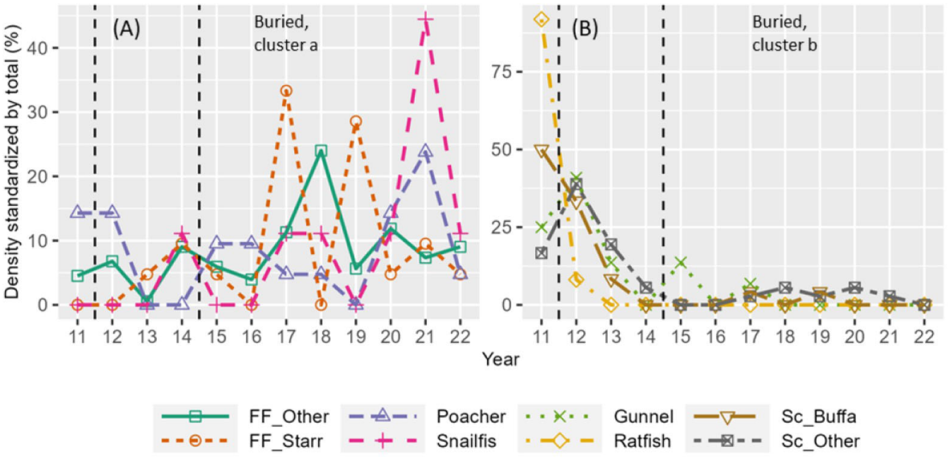

FIGURE 10
Standardized density (density in each year divided by total density across all years) versus year for fish species that changed similarly across years according to cluster analyses (see Table S2 for clusters). **(A)** Species that decreased at buried sites. **(B)** Species that increased at buried sites. See Table 2 for full species names. Vertical dashed lines show start and end of dam removal.

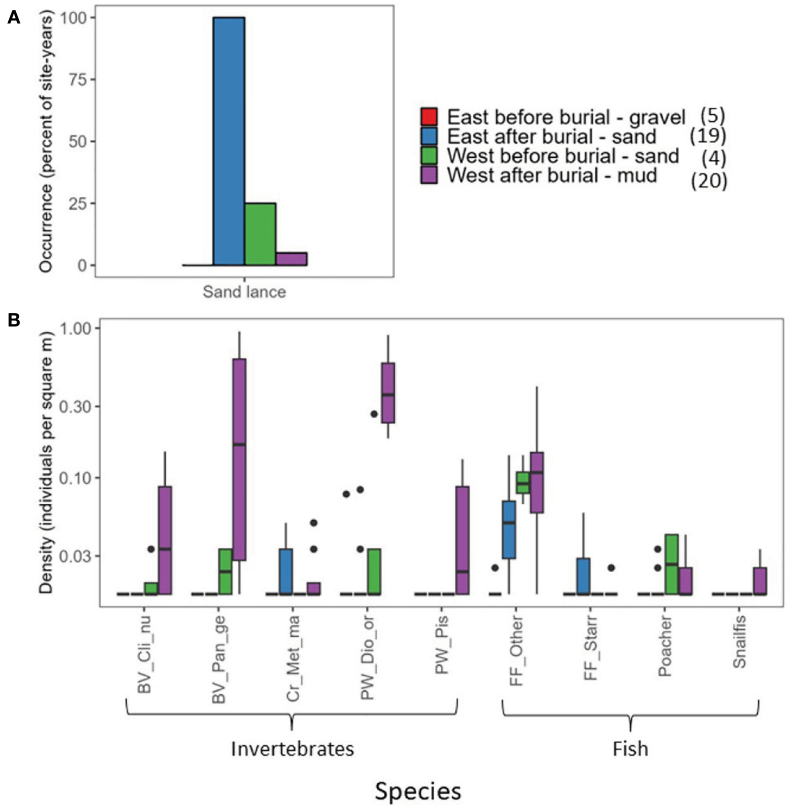

FIGURE 11
Occurrence or density at buried sites east and west of the river mouth before and after site burial for invertebrates and fish that were abundant after site burial. **(A)** Percent occurrence of Pacific sand lance. **(B)** Box and whisker plots for densities of invertebrates and fish other than sand lance; the top and bottom of boxes are the upper and lower quartiles, the line is the median, and the whiskers extends from the upper (or lower) quartile to the largest (or smallest) value no farther than 1.5 times the inter-quartile range. Numbers in parentheses in the legend are sample sizes (number of site-years).

tied to the timing of increased turbidity caused by dam removal for most species. Invertebrate density and richness did not immediately change when turbidity increased (Figures 4C, D), but overall community composition did change in 2012 (Figure 7C). Invertebrate density started to increase in 2013 and remained elevated compared to before dam removal throughout the time series (Figure 4C). For some species, increased turbidity and the loss of kelp seemed to allow them to gain a toehold at the unburied sites (Table 4; Figures S2, S3), and they were able to persist after kelp recovered and turbidity subsided (Figures 4C, 8D). Studies have shown that some filter feeders benefit from increased suspended sediment in the water column, particularly when it is correlated with an uptick in the availability of organic carbon (Dunton et al., 2006; McGovern et al., 2020). Decreases in understory algae can benefit sessile invertebrates by releasing them from competition for space (Arkema et al., 2009), or by increasing filter feeder access to food because the understory inhibits flow rates beneath it and possibly delivery of suspended particulate material as well (Eckman et al., 1989; Eckman and Duggins, 1991). For species whose abundance was positively correlated with algal cover, density tended to increase starting in 2015 (Figure 8D) when kelp started to recover.

There was no significant change in fish species composition within the unburied group, suggesting that increased turbidity and loss of kelp had little effect on the fish enumerated in our surveys. The lack of an effect of kelp density on fish abundance is contrary to other studies from kelp forest systems (Bodkin, 1988; Norderhaug et al., 2020). However, many of those studies focused on canopy-forming kelp (e.g., *Macrocystis gigantea*, *Nereocystis luetkeana*), while the kelp community in the Elwha nearshore is dominated by prostrate species, such as *Alaria marginata*, *Costaria costata*, and *Laminaria* spp. However, in some cases understory kelp too can be associated with increased fish abundance (Hamilton and Konar, 2007). There were fewer clear long-term invertebrate winners and losers within the unburied site group due to the transitory nature of the dam removal effects at these sites. The invertebrates that were able to sustain an advantage from short-term changes in turbidity and algal cover appear to be the long-term winners following dam removal.

The response of kelp, invertebrates, and fish within the buried site group was consistent with previous studies in other marine ecosystems following large sediment deposition events where communities tend to shift to an alternate state (Miller et al., 2002; Lohrer et al., 2006; Connell et al., 2008; Watanabe et al., 2016). The species response at the buried site group highlighted winners and losers due to dam removal. Species that were dependent on the gravel substrate at the eastern buried sites were lost locally and had not recovered by 2022. For the sand-dependent species, the area of

TABLE 3 Multivariate tests (distance based redundancy analyses) for associations between kelp community change and fine suspended sediment load (FSSL) or *Pycnopodia* density, and between invertebrate community change and FSSL, algal cover, or *Pycnopodia* density.

		Delta R-squared (P)				
Taxon	Site group	Site	FSSL	Algal cover	*Pycnopodia* density	R-squared
Kelp	UB	0.464***	0.102***			0.566
		0.463***			0.012*	0.476
	C	0.448***	0.034 NS			0.482
		0.435***			0.027 NS	0.474
Invertebrates	UB	0.519***	0.021***			0.54
		0.455***		0.021***		0.54
		0.508***			0.034***	0.554
	C	0.233***	0.059 NS			0.292
		0.205***		0.052 NS		0.285
		0.226***			0.071*	0.305

Site groups are unburied (UB) and control (C). NS=p>0.05, *=p<0.05, **=p<0.01, ***=p<0.001.

new habitat created by deposition of relatively fine sediment associated with dam removal resulted in density increases. Within the buried site group, kelp responded initially to the increased turbidity in 2012 and recovery was precluded due to burial and a change in habitat suitability when the cobble substrate at the eastern buried sites was buried by sand (Figure 3I), which reduced or eliminated substrate suitable for holdfast attachment. For invertebrates, the effects were more species specific, although the overall trajectory was decreased density and species richness (Figure 4). The initial increase in turbidity resulted in an increase in filter feeding sabellid worms, followed by a steep decline once the sites were buried in 2014 (Figure 8A). For other species, burial provided new habitat that was rapidly colonized by species that rely on finer grained habitat than cobble. For fish, increased turbidity at the start of dam removal in 2012 did not result in drastic changes to species density and richness or overall community composition, but burial and related grain size changes in 2013 and 2014 resulted in decreased richness and a significant change in species composition (Figures 4, 9). For some species, particularly the ecologically important forage fish Pacific sand lance, the change in habitat at the river mouth was a boon for their population (Figure 11). Frick et al. (2022) also saw an increase in sand lance at their Elwha sites after dam removal, but the increase was not significant. For all three taxonomic groups at the burial sites, despite their different initial responses to turbidity and burial, they all reached a relatively stable level of density and richness, and consistent community composition by 2016, following the peak of sediment deposition at the buried sites (Figures 3–5, 7, 9). The evolution of seafloor deposits formed during dam removal is on-going (Figure 3), with important implications for the species found within the buried site group. As the deposits of mud and sand formed during dam removal are eroded by tides and waves and the substrate coarsens (Figure 3I), it is possible that the composition of the benthic community associated with those new habitats will continue to evolve until geomorphic processes stabilize.

Within the control site group, change was unrelated to the effects of dam removal. Kelp community composition did significantly change over the course of our study, but the trajectory of change was highly variable over time (Figure 5D) and changes in density and species richness did not correspond with the timing of changes within the buried and unburied site groups (Figure 4). There were regional changes that occurred at our sites (see Other drivers of change below) that likely had a stronger effect on the variability of kelp, invertebrates, and fish within the control site group.

4.2 Other drivers of change

While dam removal was the dominant driver of change for kelp and some invertebrate and fish species from 2012-2015 for the unburied and buried site groups, dam removal was not the only disturbance playing out in the Pacific Northwest during our study period. As mentioned previously, SSWS decimated populations of *Pycnopodia* in the Strait of Juan de Fuca between our 2013 and 2014 surveys (Montecino-Latorre et al., 2016; Harvell et al., 2023) and populations had not recovered by 2022 (Figure 8C). Correlation analysis showed that the changes in the density of *Pycnopodia* was significantly negatively correlated with densities of six invertebrate species in the unburied site group, including (from strongest effect to weakest) *Mesocentrotus franciscanus*, *Saxidomus gigantea*, *Schizobranchia* sp., *Tresus capax*, *Eudistylia polymorpha*, and *Nucella* sp. (Table 4; Figure S4). *Pycnopodia* is a generalist in most subtidal communities (Duggins, 1983), so the loss of *Pycnopodia* may have affected other invertebrate species besides those we included in our analysis. We limited our analysis to those species that contributed to the overall change in invertebrate community composition within the unburied site group during our study. To the north of our study sites, but still within the Salish Sea, Schultz et al. (Schultz et al., 2016) found evidence of a trophic

TABLE 4 For Elwha unburied sites only, univariate tests (regressions) for association of fine suspended sediment load (FSSL), algal cover, or *Pycnopodia* density with kelp density (summed over species), percent algal cover, or invertebrate species densities.

Taxon	Species	FSSL	Algal cover	Pycnopodia density
Algae	Kelp	Neg*** (crv)		NS
	Algal cover	Neg*** (str)		NS
Anemone	*Halcampa* sp	Uni* (crv)	NS	NS
Bivalve	*Mya truncata*	Pos** (str)	Neg*** (str)	NS
	Other	NS	NS	NS
	Saxidomous gigantea	NS	NS	Neg*** (str)
	Tresus capax	NS	NS	Neg** (str)
Chiton	*Tonicella* sp	NS	Pos* (crv)	Pos* (str)
Crab	*Cancer productus*	Neg*** (str)	Pos** (str)	NS
	Pugettia gracilis	Neg** (str)	Uni** (crv)	NS
Hermit crab	Other	NS	NS	NS
Polychaete worm	*Diopatra ornata*	NS	NS	NS
Shrimp	*Pandalus* sp	Neg* (str)	NS	NS
Snail	*Calliostoma* sp	NS	NS	NS
	Nucella sp	Neg*** (crv)	NS	Neg* (str)
Sea star	*Henricia* sp	Pos*** (str)	Neg* (crv)	NS
	Pycnopodia helianthoides	NS	NS	
Sabellid worm	Chone *aurantiaca*	Pos*** (crv)	Neg*** (str)	NS
	Eudistylia polymorpha	NS	NS	Neg** (str)
	Eudistylia vancouveri	NS	NS	NS
	Myxicola sp	Pos* (str)	Neg*** (crv)	NS
	Schizobranchia sp	Pos* (crv)	Neg** (str)	Neg* (str)
Urchin	*Mesocentrotus franciscanus*[a]	NS	NS	Neg*** (str)

[a] *Mesocentrotus franciscanus* occurred at only on site.

Neg, negative correlation; Pos, positive correlation; Uni, unimodal (single peak; neither positive nor negative). Str = straight (linear relationship); Crv, curved relationship (when curved fit better than linear). Regression lines for significant relationships are shown in Figures S2–S4. NS=p>0.05, *=p <0.05, **=p <0.01, ***=p< 0.001.

cascade in the subtidal communities in Howe Sound following the loss of *Pycnopodia*, whereby the population of green urchins (*Strongylocentrotus droebachiensis*) increased, and kelp cover declined. Although invertebrate community composition did not change significantly across years within the control site group (Table 1; Figure 7A), community composition at control sites was significantly related to the density of *Pycnopodia* (Table 3). This mixed result provides some support for a more extensive regional effect of the loss of this important sea star predator.

For some species, density increases following the loss of *Pycnopodia* may have resulted from behavior changes rather than reduced predation mortality. Urchins sometimes come out of hiding and switch from passive to active foraging (Smith et al., 2021) and are preyed upon by and show an escape response to *Pycnopodia* (Duggins, 1983), however, susceptibility of red urchins (*Mesocentrotus franciscanus*) to *Pycnopodia* predation is greatly reduced when they reach full size (Duggins, 1983). Although we did not take size measurements, the red urchins we censused appeared to be full sized. They were usually aggregated on boulders or more spread out on gravel-cobble substrate, suggesting a change in foraging behavior rather than a release from predation.

The other regional event that coincided with the tail end of increased suspended sediment associated with the dam removal was the largest marine heatwave on record from winter 2013-2015 (Di Lorenzo and Mantua, 2016). Given the regional nature of this event, we would expect to be able to see the effects, if any, of the marine heatwave at our control sites. For kelp, there was significant change in community composition across years that was not temporally aligned with change at Elwha sites (little change from 2011-2013 at control sites compared to great change at Elwha sites; Figure 5). The waters along the outer coast of Washington, including the western entrance to the Strait of Juan de Fuca, experienced anomalously warm temperatures in 2013 and 2014 (Tolimieri et al., 2023), and canopy kelp extent was anomalously low on the outer coast and in the Strait of Juan de Fuca in 2014 (Pfister et al., 2018). Kelp density at our control sites decreased from 2013 to 2016 with some recovery in 2017 (Figure 4), and *Nereocystis leutkeana* and *Laminaria setchellii* were lost in 2014 but reappeared by 2016-2017 (Figure 6C), accounting for the large change in kelp community composition between 2013 and 2017 (Figure 5D). These results suggest some correspondence between kelp response at our control sites and regional trends in ocean temperatures and canopy kelp abundance. We would expect that regional oceanographic conditions would affect kelp at Elwha sites as well, but we were unable to separate regional from dam removal effects based on our sampling design because of the overlap of the two stressors.

The correlations we observed between community composition and the loss of sea stars (Tables 3, 4; Figure S4), along with the potential connection with climate variability (Tolimieri et al., 2023) cloud, to a degree, our ability to characterize the long-term dam removal response in the marine ecosystem, as well as to predict the ongoing trajectory of change. Invertebrate community composition within the unburied site group, for example, was indirectly related to dam removal (correlation to algal cover), but directly affected by SSWS. The relaxed predation pressure likely drove increased densities of bivalves, urchins, and some worms, suggesting that both dam removal and SSWS contributed to the response trajectory. It is possible that dam removal sparked changes in the marine community that were then further shaped by additional stressors in the system, some of which we could directly test and others that we could not.

4.3 Considerations for other dam removals

While dam removal is accelerating in the United States (O'Connor et al., 2015), the number of dam removals motivated by, or that considered, marine impacts or restoration in their management is small (Ralston et al., 2021; Cancel Villamil and Locke, 2022). The removal of the two dams on the Elwha was notable for its influence on multiple aspects of the marine system (Gelfenbaum et al., 2015; Rubin et al., 2017; Shaffer et al., 2017; Glover et al., 2019; Warrick et al., 2019). It is likely that a variety of factors contributed to those effects, including the characteristics of the impounded sediment (volume, erodibility, and grain size distribution), length and steepness of the river system, and distribution of dams within the watershed (i.e., tributary versus mainstem), which have been well characterized, particularly for dam removals in the western United States (Foley et al., 2017a; Major et al., 2017). The characteristics of marine waters into which the watershed drains—waves, currents, and bathymetry—influenced sediment dynamics in the nearshore. While data on the marine influence of dam removals besides Elwha is generally lacking, sediment dynamics in the nearshore from other sediment disturbances (e.g., land use change, landslides) have been studied (Crain et al., 2009; Erftemeijer et al., 2012; Booth, 2020; Rangel-Buitrago et al., 2023). Below we highlight processes that contributed to the geomorphic changes and ultimately ecological responses and how they may be used to consider effects of sediment disturbances, including dam removal, in other locations.

The Elwha River delivered 20 Mt of sediment to the nearshore during and immediately following dam removal, resulting in greater than 5 m of deposition near the river mouth (Figure 3E). The watershed steepness, proximity of dams to the coast, and lack of additional impoundments all contributed to the rapid flux of sediment to the nearshore and subsequent reduction following the completion of dam removal (Ritchie et al., 2018). The tidal currents in the Strait of Juan de Fuca are a dominant driver of sediment transport at the Elwha and likely contributed to a reduced amount of fine sediment retention (Warrick et al., 2008; Miller et al., 2011) compared to other systems with weaker tidal forcing. Of the 20 Mt of sediment delivered to the nearshore, approximately 60% was fine silt and clay (fine suspended sediment), which was predominantly dispersed away from the Elwha River delta by the strong tidal currents (Gelfenbaum et al., 2015). This sediment was transported predominantly to the east of the river mouth, affecting the spatial distribution of water column turbidity (Gelfenbaum et al., 2015; Foley and Warrick, 2017; Glover et al., 2019) and resulting impacts to nearshore communities (Rubin et al., 2017).

During the dam removals, the large flux of coarse sediment to the nearshore overwhelmed the littoral transport processes resulting in widespread accumulation of mostly sand-sized sediment (Figures 3E, H) that deposited on top of formerly eroding lag deposits of cobbles and boulders (Warrick et al., 2008). The two dams were operated as run of river dams, allowing for the passage of a substantial portion of fine sediment to reach the nearshore while the dams were in place, while retaining most of the sand and coarse sediment in the reservoirs. With the removal of the dams, it is likely that sand delivery to the nearshore will be greater than when the dams were in place. While the large influx of sediment initially resulted in deposition near the river mouth, those deposits are actively being reworked by tidal currents and waves, resulting in net erosion on the subaqueous delta (Warrick et al., 2019) and a coarsening of grain size (Figures 3C, F, I). The ongoing changes at the delta and the magnitude of deposition and erosion will likely affect future habitat suitability for the species in the new deposits.

Based on our observations of geomorphic and ecological response after the Elwha dam removals, the major factors to consider when evaluating the potential effects from dam removals or large sediment fluxes from watersheds to the marine environment (e.g., landslides, wildfire debris flows) include the type, magnitude, and duration of the disturbance, character of the sediment, and coastal sediment transport processes that result in dispersal and sorting of sediment in the nearshore. In the case of the Elwha, ecological change was driven by two types of effects, sediment deposition of coarser grain sediment and increased turbidity from finer grain sediment. The duration of the disturbance depended on the type of effect. Sediment deposition had longer lasting effects on the ecosystem than increased fine suspended sediment, in part due to the more variable effects of suspended sediment in space and time. In addition, species likely had different sensitivities to stressor types depending on their life history, morphological structure, mobility, and habitat needs. The magnitude of effect on the Elwha ecosystem was likely a function of both the overall sediment flux from the reservoirs to the coast as well as the hydrodynamics of the Elwha nearshore. Coastal areas without strong tidal currents would likely be most affected by burial due to a lack of transport capacity in the system, particularly if the amount of sediment being delivered is greater than background conditions. While the exact trajectories of community response to a disturbance are difficult to predict, assessing these conditions can be used to inform the development of conceptual models of potential outcomes that can inform monitoring and modeling efforts before and after dam removal.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Rubin, S.P., Elder, N.E., Miller, I.M., Beirne, M.M., and Foley, M.M., 2023, Data collected in 2008-2022 to assess nearshore subtidal community responses to increased sediment load during and after removal of the Elwha River dams, Washington State, USA: U.S. Geological Survey data release, https://doi.org/10.5066/P9NCE4FE.

Author contributions

SR, IM, JW and GG contributed to the study concept and design, SR, MF, IM, AS, JW, NE, MB and GG participated in data collection, and SR, MF, IM, AS, NE and HB in sample processing and data analysis. SR, MF, IM, AS, JW, and HB contributed to drafting and review of the submitted manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1233895/full#supplementary-material

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Using riverscape genetics to investigate the genetic response of two species and their life-history forms to dam removal

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Barriers such as hydroelectric dams inhibit migratory pathways essential to many aquatic species, resulting in significant losses of species, their unique life-history forms, and genetic diversity. Understanding the impacts of dam removal to species recovery at these different biological levels is crucial to fully understand the restoration response. We used the removal of two large dams on the Elwha River as an opportunity to characterize how restored connectivity impacts the reestablishment of two fish species, Chinook salmon (*Oncorhynchus tshawytscha*) and Steelhead/rainbow trout (*Oncorhynchus mykiss*), and their unique ocean migration return-timing life-history forms. In this study, we employed riverscape genetics to understand how restoration and the environment influence the distribution of neutral and return-timing genetic variation underlying the migratory life-history forms and species at- and between- sampling sites. We genotyped fish sampled over time and space in the Elwha River using Genotyping-in-Thousands by sequencing (GTseq) loci for both species at neutral and putatively adaptive loci in and near the major effect genic region *GREB1L/ROCK1* putatively associated with migration timing. We observed little evidence of genetic structure for either species, but a statistically significant increase in early return-timing alleles in upriver *O. mykiss* population post-dam removal. For *O. tshawytscha*, at-site genetic variation was shaped by river distance and a combination of environmental habitat differences, while between-site genetic variation was mainly shaped by river distance. For all *O. mykiss*, at- and between-site genetic variation is primarily explained by river distance. Genetic variation in juvenile and adult Steelhead, respectively, were influenced by at- and between-site environmental and habitat differences. Our study illustrates the power of using genetics to understand the implications of both demography and environment in facilitating the recovery of species and their diverse life-history forms following barrier removal.

KEYWORDS

Chinook, Steelhead, rainbow trout, dam removal, restoration, return-timing, landscape genetics, GREB1L/ROCK1

1 Introduction

Significant habitat degradation, reduced connectivity, and total isolation of suitable habitat are possible outcomes of anthropogenic barriers in freshwater environments for numerous species (Bunn and Arthington, 2002). Anthropogenic barriers can cause significant population declines, extirpations, and elimination of unique life-histories, which can have cascading ecological effects for the system across taxa (Brenkman et al., 2008; Bellmore et al., 2019; Zarri et al., 2022). Barrier removal has occurred for decades to improve accessibility and reestablish the necessary habitats for migratory animals such as salmon (Pess et al., 2012; Pess et al., 2014; Bellmore et al., 2019), which has in turn has successfully restored connectivity and contributed to population gains for key taxa in formerly blocked habitats (Brenkman et al., 2012; McHenry et al., 2017; Duda et al., 2020; Hess et al., 2020; Fraik et al., 2021; Pess et al., *In Review*). Understanding the extent to which the removal of these large barriers may ultimately lead to restored biological communities remains an important area of study (Grummer et al., 2019; Tamario et al., 2019).

Necessary ecological conditions for movement must exist for aquatic species to reestablish in their historical habitat after barrier removal. Aquatic species respond, move and disperse across riverscapes in different ways, as a function of their migration capabilities (Crozier et al., 2008; Dodson et al., 2013; Pess et al., 2014). Some species remain in one freshwater habitat for their entire lives, whereas others move between different freshwater environments (e.g., rivers and lakes) or into marine habitats (Quinn, 2018). This is exemplified in salmonids which undergo physiological transformations to migrate (Nichols et al., 2008; Hecht et al., 2012; Dodson et al., 2013; Kendall et al., 2015) and have significant intraspecific variation in their migration life-history forms. Challenges to upriver movement in freshwater environments for salmonid species include the distance to new habitat, environmental conditions, physical capacity to reach the habitat, life-history traits required to exploit the habitat, and physical barriers (Pess, 2009; Duda et al., 2020). These challenges may impact both the local population connectivity of those species still present, and the species that may reestablish the river network after local extirpation. Evaluating the impacts of barrier removal therefore requires consideration of the ecological characteristics of migratory corridors, the breadth of life-history forms expressed and the standing genetic variation underlying these life-history traits in extant populations (Gaggiotti et al., 2004; Anderson et al., 2010; Pess et al., 2012; Anderson et al., 2013).

Juvenile and adult ocean migration life-history forms of salmonids have a genetic (Nichols et al., 2008; Hecht et al., 2012; Pearse et al., 2019) and environmental basis (Docker and Heath, 2003; Heath et al., 2010; Kendall et al., 2015). In particular, there is a strong association of alleles in and near the *GREB1L* and *ROCK1* genes with ocean migration return-timing in several salmonid species (Hess et al., 2016; Prince et al., 2017; Micheletti et al., 2018; Thompson et al., 2019; Collins et al., 2020; Willis et al., 2020; Willis et al., 2021; Tigano and Russello, 2022). Previous work suggests early freshwater adult return-timing for anadromous salmonid species is an adaptation for fish migrating longer distances as they return to freshwater during higher flows, when water temperatures are cooler, producing more energetically optimal conditions compared to those experienced by later returning adult fish (Quinn et al., 2016; Waples et al., 2022). This knowledge of the genetic basis, in association with the ecological requirements, of these life-history forms is crucial for understanding the response to migratory corridor restoration. Monitoring and assessing these diverse life-history forms of salmonids, however, can be quite challenging due to variable river sampling conditions during these distinct freshwater entry-times.

Landscape genetics is a tool that allows us to examine the role specific environmental conditions have on genetic connectivity among these life history forms across a defined area (Storfer et al., 2007; Manel and Holderegger, 2013; Storfer et al., 2018). While developed specifically for terrestrial studies, landscape genetics has been applied to riverscapes to identify the impacts of shared environmental features on the movement, gene flow and structure of aquatic populations (Whiteley et al., 2004; Davis et al., 2018; Kelson et al., 2020; Rougemont et al., 2023). These methods have been employed to identify unique, population specific responses (Narum et al., 2008; Sidharthan et al., 2022) as well as inter-specific responses to shared, environmental stressors (Whiteley et al., 2004; Goldberg and Watis, 2010; Olsen et al., 2010; Emel et al., 2019). Using riverscape genetic methods, we can test the impacts of barrier removal on spatial patterns of species with life-history specific genetic variation.

Research is underway to document the implications of barrier removal on aquatic life-history diversity in the Elwha River watershed (Brenkman et al., 2019; Duda et al., 2020; Duda et al., 2021). Located in the Olympic peninsula of western Washington state, the Elwha

River basin occupies 883 rkm^2 and was once one of the more productive watersheds in the Pacific Northwest. This watershed is home to the five Pacific Salmon species (from the genus *Oncorhynchus*), as well as bull trout (*Salvelinus confluentus*), coastal cutthroat trout (*Oncorhynchus clarkii*), Steelhead/rainbow trout (*Oncorhynchus mykiss*), Pacific lamprey (*Entosphenus tridentatus*) and numerous other freshwater fish (Brenkman et al., 2008; Pess, 2009). The construction of the Elwha River (1912) and Glines Canyon (1927) dams in the lower and middle portions of the main stem without fish passage blocked upstream and downstream connectivity for fishes, leading to declines of several aquatic species (DOI, 1996; Winans et al., 2008). In particular, life-history variants of salmonid species that previously occupied the river appeared to be extirpated after dam construction, including many species' early return-timing life history forms (Brenkman et al., 2008; Pess, 2009). As a result of the Elwha River Restoration Act, dam removal of the Elwha River dams began in 2011. Following the Glines Canyon Dam removal in August 2014, a rockfall occurred in Glines Canyon and created at least a partial barrier to fish. This blockage was addressed in late 2015 with selective blasting which reopened the channel for fish passage (Ritchie et al., 2018). Over time, Chinook salmon (*Oncorhynchus tshawytscha*), Steelhead and numerous other salmonid species have ascended the river upstream of the former Glines Canyon dam, expanding their spatial distributions into the upper watershed (Duda et al., 2020; Duda et al., 2021; McHenry et al., 2022; Peters et al., 2022). However, the rates and extents of fish returning to the upper river varied, particularly across species with distinct life-history forms (Brenkman et al., 2019; Pess et al., *In Review*). One remaining question is how reestablishing connectivity in the Elwha River may affect salmonid species' distinct life-history forms and their underlying genetic variation in different ways.

In this study, we used population and riverscape genetics to investigate the distribution of neutral and return-timing genetic variation within *O. tshawytscha* and *O. mykiss* sampled from the Elwha River. First, we investigated neutral genetic structure for each species and explored associations with time and space. Second, we tested for shifts in frequencies of alleles associated with early ocean return-timing for each species. Finally, we employed riverscape genetics to test for differences in gene flow of neutral and return-timing genetic variants in each species that could be explained by freshwater environmental variation. Specifically, we compared the relationships of genetic variation with models of river distance to models of at-site and between-site environmental conditions, with the distance models representing the null hypothesis of isolation-by-distance. Overall, this study represented a unique opportunity to understand potential differences between neutral and return-timing genetic variation through space and time after large-scale dam removal, with important implications for broad restoration efforts related to connectivity.

2 Methods

2.1 Study system

We sampled two species: Chinook salmon (*O. tshawytscha*) and Steelhead/rainbow trout (*O. mykiss*). Each species exhibits multiple migration life-history forms, but the species differ in their anadromous form. *Oncorhynchus tshawytscha* are obligately anadromous, meaning that they must migrate to the ocean. *Oncorhynchus mykiss* are facultatively anadromous, exhibiting both marine migrating (Steelhead) and freshwater resident (rainbow trout) forms that spatially overlap in spawning sites and can reproduce (Behnke, 1992; Docker and Heath, 2003; Kendall et al., 2015). Both *O. tshawytsha* and *O. mykiss* express variation in the timing of their return to freshwater for spawning. Early ocean return-timing in the Elwha River is thought to occur in the spring/summer (May-June) for *O. tshawytscha* and the summer/fall (June-November) for Steelhead (Busby et al., 1996; Quinn, 2018; Denton et al., 2022a; Denton et al., 2022b). While the exact phenotype and genetic architecture for these traits are not precisely known (Ford et al., 2020; McKinney, 2020; Tillotson et al., 2021; Waples et al., 2022), the *GREB1L/ROCK1* genomic region has been repeatedly identified as a strong candidate underlying this life-history variant (Micheletti et al., 2018; Thompson et al., 2019; Koch and Narum, 2020; Thompson et al., 2020; Willis et al., 2020; Willis et al., 2021). Variant genotypes across species have been associated with freshwater entry timing, spawning site arrival timing and sexual maturation status upon start of migration (Myers et al., 2006; Hess et al., 2016; Narum et al., 2018). Due to the complexity of their life-history forms, these fish are hereafter referred to by their scientific names unless the exact phenotype (i.e. summer Steelhead or spring Chinook) is described.

2.2 Fish sampling and tissue collection for genotyping

We included both natural and hatchery-origin *O. tshawytscha* and *O. mykiss* in this study. We sampled fish from the main stem and tributaries of the Elwha River including below the former Elwha dam (BD), in between the former Elwha and Glines Canyon Dams (ID) and above the former Glines Canyon Dam (AD) (Figure 1). We sampled *O. tshawytscha* between 2014 and 2018 and *O. mykiss* between 2004 and 2022 using a variety of methods depending on the age, origin and species. Different numbers of samples, sampling resolutions (reach versus geographic point), time periods (pre and post-dam removal), spatial distributions (watershed-wide versus stream-level) and knowledge of life-history phenotypes (date of capture) were collected across species. Demographically, the hatchery composition of each species is significantly different (Denton et al., 2022a; Denton et al., 2022b). Broadly, ~98% of summer and ~75% of the winter Steelhead returning to the Elwha River are estimated to be natural-origin while overall ~90–95% of the Chinook are thought to be hatchery origin.

We sampled *O. tshawytscha* tissue from post-spawn adult carcasses found along the river margins and banks. We assigned *O. tshawytscha* sampling locations based on the downstream GPS coordinate of the reach from which a carcass was collected. Though these sites did not necessarily represent the precise spawning location, they were likely geographically proximate at the reach scale (approximately 100 m–2 km). Since we sampled adult *O. tshawytscha* as carcasses, the return-timing of individual fish was

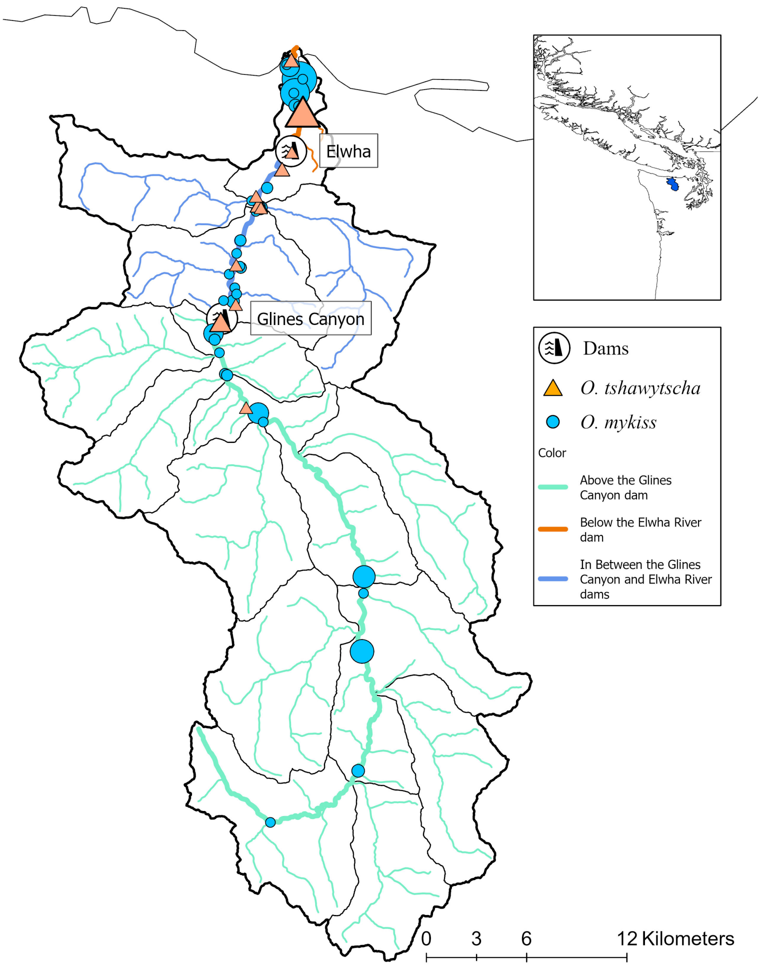

FIGURE 1
Study sites within the Elwha River basin as well as the location of the two dams removed in 2015. Each point represents a distinct sampling site for either *O. mykiss* (circles) or *O. tshawytscha* (triangles) within a broader sampling location (represented by color of the water and the relative dam location) along the Elwha River. Size of shape represents relative sample size.

unknown. All fish were sampled in 2014 or after, when the upper Elwha River Dam removal was underway. Thus, we considered all *O. tshawytscha* samples post-dam removal. However, to test if there were significant genetic differences between fish hatched pre and post-dam removal, we performed a supplementary set of analyses also assigned fish to age classes using scale ages (*Appendix Materials and Methods*). Samples taken from known hatchery-origin *O. tshawytscha*, identified by the presence of hatchery marks including otolith thermal marks, adipose clips, and coded wire tags (CWT), were included in this study. The *O. tshawytscha* hatchery broodstock are a native lineage broodstock program developed from fish caught in the Elwha; hatchery managers intentionally avoided releasing non-local stocks (Brannon and Hershberger, 1984). Both hatchery-origin and natural-origin fish were used for hatchery spawning, but it was not possible to target either origin for preferential spawning because most fish were not externally marked; hence hatchery-origin fish were not readily identifiable at spawning.

We sampled tissue from adult resident rainbow trout, adult Steelhead of both return migration times (early and late), outmigrating smolts (herein included in counts for Steelhead) and juvenile *O. mykiss* of unknown life-history forms across the watershed, prior to and post-dam removal, from fish returning from January through October (Table S1). We sampled juvenile *O. mykiss* using both backpack electrofishing and smolt traps (Pess et al, *In Review*). We designated trout fry as unknown life-history phenotypes unless recaptured as an adult or defined as a smolt (Fraik et al., 2021). We sampled hatchery-origin Steelhead samples from the Lower Elwha Klallam Tribe's hatchery program, which was founded from native lineage broodstock developed from eyed eggs from naturally spawned adult *O. mykiss* sampled downstream of Elwha River dam from 2005–2011 (LEKT, 2012; Winans et al., 2016; Fraik et al., 2021). Hatchery-origin samples were included in this study. We collected natural-origin, adult *O. mykiss* via hook and line sampling and in steam netting (Denton et al., 2022b). We distinguished adult Steelhead from adult rainbow trout primarily based on body coloration and a size threshold (Steelhead fork length > 500 mm, rainbow trout fork length < 500 mm). Adult Steelhead were sampled in the main-stem Elwha River while migrating to their spawning sites or emigrating back to the sea after spawning.

Thus, for *O. mykiss*, sampling location may not necessarily represent their exact spawning location. We assigned fish as pre-dam removal if they were sampled before 2013 and post-dam removal if they were sampled 2013 and beyond (Table S1). As scale ages were not available for *O. mykiss*, we could not assign *O. mykiss* to fish hatched pre and post-dam removal.

2.3 DNA sequencing, genotyping, and quality control

In total, 380 *O. tshawytscha* and 1,741 *O. mykiss* were sampled and prepared for Genotyping-in-Thousands by sequencing (GTseq). Sequence data for *O. tshawytscha* was obtained from McKinney et al. (*In Prep*), NCBI Bioproject PRJNA1020840, and reanalyzed for this study. DNA was extracted from *O. tshawytscha* and *O. mykiss* tissue punches stored on Whatman paper using the Promega Wizard SV genomic DNA extraction kit. All GTseq libraries were constructed separately for each species following the methods in Campbell et al. (2015). The *O. tshawytscha* GTseq panel contains 332 loci, 298 of which are putatively neutral and commonly used for population genetic studies, one sex identification marker, and 33 markers associated with return-timing variation in *GREB1L/ROCK1* region (Hess et al., 2016; Thompson et al., 2019; Koch and Narum, 2020; Thompson et al., 2020). Genotypes for both species were called using the custom scripts in the GTScore pipeline (McKinney et al., 2020, available at GitHub - gjmckinney/GTscore: Pipeline for GTseq genotyping and quality control). *Oncorhynchus mykiss* samples were genotyped with the GTseq panel developed by Campbell et al. (2015) that contains 367 SNPs, of which 241 are putatively neutral and commonly used for population genetic studies, one is for sex identification, three are for diagnosing cutthroat trout (*O. clarkii*) and 122 markers that are putatively adaptive, of which 13 are associated with return-timing variation (Collins et al., 2020). Across both data sets, loci were filtered to remove potential and known tetrasomic loci. Samples with a high likelihood of DNA contamination (contamination score > 90%) and pairs of samples with duplicate genotypes (> 80% genotypes identical between each pair of individuals) were filtered out. For *O. mykiss*, we also removed individuals that had at least one cutthroat trout allele at one of the three species diagnostic loci.

Subsequent filtering for each species was performed in R v4.1.2 (R Core Team, 2022) using the package "adegenet" (Jombart, 2008; Jombart and Ahmed, 2011) for all the remaining SNPs. Using the *minorAllele* function we identified and removed 18 monomorphic loci from the *O. tshawytscha* and zero loci from the *O. mykiss* dataset. Next, we removed loci that were missing > 0.3 data among genotyped individuals (zero loci were removed from *O. tshawytscha* and five loci from the *O. mykiss* dataset) and individuals missing > 0.4 genotype data across loci (zero *O. tshawytscha* and 102 *O. mykiss* individuals*)*.

The filtered SNPs for each species were then divided into two data sets: loci putatively involved in migration return-timing and putatively neutral loci. Given the specificity of our study question, we considered loci located in *GREB1L/ROCK1* regions to be involved in migration return-timing, and the other adaptive loci were classified into the neutral genetic matrix. This also prevented loci that were adaptive in one system from being erroneously classified as adaptive in the Elwha River populations due to the geographic range of previous genomic outlier tests. Loci found in/near *GREB1L/ROCK1* and previously identified as candidates for migration return-timing life-history variants included 28 SNPs in the *O. tshawytscha* panel and 11 SNPs in the *O. mykiss* panel that passed missing data thresholds (Campbell et al., 2015; Hess et al., 2016). We applied a Hardy-Weinberg equilibrium test to all of the remaining neutral loci in each species' panel to identify loci deviating from expectations of Hardy-Weinberg equilibrium (HWE) using *hw.test* function in the R package "pegas" (Paradis, 2010). We applied a strict Bonferroni adjustment (Dunn, 1961) for multiple tests to generate the final list of putatively neutral loci for downstream analysis.

2.4 Population genetic and structure analyses across species

To investigate changes to the population genetic structure of *O. mykiss* and *O. tshawytscha*, we performed Discriminant Analysis of Principal Components (DAPC) using "adegenet" in R. For these analyses, we conducted four independent DAPC analyses for *O. mykiss* and one for *O. tshawytscha*. In the first two DAPCs for *O. mykiss*, we used the set of putatively neutral loci as determined by the HWE test for pre and post-dam removal fish (303 SNPs). In the second two DAPCs for *O. mykiss*, we once again separated samples temporally, but only retained loci explicitly designated as neutral in the GTseq panel (212 SNPs). We ran DAPC analyses on each set of putatively neutral loci in *O. mykiss* to compare the neutral genetic structure between our filtered loci and those identified as neutral in the panel. There were no putatively adaptive loci outside of the return-timing loci in the *O. tshawytscha* GTseq panel, therefore we only conducted one DAPC for all post-dam removal fish (271 SNPs). The number of genetic clusters (K) used in the DAPC analyses was informed by returning successive K-means with an increasing number of clusters. We considered the optimal K based on the lowest Bayesian Information Criterion (BIC) or within 2 ΔBIC (Jombart et al., 2010).

To estimate changes in population genetic diversity over time and space, we divided these temporal sets by sampling location relative to the location of the former dams (AD, ID and BD). Next, we divided our genetic data sets temporally pre and post-dam removal for *O. mykiss*. We included temporal comparisons of population genetic structure and diversity analyses for *O. tshawytscha* using scale analysis assignments in the Appendix (Appendix Figures 1–2, Appendix Tables 1–2). We tested the observed heterozygosity (H_O), the inbreeding coefficient (F_{IS}), and fixation index (F_{ST}) using the R package "hierfstat" (Goudet, 2005). We bootstrapped F_{IS} values 100 times using *boot.ppfis()* to generate the 95% confidence interval for F_{IS}. We assessed the significance of F_{IS} by determining if the 95% confidence interval overlapped 0 (Goudet, 2005). KING relatedness statistics were calculated with neutral loci using vcftools (Danecek et al., 2011) "–relateness2" option. We also performed a permutation test with 1000 iterations to test the significance of F_{ST}. The p-value of F_{ST} was calculated by looking at the proportion of the permuted values that were greater than or equal to the observed values. We also estimated changes in the effective number of breeders (N_b) using the software "NeEstimator" 2.1 (Do et al., 2014). Input files were generated by modifying the *genind_to_genepop* function of the R package "graph4lg" (Savary et al., 2021) to allow for both indels and SNPs as the alternative allele. We calculated N_b using a random mating model of *Linkage Disequilibrium* method with a critical value of 0.05. We determined the statistical significance of our estimates using 95% critical intervals derived from jackknife estimates of N_b.

2.5 Riverscape genetics modeling

We tested two types of riverscape genetic models - Isolation by Environment (IBE) and Isolation by Resistance (IBR) using post-dam removal individuals (Figure 2). IBE represents spatial genetic variation created by the interactions between organisms and environments "at sites" (Wang and Bradburd, 2014). If this is the case, the genetic distances are correlated with the environmental differences at sites as heterogeneous environments influence gene flow. On the other hand, IBR represents a positive relationship between genetic distances and resistance distances focused on the environment "between sites". Based on circuit theory, IBR calculates resistance distances, or cost distances, across the geographic range from factors interfering with migration (McRae, 2006). As IBE and IBR models test associations of genetic variation with variables "at sites" where fishes stay and "between sites" where fishes travel, respectively, these two riverscape genetic models can complement each other in their capture of both site-specific and corridor-specific environmental heterogeneity. The null model, or hypothesis, to both the IBE and IBR hypotheses was Isolation by

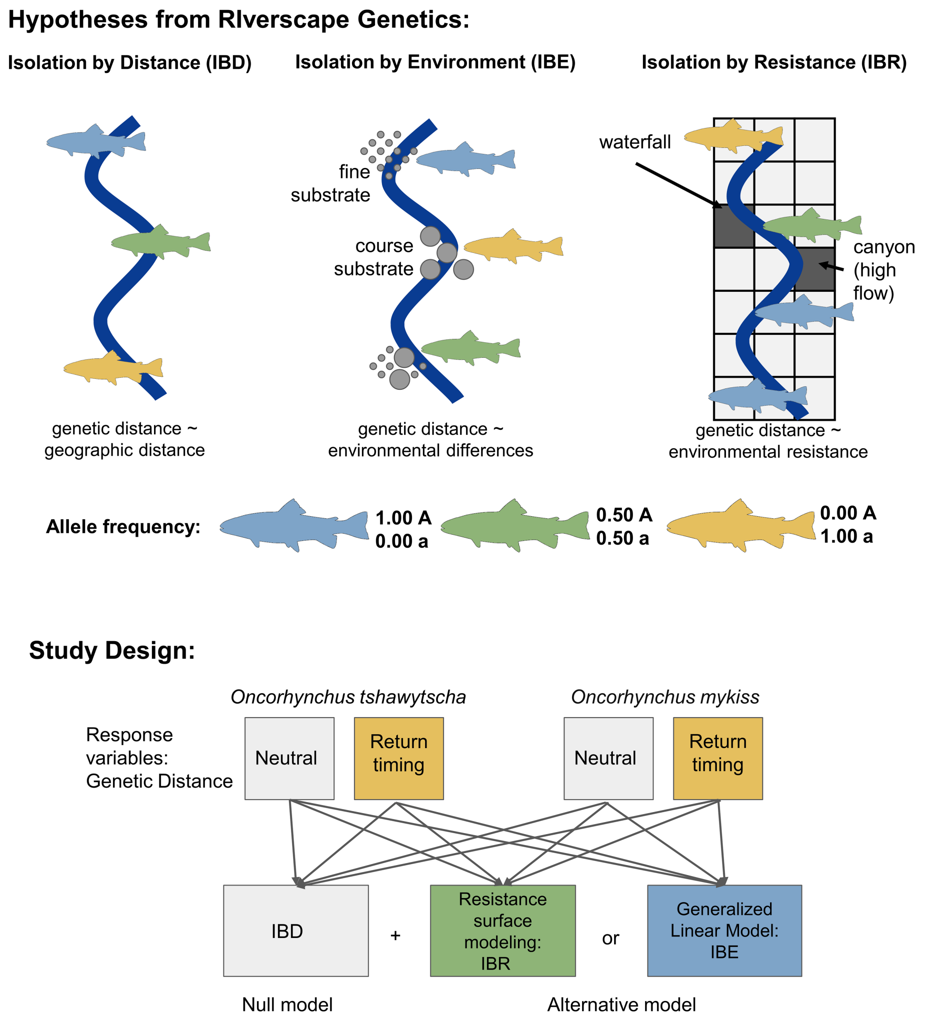

FIGURE 2
Schematic of the landscape genetics hypotheses tested in our study design. Isolation by distance (IBD) is a pattern of decreasing genetic similarity as geographic distance increases due to limitations in movement and gene flow. Isolation by environment (IBE) is a pattern where genetic similarity is influenced by the environment at a location instead of the geographic distance. Conversely, isolation by resistance (IBR) is a pattern of decreasing genetic similarity based on the landscape between two sites. Isolation by distance represents the null hypothesis to isolation by environment and isolation by resistance. In this study, the response variable for each model is neutral or return-timing genetic distance for each species.

Distance (IBD). This served as our null hypothesis as the expected relationship is a decrease in relatedness with increasing distance (Rousset, 1997) and following with Tobler's First Law of Geography that things closer in space are more similar. We also expected this to explain patterns of gene flow for return-timing genetic distance as we expect that early-return life-history forms evolved in part to exploit favorable environmental conditions coinciding with earlier arrival for fish that must migrate long distances. We quantified this in our IBD models as river kilometer (rKm) or distance from the mouth of the river (Benda et al., 2007) (Figure 2). If IBD represents the best model, genetic distance should be proportional with rKm (Selkoe et al., 2016). Alternative models and the environmental variables included in each model are listed in Table 1.

2.5.1 Genetic distance matrix generation for landscape genetics models

We generated two sets of neutral and return-timing genetic distance matrices for each species: one for IBE models and one for IBR models. We tested neutral and return-timing genetic distances separately to examine how riverscape variables may affect both neutral and return-timing genetic variation. For IBE models we calculated neutral genetic distance using the loading scores of the first principal component from the DAPC analysis that characterized the underlying genetic structure of post-dam removal individuals. The proportion of early return-timing alleles in each individual was used to generate the return-timing genetic distance matrices. For IBR models, both neutral and return-timing genetic distances were calculated among every sampling site as Roger's/Classical Euclidean distance (Rogers, 1972; Avise, 1994) using the *dist.genpop* function of the R package "adegenet" with the method argument set to 4 (Jombart, 2008). We also calculated Nei's distance (method = 1) (Nei, 1972; Nei, 1978; Avise, 1994) but only used Roger's/Classical Euclidean genetic distance for downstream analyses due to the high correlation between them ($r > 0.97$).

Given that *O. tshawytscha* were only sampled as adults and *O. mykiss* were sampled as adults, juveniles and unknown life-history forms, we tested one *O. tshawytscha* dataset and three *O. mykiss* datasets: all *O. mykiss*, adult Steelhead, and juvenile *O. mykiss*.

2.5.2 Isolation by environment modeling: at-site characteristics

To test if environmental differences at spawning sites influence genetic variation in our study species, we centered and scaled the uncorrelated environmental variables describing the stream temperature, flow, habitat, and riverbed substrate at our sampling sites where individuals were sampled post-dam removal. We subset our environmental variables into five models: (1) null, including only river kilometer, (2) climate, including MWMT (maximum weekly maximum temperature) and precipitation, (3) flow, including flow velocity, (4) habitat, including canopy cover, slope, intrinsic habitat potential, pool frequency, number of logjams per 100m, and amount of spawnable habitat, and (5) full, including all variables except river kilometer (Table 1). For all five models, we rechecked for multicollinearity using variance inflation factor (VIF) (Naimi et al., 2014) and removed the variable with the greatest VIF until all remaining variables had a VIF of less than 5. The resulting model subsets are described in Table 1. We used linear models for neutral response variables and generalized linear models with a binomial distribution for return-timing response variables due to their bimodal distribution using the "stats" in R package (R Core Team, 2022). Model residuals were visually inspected for model assumptions. We compared each suite of IBE models using Akaike information criterion (AIC) (Burnham and Anderson, 2002).

2.5.3 Isolation by resistance modeling: between-site characteristics

To test if environmental characteristics between spawning sites influence genetic variation in our study species, we fit IBR models to our data. These included: (1) null model/IBD where distance and not environment drives patterns of genetic distance, represented by river kilometers between sites, (2) climate model, including MWMT (maximum weekly maximum temperature) and precipitation, (3) flow model, including flow velocity, (4) habitat model, including canopy cover, slope, intrinsic habitat potential, pool frequency, number of logjams per 100m, and amount of spawnable habitat, (5) subset of the habitat model, including canopy cover, slope, and intrinsic habitat potential, excluding pool frequency, number of logjams per 100m, and amount of spawnable

TABLE 1 Environmental variables included for each isolation by environment (IBE) and isolation by resistance (IBR) riverscape genetics model tested.

Model	Variables included in IBR models	Variables included in IBE models
Full	MWMT, PRECIP, FlowVel, IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY, Pool_frequency, Logjams, spawnable_area_steelhd	MWMT, PRECIP, FlowVel, IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY, Pool_frequency, spawnable_area_steelhd
Subset Full	MWMT, PRECIP, FlowVel, IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY	MWMT, FlowVel, CANOPY, Pool_frequency, spawnable_area_steelhd
Climate	MWMT, PRECIP	MWMT, PRECIP
Flow	FlowVel	FlowVel
Habitat	IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY, Pool_frequency, Logjams, spawnable_area_steelhd	IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY, Pool_frequency, Logjams, spawnable_area_steelhd
Subset Habitat	IP_STEELHD or IP_CHINOOK, SLOPE, CANOPY	IP_STEELHD or IP_CHINOOK, CANOPY, Pool_frequency, spawnable_area_steelhd
IBD	OUT_DIST	OUT_DIST

See Table S3 for the definitions of variable acronyms.

habitat which had a narrow range of cells, (6) full model, including all variables except river kilometer, (7) subset of the full model, including all variables except river kilometer, pool frequency, number of logjams per 100m, and amount of spawnable habitat (Table 1).

We used the R package "ResistanceGA" (Peterman, 2018) for modeling which uses a machine learning algorithm inspired by the process of natural selection genetic algorithm (Forrest, 1993), and maximum likelihood population effects regression (MLPE) that accounts for non-independence of data from the same populations (Clarke et al., 2002) in resistance surface optimization. Variables identified as uncorrelated were cropped to the Elwha river region and reprojected to the same geo-reference system (NAD83) of Elwha template raster derived from the NorWeST's Washington Coast shapefile (Isaak et al., 2017) using the R package "terra"(Hijmans, 2022). Shapefiles were rasterized to a SpatRaster with a resolution of 0.001 degree. We then converted to RasterLayer and RasterStack using the R package "raster" (Hijmans, 2023), which is required by ResistanceGA. The "NA" values in each raster layers were set to 10 * maximum value of the layer for resistance surface computation due to the requirements of the ResistantGA algorithms.

We applied the "commuteDistance" option and "log-likelihood" as the objective function in ResistanceGA to optimize the effective resistance distance and resistance surface. Bootstrapping with 1,000 iterations was conducted to compare among successfully optimized models and choose the most likely one. IBR models with juvenile *O. mykiss* genetic distances were compared without bootstrapping due to an insufficient number of populations in the subsequent MLPE step. Models with each genetic distance were compared based on AIC calculated within ResistanceGA and optimal models with ΔAIC less than 2 were presented for each genetic distance.

3 Results

3.1 Genotype filtering to generate neutral and return-timing genetic datasets

After filtering, we retained a total of 278 SNPs and 354 *O. tshawytscha* individuals and 314 SNPs and 1,363 *O. mykiss* individuals (Supplementary Table S1). Of those filtered loci, 28 SNPs from the *O. tshawytscha* panel and 11 SNPs from the *O. mykiss* panel found in or near the *GREB1L* and *ROCK1* genes, previously identified as candidates for migration return-timing life-history variants, were retained (Campbell et al., 2015; Hess et al., 2016). We ultimately removed one *O. tshawytscha* SNP (Bonferroni adjusted p-value < 0.00015) and 12 *O. mykiss* SNPs (Bonferroni adjusted p-value < 0.00015) that were out of HWE for downstream population and riverscape genetic analyses. Ultimately, this allowed us to retain 250 and 303 putatively neutral *O. tshawytscha* and *O. mykiss* SNPs.

3.2 Neutral genetic structure across species and space

Based on BIC, our population genetic structure analysis supported different numbers of genetic clusters or populations between species over time (Figure 3, Figures S1, S2, Appendix Figures 1–2). For *O. tshawytscha*, we identified one cluster post-dam removal (Figure 3C, Figure S1E) and no pairwise F_{ST} values between any pair of populations were significant (Table S2). Pre-dam removal DAPC analysis supported four to six clusters of *O. mykiss* pre-dam removal (Figures S1A, C) that we visualized as five clusters (Figures 3A, B). Post-dam removal, however, we detected five to ten clusters amongst our *O. mykiss* samples (Figures S1B, D). Pairwise spatial and temporal estimates of F_{ST} in *O. mykiss* supported significant, but small, changes in genetic structure across both space and time. We observed few differences in patterns of genetic diversity among species when looking at each time period or sampling location (Table 2). For *O. tshawytscha*, we observed no evidence of significant inbreeding across sampling locations as measured by FIS statistics with 95% confidence interval overlapping zero, when considering individuals from all sampling locations. For *O. mykiss*, we observed small positive F_{IS} statistics with 95% confidence intervals significantly greater than zero, when considering individuals from all sampling locations, below dam only, and in-between dam only. There were no changes in the direction or significance of the F_{IS} statistic over time or space in *O. mykiss*. We observed no significant relatedness, as measured by the KING statistic, in either *O. tshawytscha* or *O. mykiss* when samples were grouped by space and time.

For *O. tshawytscha*, sampling location had no association with genetic clustering (Figure 3C). There was also no association of sampling location with *O. tshawytscha* genetic clustering when *O. tshawytscha* samples were classified as individuals hatched pre-dam removal or post-dam removal (Appendix Figures 1–2). For *O. mykiss*, some individuals collected from ID were highly discriminated from other sampling locations pre-dam removal (Figure 3A), while some individuals collected from BD were highly discriminated from other sampling locations post-dam removal (Figure 3B). For *O. mykiss*, genetic clusters tended to differentiate individuals collected BD from individuals collected AD post-dam removal along the second principal component axis (Figure 3B). We identified similar genetic clustering restricting our DAPC analyses to the 212 loci classified as neutral in the *O. mykiss* panel (Figure S2).

3.3 Three return-timing haplotypes were detected in both species

On average, single nucleotide polymorphisms (SNPs) in and near the *GREB1L/ROCK1* genes genotyped using the GTseq panel were in linkage disequilibrium and phased into haplotypes (*O. tshawytscha* r^2 = 0.48; *O.mykiss* r^2 = 0.50). We identified three distinct haplotypes in each species post-dam removal: late return-timing (Fa, Win), early return-timing (Sp, Su) and recombinant haplotypes (FaR, WinR) for *O. tshawytscha* and *O. mykiss* (Figures 4, 5).

For *O. tshawytscha,* recombinant haplotypes were the most common (FaR.) (N = 410), followed by late return-timing (Fa) (N = 175) and then early return-timing (Sp) (N = 123) haplotypes (Figure 4B). Early return-timing (Sp) haplotypes had 85.7% early

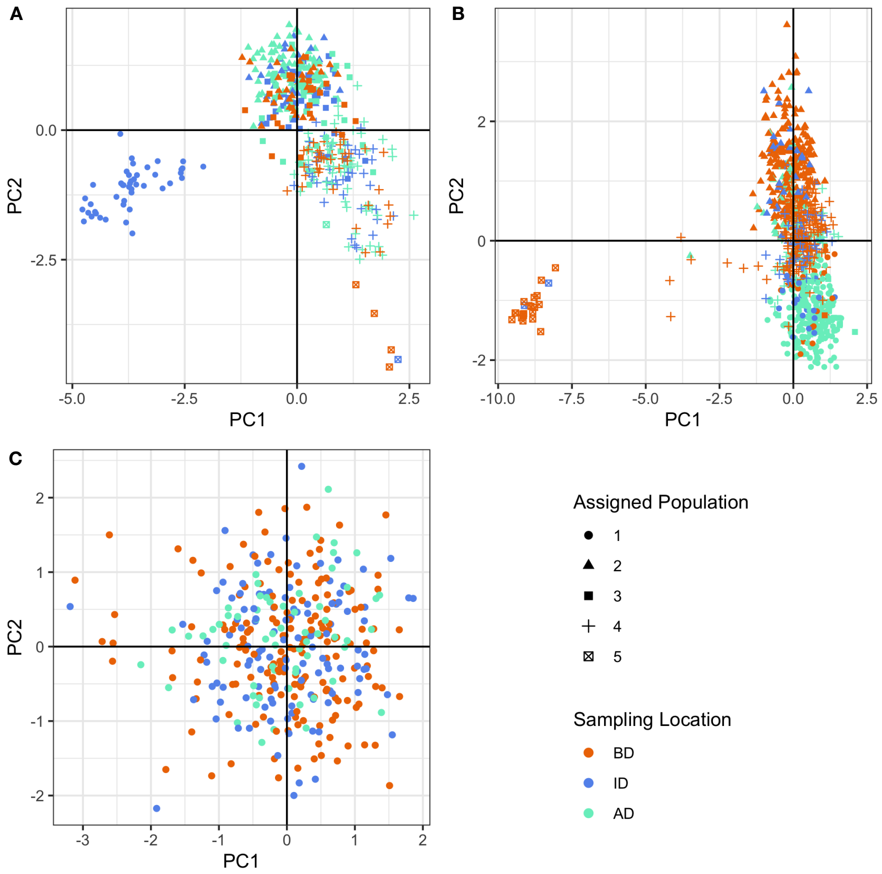

FIGURE 3
Discriminant analysis of principal components (DAPC) clusters using neutral loci for **(A)** *O. mykiss* pre-dam removal, **(B)** *O. mykiss* post-dam removal, and **(C)** *O. tshawytscha* post-dam removal. Colors represent sampling locations (BD: Below the Elwha River Dam, ID: In between the Elwha River and Glines Canyon Dams, AD: Above the Glines Canyon Dam). Shapes represent assigned populations.

TABLE 2 Summary of relative levels of inbreeding (F_{IS}, 95% confidence intervals in brackets with the bold significant results), mean relatedness statistic (KING, 95% confidence intervals in brackets), population genetic diversity (H_O), and effective population size (N_b, 95% confidence intervals in brackets) for both salmonid species *O. tshawytscha* and *O. mykiss* pre and post-dam removal above dams (AD), in between the dams (ID) and below the dams (BD).

Species	Time	Location	Inbreeding Coefficient (F_{IS})	Mean Relatedness Statistic (KING)	Observed Hetero-zygosity (H_O)	Effective Number of Breeders (N_b)
O. tshawytscha	Post-Dam Removal	All Sampling Locations (354)	0.0073 (−0.0052, 0.015)	−0.004 (−0.169, 0.161)	0.3951	653.6 (526.6, 847.9)
		BD (170)	−0.0068 (−0.020, 0.0056)	0.007 (−0.183, 0.197)	0.3010	767.7 (490.9, 1651.3)
		ID (121)	**0.019** (0.0007, 0.035)	−0.017 (−0.184, 0.151)	0.2905	462.1 (292.5, 1011.1)
		AD (63)	0.0099 (−0.011, 0.028)	−0.005 (−0.177, 0.168)	0.2938	1370.5 (410.0, Infinite)
O. mykiss	Pre- and Post-Dam Removal	All Sampling Locations (1363)	**0.040** (0.023, 0.059)	−0.080 (−0.486, 0.327)	0.296	109.8 (72.8, 160.4)
	Pre-Dam Removal	All Sampling Locations (454)	**0.038** (0.016, 0.050)	−0.062 (−0.366, 0.242)	0.299	119.5 (92.6, 155.9)
		BD (97)	**0.052** (0.027, 0.081)	−0.030 (−0.229, 0.169)	0.2941	94.9 (62.9, 164.6)

(Continued)

TABLE 2 Continued

Species	Time	Location	Inbreeding Coefficient (F_{IS})	Mean Relatedness Statistic (KING)	Observed Hetero-zygosity (H_O)	Effective Number of Breeders (N_b)
		ID (157)	**0.054** (0.033, 0.071)	−0.070 (−0.391, 0.251)	0.2926	245.0 (181.4, 360.8)
		AD (200)	0.009 (−0.012, 0.028)	−0.028 (−0.226, 0.169)	0.3091	56.3 (42.4, 76.1)
	Post-Dam Removal	All Sampling Locations (909)	**0.036** (0.024, 0.058)	−0.095 (−0.558, 0.369)	0.2943	82.6 (55.5, 119.7)
		BD (490)	**0.050** (0.030, 0.067)	−0.096 (−0.669, 0.477)	0.2931	207.9 (169.3, 259.1)
		ID (101)	**0.041** (0.020, 0.056)	−0.071 (−0.487, 0.346)	0.2974	203.5 (124.8, 455.1)
		AD (318)	0.016 (−0.0073, 0.033)	−0.036 (−0.202, 0.131)	0.2926	24.9 (13.8, 41.5)

Numbers in parentheses in the location column cells represent the total number of fish included in each of these analyses.
Bold values indicate statistically significant results as the confidences intervals do not cross zero.

return-timing alleles on average (range = 0.71–1.00, σ = 0.008), while recombinant (FaR: μ = 0.158, range = 0.07–0.35, σ = 0.0011) and late return-timing haplotypes (Fa: μ = 0.08, range = 0.036–0.14, σ = 0.0013) had substantially fewer alleles on average. For *O. tshawytscha*, this included mostly recombinant haplotypes (FaR) (N = 198), followed by late return-timing (Fa) (N = 75), and then early return-timing (Sp) (N = 55) haplotypes (Figure 4). Fish hatched pre-dam removal mostly had mostly recombinant *O. tshawytscha* haplotypes (FaR) composed of 15.0% early return-timing alleles on average (Appendix Figure 3).

For *O. mykiss*, late return-timing haplotypes were also the most frequently detected post-dam removal (Win) haplotypes (N = 868), followed by early return-timing (Su) haplotypes (N = 517) and then recombinant (WinR) (N = 431) haplotypes (Figure 5B). The early return-timing (Su) haplotypes were composed of 86.8% early return-timing alleles on average (range = 0.64–1.00, σ = 0.005), while recombinant (WinR: range = 0.09–0.73, σ = 0.002) and late return-timing haplotypes (Win: range = 0–0.36, σ = 0.002) were composed of 25% and 2.1% early return-timing alleles on average respectively.

We did not detect any significant differences in the frequency of early return-timing alleles among *O. tshawytscha* spatially post-dam removal (Figure 6A) or over time (Appendix Figure 4). However, we identified a number of statistically significant pairwise comparisons of early return-timing allele frequencies across *O. mykiss*, sampled from different parts of the river over time (Figure 6B). Pre-dam removal, we found that BD fish (μ_{AF} = 0.15) had significantly lower early return-timing allele frequencies compared to AD (μ_{AF} = 0.26; Wilcox test, Bonferroni adjusted p-value = 0.002), but not ID fish (μ_{AF} = 0.16; Wilcox test, Bonferroni adjusted p-value = 0.006). Post-dam removal, we observed statistically significant differences in the allele frequencies observed across all geographic pairwise comparisons (Wilcox test, Bonferroni adjusted p-value < 0.05). We found that fish sampled AD (μ_{AF} = 0.608) had significantly higher frequencies of early return-timing alleles than those sampled BD (μ_{AF} = 0.108; Wilcox test, Bonferroni adjusted p-value = 9.24e-71) and ID (μ_{AF} = 0.207); ID fish had significantly higher early return-timing alleles than BD (Wilcox test, Bonferroni adjusted p-value = 0.021). Early return-timing alleles were more frequent in fish sampled AD post-dam removal (μ_{AF} = 0.608) than those sampled pre-dam removal (Wilcox test, Bonferroni adjusted p-value = 7.21e-25). We detected the highest proportions of both early return-timing haplotypes and genotypes in adult Steelhead sampled AD post-dam removal between July and October (Figure S3).

3.4 Reduced environmental dataset retained for riverscape genetics models

We ultimately retained 11 out of the 26 environmental variables after testing for correlations for use in our riverscape genetic models for both O. *tshawytscha* and *O. mykiss* (Table S3, Figures S4–S6). These included stream temperature (Maximum Weekly Maximum Temperature between 2015–2017; MWMT), flow velocity, habitat intrinsic potential for O. *tshawytscha*, habitat intrinsic potential for Steelhead, slope, riparian canopy, pool frequency, logjams per 100 m and spawnable habitat (Table 1, Table S3, Figure S7). This subset represented summarized measures of dynamic variables (i.e., stream temperature), predicted metrics based on geometry (i.e., flow velocity), and single measures of relatively static variables (i.e., slope and canopy) that change on the scale of years to decades.

3.5 IBD as a strong explanatory variable across IBE and IBR models

3.5.1 IBE indicates at-site environment and IBD influence genetic differentiation

Isolation by Environment (IBE) models identified at-site environmental variables associated with neutral and return-timing

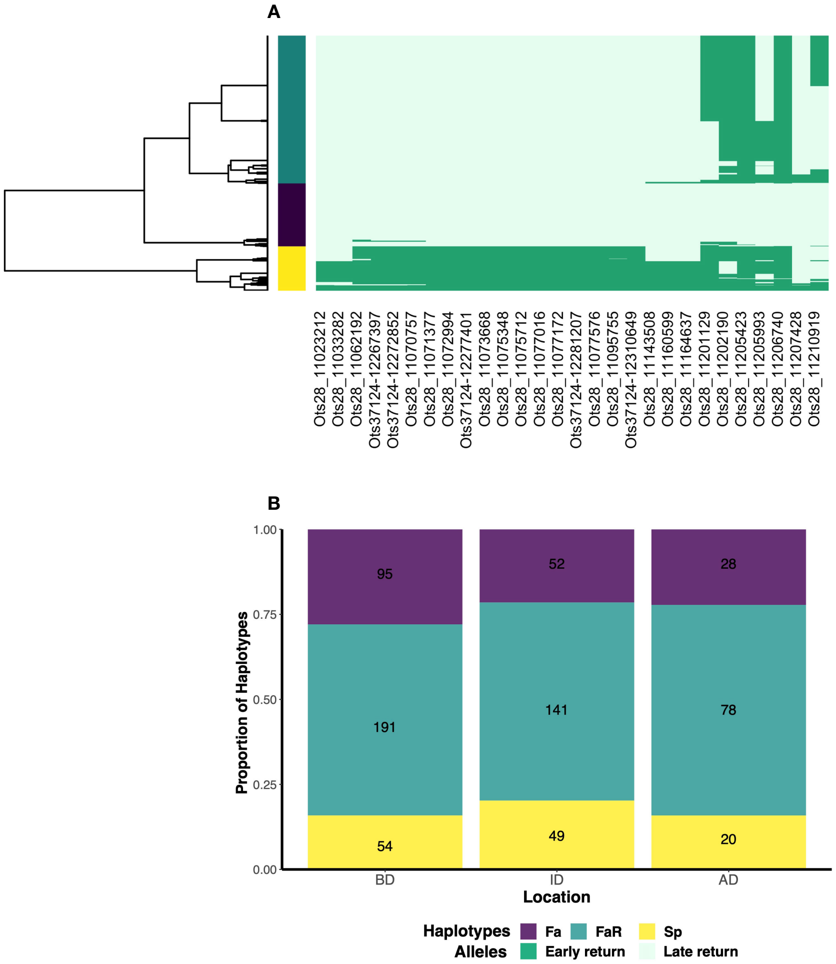

FIGURE 4
(A) Three haplotypes are detected post-dam removal in *O. tshawytscha*. Each column of the heat map represents one of the 29, putatively adaptive return-timing loci with each color of the heat map representing the early return-timing alleles or late return-timing allele. Each row represents one individual, with the dendrogram on the x-axis showing the most parsimonious clustering of individuals based on the haplotypes phased from the early return-timing loci. The vertical bar represents the haplotype called for each individual with haplotypes primarily containing early return-timing alleles, late return-timing alleles and a combination of the two. **(B)** The proportion of the three haplotypes in *O. tshawytscha* sampled below (BD), in-between (ID) and above (AD) the former dams post-dam removal. The numbers represent the sample size for each haplotype. (Fa: Fall, FaR: Fall Recombinant, Sp: Spring).

genetic differentiation in *O. mykiss* individuals sampled post-dam removal. For *O. tshawytscha*, while no individual environmental variable was statistically significant, the IBD model, followed by the climate and flow models, had the lowest AICs to explain neutral, at-site, genetic differentiation. The habitat and full models had the lowest AICs to explain return-timing genetic differentiation for *O. tshawytscha*, also with no statistically significant individual environmental variable (Table 3). When combining all *O. mykiss* life-stages in one model, the IBD model had the lowest AIC to explain neutral and return-timing genetic differentiation (Table 3). For just adult Steelhead, the habitat and full models had the lowest AIC to explain neutral genetic differentiation, while the IBD, the habitat model, and full model equally explained return-timing genetic differentiation (Table 3). Within these top models for return-timing genetic variation, river kilometer and pool frequency both had significant positive relationships with the proportion of early return-timing alleles. For juvenile *O. mykiss*, the habitat and full models equally explained both neutral and return-timing genetic differentiation (Table 3). Within these full models, canopy cover and intrinsic habitat potential had significant positive and negative relationships respectively with the proportion of early return-timing alleles (Table 3, Supplementary Data File 1).

3.5.2 IBR modeling indicates IBD best explains genetic variation

We tested four IBR models for *O. tshawytscha* and twelve IBR models for *O. mykiss*, similar to IBE models to account for differences in the life-history stage and methods of sampling included for each species (Figure 2, Table 4). Across both species and both genetic distance types, IBD was the best model for all the cases of IBR modeling conducted (Figure 7, Table 4, Supplementary Data File 2). The optimized resistance surface even displayed the same value of “1” all over the extent in some cases (Figures 7A, B, H), which indicated that genetic distances could not be explained

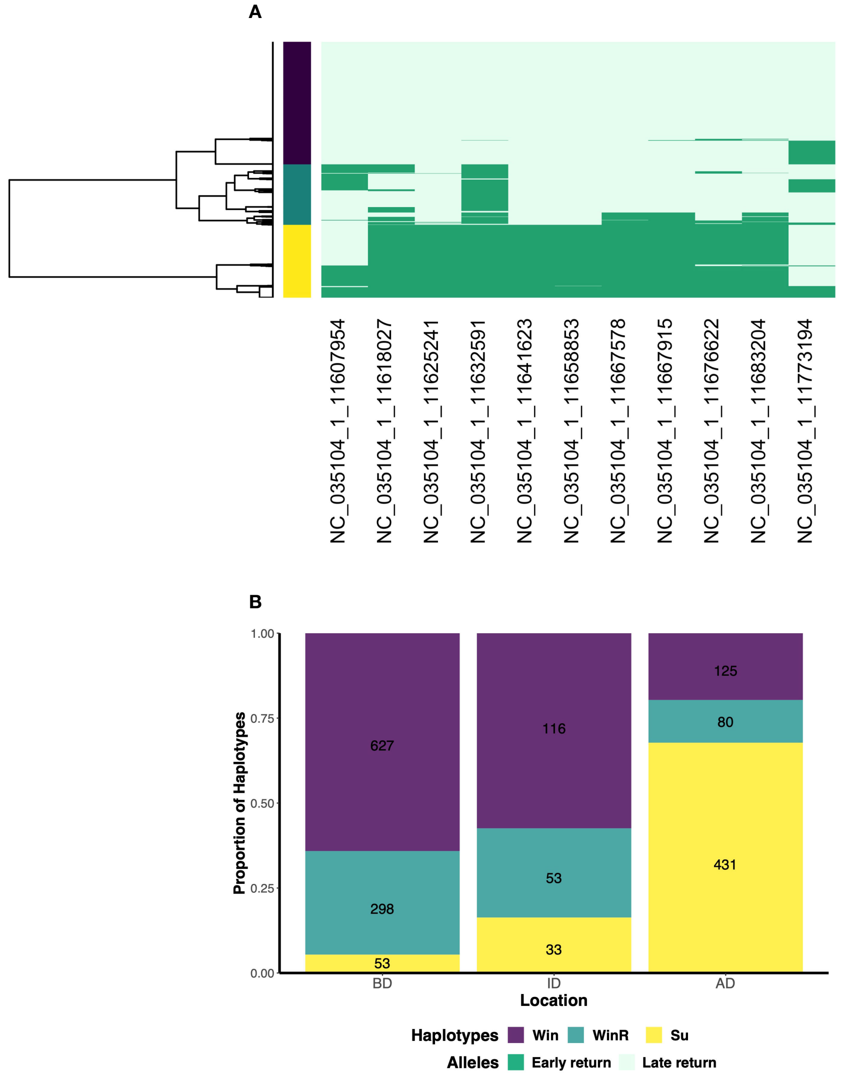

FIGURE 5
(A) Three haplotypes are detected post-dam removal in *O. mykiss*. Each column of the heat map represents one of the 11, putatively adaptive return-timing loci with each color of the heat map representing the early return-timing alleles (dark green) or late return-timing allele (light-green). Each row represents one individual, with the dendrogram on the x-axis shows the most parsimonious clustering of individuals based on the haplotypes phased from the early return-timing loci. The vertical bar represents the haplotype called for each individual with the yellow haplotype containing primarily early return-timing alleles, the purple primarily late return timing alleles and the green appears to be a combination of the two. **(B)** The proportion of the three haplotypes in *O. mykiss* sampled below (BD) in-between (ID) and above (AD) the former dam populations post-dam removal. The numbers represent the number of individuals containing each haplotype. (Win: winter, WinR: Winter Recombinant, Su: Summer).

better than the Euclidean geographic distances (Table 4). Second and third optimal models (ΔAIC < 2) were identified for several cases, including all *O. mykiss* neutral (flow model), all *O. mykiss* return-timing (flow and climate model), adult Steelhead neutral (flow model), and juvenile *O. mykiss* return-timing (flow model) genetic distances (Figure S8).

4 Discussion

In this study, we leveraged the removal of two large dams on the Elwha River to understand how habitat restoration impacted the return and reestablishment of distinct ocean migrating life-history forms of *O. tshawytscha* and *O. mykiss* to their historical distribution. While we observed no difference in the proportion of early return-timing alleles in *O. tshawytscha* across the watershed, we observed significant differences for *O. mykiss* across the watershed for samples collected both pre- and post-dam removal. Specifically, the proportion of early return-timing alleles was greater in *O. mykiss* sampled above dam locations than below dam locations. Using riverscape genetics analyses, we found that return-timing genetic variation was more strongly influenced by environmental differences compared to neutral variation. By exploring the relationships of at- and between-site environmental characteristics, we identified significant patterns of spatial genetic variation in *O. mykiss*. For both species, the patterns and processes are still actively shifting in response to these restoration efforts; however, we show here early evidence of the importance of

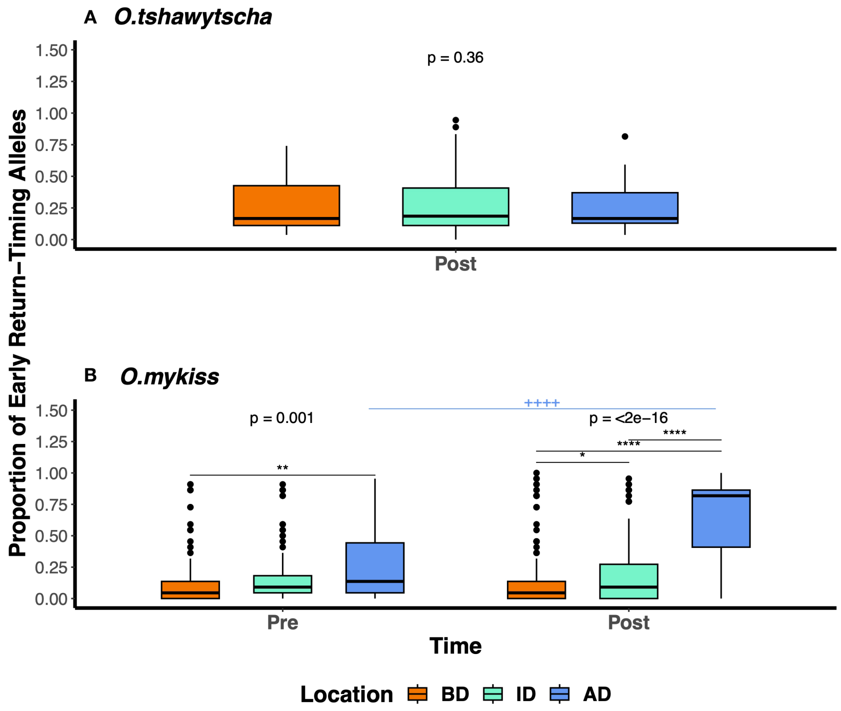

FIGURE 6
The proportions of early return-timing alleles in *GREB1L* in **(A)** *O. tshawytscha* and **(B)** *O.mykiss* post-dam removal below (BD), in-between (ID), and above (AD) the dam. The Bonferroni adjusted p-values generated by Kruskal test across three locations were labeled above each time period. The asterisk (*) represents statistically significant pairwise comparisons with the Bonferroni adjusted p-values reported across sampling locations within the same time period. The plus (+) represents statistically significant pairwise comparisons with the Bonferroni adjusted p-value reported among fish sampled from the same sampling locations, across time (cutpoint for p-values: */+=0.05, **/++=0.01, ****/++++=0.0001).

TABLE 3 IBE model results representing the influence of environmental variables on neutral and return-timing genetic variation.

Genetic Distance	Model	AIC	ΔAIC	LogLik	Model Fit	Significant coefficients (95% CI)
O. tshawytscha Neutral	IBD	−123.145	0	−438.7	−0.001	None
	flow	−122.736	0.410	−438.9	−0.003	None
	climate	−121.776	1.369	−438.4	−0.003	None
O. tshawytscha Return-timing	habitat	275.89	0	−132.9	0.013	None
	full	276.00	1.10	−132.5	0.017	None
All *O. mykiss* Neutral	IBD	−854.556	0	−792.4	0.096	rKm: 0.199 (0.159, 0.240)
All *O. mykiss* Return-timing	IBD	487.211	0	−241.6	0.417	rKm: 1.286 (1.090, 1.482)
Adult Steelhead Neutral	habitat	−525.938	0	−513.9	0.022	None
	full	−525.819	0.119	−514.9	0.024	canopy: −0.134 (−0.225, −0.044)
Adult Steelhead Return-timing	IBD	210.925	0	−103.5	0.148	rKm: 1.768 (1.082, 2.454)
	habitat	211.297	0.371	−100.6	0.171	pool frequency: 0.959 (0.501, 1.418)
	full	211.349	0.424	−99.7	0.179	None
Juveniles *O. mykiss* Neutral	habitat	−365.75	0	−204.8	0.144	pool frequency: −0.104 (−0.196, −0.012)
	full	−365.75	0	−204.8	0.144	

(Continued)

TABLE 3 Continued

Genetic Distance	Model	AIC	ΔAIC	LogLik	Model Fit	Significant coefficients (95% CI)
						MWMT: −0.273 (−0.536, −0.010) FlowVel: 0.549 (0.066, 1.031)
Juveniles *O. mykiss* Return−timing	habitat	248.476	0	−120.2	0.330	canopy: 1.536 (0.877, 2.195) IP_Steelhd: −1.122 (−2.016, −0.229)
	full	248.476	0	−120.2	0.330	None

AIC, Akaike Information Criterion; LogLik, log-likelihood. Model fit for neutral models is adjusted R-squared and model fit for return-timing models is McFadden's R-squared. The coefficient and 95% CI for significant explanatory variables in models are listed.

considering adaptive potential of ocean return-timing and neutral genetic variation in understanding species responses to restoration efforts.

Lack of population genetic structure and decreases in genetic diversity observed in *O. mykiss* may be, in part, an artifact of the study design. Previous work documenting Elwha River *O. mykiss* using microsatellite and tens of thousands of SNP loci found that both dams and anadromous barriers generated significant genetic structure pre-dam removal (Winans et al., 2016). Post-dam removal, structure appeared to decrease as gene flow resumed

TABLE 4 IBR model results representing the influence of environmental variables on neutral and return-timing genetic variation.

Genetic distance	Model	AIC	ΔAIC	LogLik	Model Fit	MLPE.coeff (95% CI)
O. tshawytscha Neutral	IBD	−146.105	0	164.330	0.001	−0.002 (−0.008, 0.004)
O. tshawytscha Return-timing	IBD	−79.881	0	93.028	0.010	0.008 (−0.010, 0.026)
All *O. mykiss* Neutral	IBD	−557.829	0	516.591	0.033	0.015 (0.007, 0.023)
	Flow	−556.102	1.727	515.469	0.032	0.014 (0.006, 0.022)
All *O. mykiss* Return-timing	IBD	−38.623	0	40.332	0.199	0.098 (0.066, 0.129)
	Flow	−37.723	0.900	39.664	0.188	0.095 (0.064, 0.127)
	Climate	−37.102	1.521	43.850	0.287	0.121 (0.087, 0.155)
Adult Steelhead Neutral	IBD	−317.141	0	301.755	0.007	0.007 (−0.002, 0.017)
	Flow	−316.777	0.364	301.490	0.009	0.008 (−0.004, 0.020)
Adult Steelhead Return-timing	IBD	−45.285	0	47.759	0.142	0.071 (0.039, 0.102)
Juvenile *O. mykiss* Neutral	IBD	−52.412	0	30.206	0.909	0.068 (0.042, 0.094)
Juvenile *O. mykiss* Return-timing	IBD	−3.956	0	5.978	0.757	0.235 (0.138, 0.332)
	Flow	−3.956	0	5.978	0.757	0.235 (0.138, 0.332)

The optimal models were determined based on the minimum AIC after 1,000 iterations of bootstrapping, except juvenile Oncorhynchus mykiss genetic distances whose optimal models were determined based on the non-bootstrapped minimum AIC. The values of associated information (LogLik, Model Fit, MLPE.coeff) are non-bootstrapped original values. Model fit for models is pseudo marginal R-squared. AIC, Akaike Information Criterion; LogLik, Log-Likelihood; MLPE.coeff, coefficient of the resistance surface estimated by Maximum Likelihood Population Effect regression. The 95% CI for the MLPE coefficient is presented in brackets.

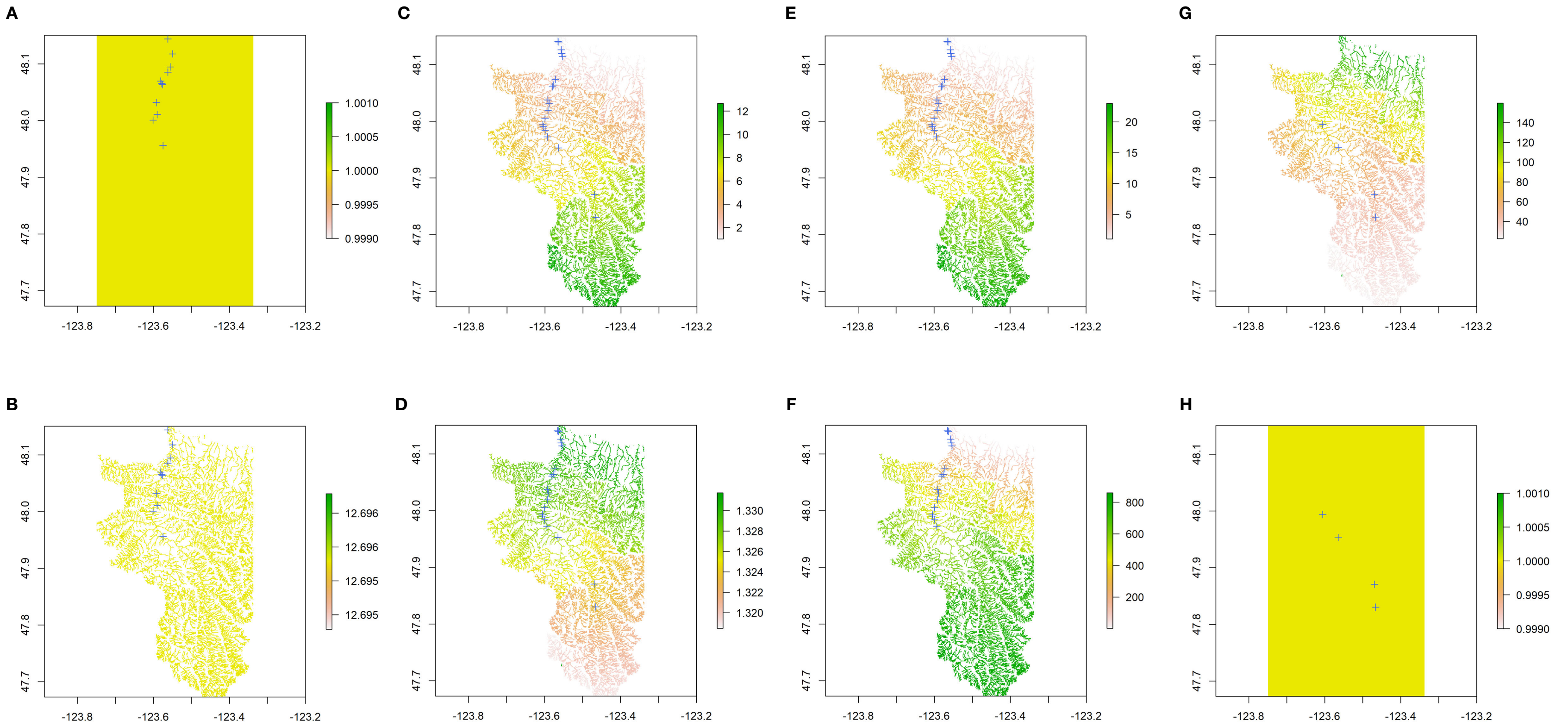

FIGURE 7

The best optimal resistance surfaces by ResistanceGA for each response matrix of **(A)** *O. tshawytscha* neutral, **(B)** *O. tshawytscha* return-timing, **(C)** all *O. mykiss* neutral, **(D)** all *O. mykiss* return-timing, **(E)** adult Steelhead neutral, **(F)** adult Steelhead return-timing, **(G)** juvenile *O. mykiss* neutral, **(H)** juvenile *O. mykiss* return-timing genetic distance. Green colors represent higher resistance values while yellow to red represent lower resistance values. Optimized resistance values for **(A, H)** were homogeneous across the geographic extent, implying their genetic distances could not be explained by environmental variables, any better than euclidean-distance-based Isolation by Distance.

between formerly allopatric populations (Fraik et al., 2021). While we know the natural-origin Steelhead populations in the upper river have significantly increased post-dam removal (Denton et al., 2022b; Peters et al., 2022; Pess et al., *In Review*). We observed diminished N_b above the former dams, but an increase below the former dams. Biologically, this might reflect down river movements of resident rainbow trout after dam removal and greater overall admixture. Alternatively, this could be an artifact of sampling location and design since Steelhead may not have been sampled at spawning sites. Ascertainment bias in the genotyping panels utilized for this study could also explain deviations from previous work. One half of the neutral loci in the *O. mykiss* GTseq panel (92 SNPs) were selected to delineate genetic stocks at a river basin or watershed level, across reporting groups in the Columbia River and across the US West Coast (Narum et al., 2010; Abadía-Cardoso et al., 2011; Limborg et al., 2012). Given the geographic focus of our study is considerably smaller than the target spatial scale of the panels, we may be observing higher genetic covariance amongst the SNP genotypes of fish from the Elwha River watershed, in line with the intended purpose of the panel.

Similar to *O. mykiss*, we did not observe significant evidence of genetic structure in *O. tshawytscha*. The reestablishing *O. tshawytscha* in the Elwha are heavily dominated by hatchery spawners that were generated from the small, natural-origin population that remained below the dams decades after dam removal (McHenry et al., 2022). We have evidence that eleven of the *O. tshawytscha* sampled in the Elwha River might represent strays (McKinney et al., *In Prep*) and may encompass greater genetic diversity. As the neutral loci in the *O. tshawytscha* panel were designed to delineate genetic stocks, we may be capturing the introduction of straying fish admixing with Elwha River endemic *O. tshawytscha*. While there is limited data to determine how genetic diversity and structure changed over time (Appendix Table 2), these genotypes provide an important baseline for *O. tshawytscha* as limited genetic studies have been published on Elwha and surrounding Puget Sound populations to date (McKinney et al., *In Prep*; Ruckelshaus et al., 2006; Winans et al., 2008).

While we did not find evidence of significant neutral genetic structure between locations, there were significant deviations in the return-timing allele frequencies across the watershed in *O. mykiss*, but not *O. tshawytscha* (Figure 6). In *O. mykiss*, there were higher frequencies of the early return-timing haplotypes and alleles in fish sampled above the former dams compared to below the dams post-dam removal (Figures 5, 6). In the Elwha River, both early return-timing life-history forms of each species were extirpated following dam construction (DOI, 1996). The resident form of *O. mykiss*, rainbow trout, was able to persist in the middle and upper watershed, while *O. tshawytscha* and the anadromous form of *O. mykiss*, Steelhead, were limited to seven river kilometers of spawning habitat below the dams (McHenry et al., 2017). While Steelhead were not able to return to spawn above the dams, these land-locked *O. mykiss* harbored high proportions of the early return-timing alleles and maintained high levels of standing genetic variation river-wide (Hiss and Wunderlich, 1994; Winans et al., 2016; Fraik et al., 2021; Fraik et al., 2022). Steelhead reestablished in the upper river before *O. tshawytscha* (Duda et al., 2020; Duda et al., 2021), with the first early return-timing Steelhead detected in 2013 (Personal Comm. J. McMillan) and Chinook detected in 2022 (Personal Comm. R. Peters). A high proportion of these summer Steelhead ascending the former dammed river have been shown to be descendants of the land-locked, above-dam ancestries (Fraik et al., 2022). The preference for summer Steelhead to spawn in colder, snow-melt fed water (Busby et al., 1996) may also suggest there is pleiotropy at the return-timing genetic locus for local adaptation (Micheletti et al., 2018).

Riverscape genetic models indicated that patterns of return-timing variation in *O. mykiss* were affected by sampling site environmental differences. Variation in frequencies of early return-timing alleles in adult Steelhead and juvenile *O. mykiss* at sampling sites were best explained by habitat and full models. Pool frequency was a significant covariate in the habitat model for adult Steelhead, suggesting that spawning Steelhead adults with different early return-timing genotypes may be differentially impacted by spawning ground habitat characteristics. Similarly, juvenile *O. mykiss* return-timing, as well as neutral genetic variation, was best explained by habitat variables (pool frequency and canopy) across rearing habitat. When considering all *O. mykiss* cumulatively, the significance of these models diminished. Consistent influence of habitat characteristics across age classes and genetic response variables suggests that these covariates may be biologically significant, reflecting age class specific responses.

Broadly, we found that geographic distance best explained patterns of neutral gene flow both at-site (IBE) and between-site (IBR) for most species' models. The full and habitat IBE models were the optimal neutral models for Steelhead and juvenile *O. mykiss*, but not for *O. tshawytscha*. The lack of environmental influence observed in the *O. tshawytscha* models most likely reflects the limited, or lack of, environmental heterogeneity among *O. tshawytscha* sampling sites. While water temperature is usually a significant environmental factor influencing growth, migration and movement in salmonids (Brewitt and Danner, 2014; Kendall et al., 2015; Armstrong et al., 2021; Pitman et al., 2021), temperature variation throughout the Elwha is not physiologically limiting (Myrick and Cech, 2005; Siegel et al., 2022; Siegel et al., 2023) and probably not impacting gene flow. Alternatively, these differences could be the by-product of how *O. mykiss* were sampled at specific sampling sites at known age classes compared to *O. tshawytscha*, which were sampled across river reaches post-spawning. For example, MWMT stream temperature standard deviation for *O. mykiss* was 0.44 Celsius (n = 19, mean = 16.1 Celsius, range = 15.1–16.5 Celsius) and *O. tshawytscha* was 0.37 Celsius (n = 9, mean = 16.6 Celsius, range = 16.3–17.4 Celsius), reflecting a narrow range of environmental variation across the sampling locations. However, these differences in stream temperature could also reflect the statistical uncertainty around the derivation of environmental point estimates from stream reaches rather than geographic points. Regardless, we may simply lack the statistical power to detect the influence of the environment on neutral variation due to a more homogenous resistance surface.

In this study, we explicitly did not conduct any direct comparisons between *O. tshawytscha* and *O. mykiss* because of several important differences in the founding populations, sampling methods, and stage of recovery of the two species in the Elwha River. First, the founding Elwha *O. tshawytscha* is not only smaller than the *O. mykiss* population but represents lower return-timing genetic diversity compared to *O. mykiss* (Figures 4, 5). Both species populations are bolstered by hatchery programs that were founded from below dam, natural-origin Elwha broodstock that do not necessarily select for diversity at the *GREB1L/ROCK1* locus. While these hatchery fish make up a large proportion of the reestablishing *O. tshawytscha* population, they make up less of the Steelhead population (Pess et al., *In Review*; Denton et al., 2022a; Denton et al., 2022b; McHenry et al., 2022; Peters et al., 2022). Reestablishing Steelhead possess ancestry from below dam, similar to those of hatchery fish, as well as formerly above and in-between dam ancestries that contain greater return-timing genetic variation (Fraik et al., 2021). Second, the temporal and spatial extent of sampling was more limited for *O. tshawytscha* than for *O. mykiss*. The relatively short time frame of sampling for *O. tshawytscha* and the majority of samples coming from the lower reaches of the Elwha is a direct result of this species being in an early stage of reestablishment in the Elwha River. While these sampling limitations do impede the power of temporal and spatial analyses for *O. tshawytscha*, our study was able to document contemporary patterns, or the lack thereof, of genetic variation in the study area. For example, while IBD models were the most optimal for *O. tshawytscha*, the coefficients were not significantly different from zero reflecting no clear association or return-timing variation with river kilometer. Thus, we may be observing an artifact of a founder effect generated by genetic stochasticity rather than IBD (Gaggiotti et al., 2004; Weigel et al., 2013). In contrast, we observed a positive association between geographic distance and return-timing genetic distance and resistance in *O. mykiss*, regardless of age class. These results may occur because distance can represent a proxy for the cumulative differences in environmental conditions experienced by each return-timing life-history as individuals move further upriver from the ocean (Rougemont et al., 2023), and our sampling sites for *O. mykiss* extended over twice the distance upstream compared to *O. tshawytscha* sampling sites.

Our study provided a framework for testing the impacts of a significant environmental change, large barrier removal, on the recovery of two important species and their key life-history forms. The reservoir of neutral and return-timing genetic variation maintained in resident rainbow trout above the dams appeared to allow for rapid, robust reestablishment of diverse *O. mykiss* life-history forms river wide post-dam removal. While we did not have phenotype data to characterize recovery of each life-history form in the watershed, we were able to infer how adaptive potential underlying these life-history forms is distributed (Hess et al., 2016; Prince et al., 2017; Micheletti et al., 2018; Narum et al., 2018; Thompson et al., 2019; Collins et al., 2020; Ford et al., 2020; Koch and Narum, 2020; McKinney, 2020; Willis et al., 2020; Willis et al., 2021; Tigano and Russello, 2022; Waples et al., 2022). We observed species and age-class specific patterns of genetic distances structured among sites that shows how at- and between-site environmental heterogeneity may influence *O. mykiss*. Given that *O. tshawytscha* were extirpated from the river above the former dams, we are still in the early stages of observing their reestablishment in the upper watershed. We were able to test biologically informative hypotheses about environmental heterogeneity that influence species, population and life-history specific gene flow. However, differences in the geographic scale, time frame and sampling methodologies for each species must be considered in the interpretation of results in this study. Future studies should continue to monitor *O. tshawytscha* to study the long-term impacts of different demographic and environmental factors on reestablishment.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: NCBI BioProject, PRJNA1021324.

Author contributions

TS, AKF and GM conceptualized the study, organized the course planning and solicited help from the 2022 Landscape Genetics Distributed Graduate Seminar course. JHA, KMN, TRS, GM and GP coordinated the field planning, study design, and metadata collection for both species. KD, JHM, JHA, HC, MM, and TB coordinated and collected, aggregated and disseminated the field samples and metadata for both species. DK, KMN, AKF, GM, and TRS conducted and oversaw the lab work and genotyping. AKF and GM genotyped the genetic data. AKF, TS, and GM oversaw and directed the graduate work. AHF and GP contributed to the environmental data collection, aggregation and analyses. KJL, YS, and JYJ performed all data analyses, data visualization and results presentation. KJL, YS, JYJ, and AKF contributed to the writing. All authors contributed to the articleand approved the submitted version.

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Conflict of interest

Author KD was employed by the company K. Denton and Associates, LLC.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1225229/full#supplementary-material

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Dam removal enables diverse juvenile life histories to emerge in threatened salmonids repopulating a heterogeneous landscape

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Human stressors block, eliminate, and simplify habitat mosaics, eroding landscapes' life history diversity and thus biological resilience. One goal of restoration is to alleviate human stressors that suppress life history diversity, but life history responses to these efforts are still coming into focus. Here, we report life history diversity emerging in threatened salmonids (*Oncorhynchus* spp.) repopulating the recently undammed Elwha River (WA, United States) in adjacent but environmentally distinct tributaries. The ~20km tributaries entered the Elwha River <1km apart, but one had a colder stream temperature regime and swifter waters due to its high, snow-dominated elevation and steep valley gradient (~3%), while the other had a warmer stream temperature regime and slower waters because it drained a lake, was at lower elevation, and had a lower stream gradient (~1.5%). Following the 2012 removal of Elwha Dam, the tributaries' salmonids generally became more abundant and expressed diverse life histories within and among species. The warmer, low-gradient tributary produced more age-1+coho salmon and steelhead. Additionally, salmonids exiting the warmer tributary were older and possibly larger for their age class, emigrated ~23 days earlier, and included age-0 Chinook salmon that were larger. Also, assemblage composition varied among years, with the most abundant species shifting between Chinook salmon and coho salmon, while steelhead abundances generally increased but were patchy. These patterns are consistent with a newly accessible, heterogeneous landscape generating life history diversity against the backdrop of patchy recruitment as salmonids—some with considerable hatchery-origin ancestry—repopulate an extirpated landscape. Overall, dam removal appears to have promoted life history diversity, which may bolster resilience during an era of rapid environmental change and portend positive outcomes for upcoming dam removals with similar goals.

KEYWORDS

Elwha river, habitat mosaic, restoration, thermal regime, phenology

Introduction

Diversity promotes ecological resilience and efforts to restore connected, functional habitats often seek to rebuild aspects of diversity that have been depleted. Diverse habitats enable varied life histories, creating biological systems that spread risk, locally process disturbances, and exploit unpredictable opportunities (Levin, 1992; Tilman and Downing, 1994; Schindler et al., 2015). In this way, diversity helps promote stability over greater temporal and spatial scales, which is key to reliable ecosystem services (Greene et al., 2010; Schindler et al., 2010). Human stressors can suppress diversity within and among species, which has prompted attempts to rehabilitate biological diversity by reconnecting and restoring impaired habitats (e.g., Boughton et al., 2022; Soulodre et al., 2022). However, empirical outcomes of such efforts are still coming into focus.

Rebuilding diversity is critical for Pacific salmon and trout (*Oncorhynchus* spp.; hereafter: salmonids). Salmonids are culturally, ecologically, and economically significant taxa native to the Pacific Rim. They are often migratory and adapted to diverse habitat mosaics across a wide range of landscapes (Quinn, 2018). Within and among species, life history attributes such as differences in timing (e.g., age at ocean entry, age at maturity, and spawning season) and habitat use (e.g., low elevation vs. high elevation spawning) are sustained through variable physical environments and genetics, contributing to population stability and increasing the reliability of fisheries (Greene et al., 2010; Schindler et al., 2010; Hodge et al., 2016). A suite of diverse life histories—using a variety of habitats at different times for different reasons—can help buffer annual and seasonal variation in population survival, which is critical for salmon given their naturally high mortality rates (Quinn, 2018). For example, Alaska's comparatively undeveloped landscape and its varied, functional habitats support substantial life history diversity that contributes to more sustainable production and more consistent fisheries (Hilborn et al., 2003; Schindler et al., 2010; Brennan et al., 2019). In contrast, human stressors across highly-modified habitats in California have eroded the diversity and resilience of what was once a reliable fishery and made it more susceptible to drought and temperature fluctuation (Carlson and Satterthwaite, 2011; Munsch et al., 2022).

Human modifications and stressors have imperiled salmonids, particularly across their southern range (Nehlsen et al., 1991). Consequently, many efforts have sought to restore lost habitat and rebuild life history diversity to improve productivity, resilience, and viability, especially against the backdrop of increasing climatic impacts (e.g., rising temperatures and shifting streamflow patterns; Beechie et al., 2013). One particularly promising approach to improve salmonid life history diversity is the removal of impassable dams to restore formerly connected habitats. Restored connectivity can increase the variety of habitats salmon use, within a species range of preference, and provide salmon with greater potential for expressing diversity across landscapes (Pess et al., 2014). For instance, deep-bodied coho salmon (*O. kisutch*) prefer slow-moving pools in low-gradient streams whereas cylindrical-shaped steelhead (*O. mykiss*) prefer shallower, faster waters in steep streams, and Chinook salmon (*O. tshawytscha*) are more intermediate (Bisson et al., 1988). Further, each species generally remains in freshwater for different periods of time and migrates to sea at different ages and sizes (Quinn, 2018). Because survival, movement, and migration timing partly depends on juvenile growth in freshwater, however, different habitats can produce slightly different life history trajectories within each species. For example, water temperature strongly influences incubation and growth rates, and thermal regimes can vary extensively within and across stream networks (Hawkins et al., 2020). Given adequate food, salmonids tend to grow fastest as water temperatures increase up to and within their thermal optimum (Brett et al., 1969). Additionally, eggs incubate faster in warmer water (Murray and McPhail, 1988). Salmonids often move and migrate when they exceed a threshold size (e.g., reaction norm: Bjornn et al., 1968; Peven et al., 1994), ostensibly to optimize differential tradeoffs in growth and mortality regimes in freshwater and marine habitats, which is mediated by size-selective mortality (Quinn, 2018). As a result, juvenile salmonids often outmigrate earlier (Roper and Scarnecchia, 1999) and at younger ages (Cline et al., 2019) in warmer years and warmer systems that do not frequently exceed the species thermal optimum (Liermann et al., 2017). Accordingly, different temperature regimes across landscapes are likely to promote different growth and migration patterns, and restoring access to a broader range of temperature regimes may therefore help salmon increasingly realize greater life history diversity.

Here, we quantify the life history attributes of salmonid assemblages in two newly accessible, adjacent, but environmentally-distinct tributaries following dam removal. We focus on the species-specific outmigration timing, age structure, and length at date of seaward migration in juvenile coho salmon, Chinook salmon, and steelhead. The research was conducted in the Elwha River (WA, United States) where dams previously blocked 95% of anadromous habitat and dam removal in 2012 restored habitat access for the first time since 1912. Previous work indicates the diversity and abundance of salmonids has increased as they access former habitats and resume life histories that require a connected river system (e.g., Quinn et al., 2017; Duda et al., 2021; Fraik et al., 2021). However, most of that research was centered on the adult life stage. For juveniles, Liermann et al. (2017) found a warmer, low-gradient stream produced more coho salmon smolts and earlier-outmigrating coho salmon fry compared to a colder stream. Building on this, our goal was to use new data to quantify and compare juvenile life history expression in newly opened habitats with contrasting features. Specifically, we focus on the juvenile life stage and analyze data collected from 2016 to 2021 to characterize and compare the timing of juvenile migration, age structure, and growth trajectories of all salmonid species that were commonly found during sampling. These results may inform expectations in other systems where dam removal and other restoration actions seek to improve access to diverse landscapes and increase life history diversity.

Methods

Study region and species

The 72 km Elwha River drains an old-growth, forested landscape within Washington State that connects perennial snowfields in the Olympic Mountains to the Salish Sea (Figure 1). The Elwha River's tributaries are generally shaded, primarily by Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), while understory vegetation includes sword fern (*Polystichum munitum*) and Oregon grape (*Mahonia* spp.), among others (Munn et al., 1999). Substrate size varies across the basin with local habitat

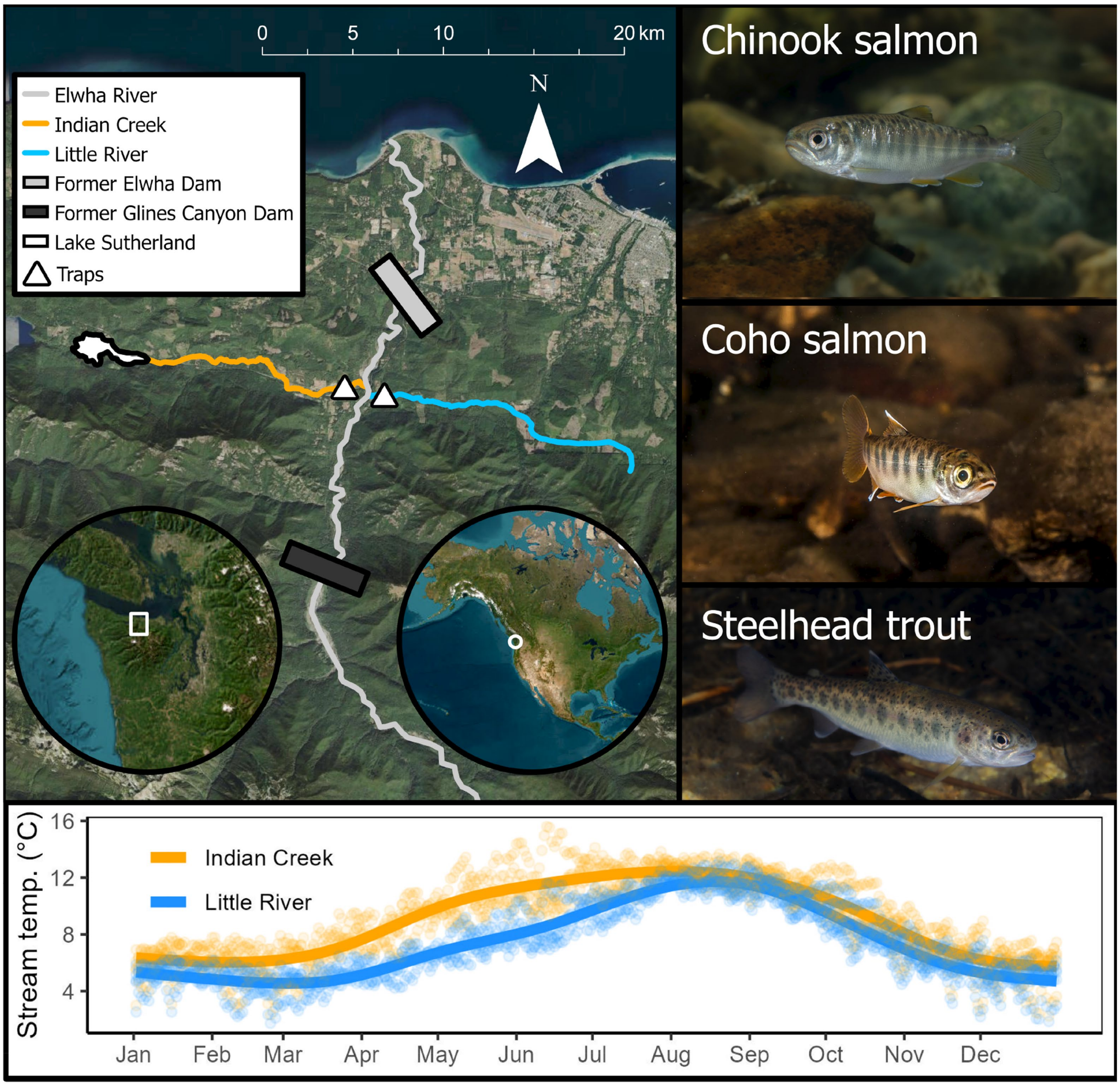

FIGURE 1
Study region, focal species, and tributary temperature regimes. Lines describing temperature regimes are cubic regression splines fit to the points as a visual aid. Here and after, we follow the convention that Indian Creek, which is warmer, is depicted in orange, while Little River, which is cooler, is depicted in blue. Photographs by Morgan H. Bond.

type (e.g., riffle and run) and stream order, with mean sizes ranging from ~10–170 mm (Munn et al., 1999; their Figure 11). For millennia, people including the Lower Elwha Klallam Tribe shared this landscape with an abundance and diversity of salmonids that enabled sustenance, identity, and culture (reviewed by Guarino, 2013). In 1912, Olympic Power and Development Company constructed the Elwha Dam on the river's mainstem at rkm 7.9, blocking ~95% of accessible habitat to salmonids (Olympic Power also constructed an additional dam, Glines Canyon, upstream in 1925; Brenkman et al., 2019). In 1992, following declines in salmonid production, tribal advocacy, and legal proceedings, U.S. Congress passed the Elwha River Ecosystem and Fisheries Restoration Act, authorizing the eventual removal of the dams in 2012. Notably, much of the watershed drained by the Elwha River remains undeveloped as it is located in Olympic National Park. This effort constituted the largest dam removal project in the world and is arguably the most direct attempt ever to recover a human-stressed landscape's natural potential to produce abundant, diverse salmonids.

Despite its history of stressors, the Elwha River is inhabited by many species of Pacific salmon and trout (Duda et al., 2021). Among these species are Chinook salmon, coho salmon, and steelhead, which rear in streams and are the focus of this study (Figure 1). The Chinook salmon and steelhead populations in this system are listed as threatened under the U.S. Endangered Species Act. These anadromous species express considerable variation in their juvenile life histories, including their seasonal outmigration timing and length of freshwater rearing (Quinn, 2018). In addition to the species that we focus on here because they were abundant in the observed tributaries, chum salmon

(*O. keta*), pink salmon (*O. gorbuscha*), cutthroat trout (*O. clarkii*), bull trout (*Salvelinus confluentus*), sculpins (Cottidae), and lamprey (*Entosphenus tridentatus*) inhabit the Elwha River system.

Dam removal restored access for salmonids to the Elwha River's environmentally-distinct tributaries Indian Creek and Little River. They are the first major tributaries encountered by salmon swimming upstream, enter the Elwha River mainstem within ~1 km of one another, and drain similar areas (Indian Creek: 60 km^2, Little River: 52 km^2). However, they support markedly different habitats—one being cold and steep, the other being warmer and lower-gradient. Little River has a colder stream temperature regime (annual mean: 7.5°C Washington Department of Ecology, 2016; Figure 1) due to its elevation, including the snow dominated zone with perennial snowfields, and steeper valley gradient (~3%). In contrast, Indian Creek has a warmer stream temperature regime (annual mean: 9°C, Washington Department of Ecology, 2016; Figure 1) because it drains Lake Sutherland, is at lower elevation, has a lower stream gradient (~1.5%), and has ample beaver activity. Note: the tributaries' daily temperature values in Figure 1 are a combination of empirical observations and imputed values estimated by quantifying statistical relationships between temperature in the tributaries and the Elwha River mainstem and neighboring Quinault River, for which more complete time series were available (details: Liermann et al., in review, this issue).

Also of note, hatcheries have in some years transported adults from the lower Elwha River to Indian Creek and Little River. Specifically, 179 and 117 Chinook salmon were relocated to Indian Creek in 2012 and 2013, respectively; 11 and 35 steelhead were relocated to Indian Creek in 2012 and 2016, respectively; and 35, 88, and 59 steelhead were relocated to Little River in 2012, 2013, and 2014, respectively (details: Pess et al. in review; this issue). Additionally, hatcheries seeded Indian Creek in 2011–2014, 2016, 2017, and 2021 and Little River in 2011–2013 with surplus adult coho salmon to accelerate recovery (McHenry et al., 2022). Furthermore, adult Chinook salmon returning to the Elwha River system at present are predominantly hatchery origin (Pess et al., in review, this issue). That is, juveniles emigrating from Indian Creek and Little River are natural-origin, but their ancestors, including some of their parents, were likely raised by hatcheries.

Data collection

Screw trap observations quantified attributes of salmonids migrating from Indian Creek and Little River. Traps were located at river kilometer (rkm) 0.5 in Little River and 0.7 rkm in Indian Creek and were monitored from late winter to late summer 2016–2021. Fieldworkers identified and measured individual lengths, and Chinook and coho salmon were classified as age-0 or age-1+ based on length cutoffs (80 and 60 mm for coho and Chinook salmon, respectively). However, in a separate analysis on a subset of these outmigrants, we explored the possibility that some coho salmon and steelhead were age-2. Indeed, steelhead were not assigned age classes in the field because of their complex age structure and phenology that produces a less obvious break in length distributions (given the date) between age classes. Instead, we attempted to make these assignments and make primary inference about individual ages in a more rigorous modeling analysis described below.

Tributaries were inhabited by the anadromous (steelhead) and resident (rainbow trout) forms of *O. mykiss*. Fieldworkers followed the convention of only identifying smolting individuals (characterized by silver coloration adapted to marine habitats) as steelhead and not identifying individuals under 55 mm as steelhead, because *O. mykiss* and sympatric cutthroat trout (*O. clarkii*) are not visually distinguishable below that length.

Trap efficiency was measured by mark-recapture procedures whereby fieldworkers dyed 100–200 age-0 fish with Bismarck brown and released them upstream of the trap, enabling calculation of weekly efficiency as the proportion of recovered marked fish. The procedure was repeated weekly and marked fish recaptured in the trap usually arrived within 3–4 days after release. Typically, marked fish were natural-origin (i.e., not hatchery-origin) Chinook salmon, coho salmon, and steelhead. To calculate capture efficiencies during periods of low natural abundance, juveniles transported from hatcheries were used as surrogates. We divided daily counts by efficiency to estimate total outmigration counts. We inferred that juveniles were natural origin because (1) hatcheries on the Elwha River are below the former Elwha Dam location and thus below the tributary mouths and (2) hatchery coho salmon and steelhead were identifiable via clipped adipose fins and traps caught zero clipped fish.

In addition, fieldworkers enumerated Chinook salmon redds (egg nests) across the tributaries during the spawning season. We chose to include these data *post hoc* after noticing substantial annual variation in juvenile Chinook salmon that we thought may be due to variation in adult spawning abundances.

Analyses

We used mixed effects models to (1) compare the abundances of salmonids between tributaries, (2) compare the timing of median annual outmigration date between tributaries, and (3) examine for effects of density dependence on Chinook salmon length. Models comparing abundances and outmigration timing were similarly parameterized as:

$$\mu = \beta_0 + \beta_1 X_1 + a_c$$

$$a_c \sim N\left(0, {\sigma^2}_c\right)$$

where log(abundance+1) or median migration date μ was a function of an intercept β_0, an effect β_1 of tributary X_1, and random intercepts a_c. Here and after, tributaries were categorical variables, meaning their model parameters were informed by binary vectors of whether (1) or not (0) observations occurred in a given tributary. For abundance models, *c* indicated different years and for the outmigration model, c indicated different combinations of years, species, and fishes' identifiable age class (e.g., 2016 Chinook age-0, 2020 steelhead smolt). For the latter, we combined these variables rather than including separate random intercept parameters for year and salmonid type to avoid a scenario whereby models attempted to fit random effects to variables with few levels for each variable (Bolker et al., 2009), while following the guiding premise that the model should account for fish of the same type and within the same year outmigrating at similar times to better isolate differences in timing among tributaries. Also for the outmigration timing model, we only compared combinations of years, species, and identifiable age classes when abundances in both tributaries' traps were in the top 33rd percentile of abundances (5,804 individuals) relative to each combination of year, species, age class, and tributary to focus on comparisons with more robust sample sizes. Initial explorations suggested that this was a natural cutoff below which counts were too few or patchy for medians and cumulative distribution functions to informatively describe outmigration timing.

Then, we used non-metric multidimensional scaling (NMDS) to compare the composition of salmonid types (each species and identifiable age class; hereafter "assemblage") between tributaries and among years. The NMDS was fit to two dimensions using a Bray–Curtis dissimilarity matrix. The format of this data was rows: years, columns: salmonid types (e.g., Chinook age-0, Coho age-1), and cell data: summed abundance. To test for differences in composition between assemblages, we used a permutational ANOVA (PERMANOVA; Anderson, 2001), which was also implemented using a Bray–Curtis dissimilarity matrix and included the categorical explanatory variables of tributary and year.

Next, we used Bayesian mixture models to assign salmonids to age classes and quantify differences in length between tributaries. Formally, these models were parameterized where the age, $a[i]$, of fish i, followed a categorical distribution with a dirichlet prior on p. The resulting age then determined the age specific length distributions.

$$L_i \sim normal\left(\mu_{a[i]}, \sigma_{a[i]}\right)$$

$$a[i] \sim cat(p)$$

$$p \sim dirichlet(\alpha)$$

The mean age specific fish length was modeled using year and tributary specific effects (Y_y and T_t) along with a linear relationship with julian date ($a \cdot d_i$).

$$\mu_{a[i]} = S_{a[i]} e^{Y_{y[i]} + T_{t[i]}} + a \cdot d_i$$

The year effect, $Y_{y[i]}$, was modeled hierarchically using a normal distribution with mean 0 and estimated standard deviation. The tributary effect, $T_{t[i]}$, was modeled with normal priors. See Supplementary material for more details.

While steelhead often outmigrate at age-2 (Busby et al., 1996) and preliminary data explorations suggested their lengths followed a relatively clear trimodal distribution (ages 0–2), this was not the case with coho salmon. This assemblage included distinct age-0 and age-1 individuals, but also—particularly in Indian Creek—markedly larger individuals. We therefore fit coho salmon lengths to a trimodal mixture model as we did for the steelhead, but refer to the largest coho salmon tentatively as "age 2?" and address this uncertainty in the Discussion.

Additionally, in the case of Chinook salmon, which were almost entirely age-0, we used a linear mixed effects model to quantify differences between tributaries in size at date. Formally, this model was parameterized as

$$\mu = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + a_c$$

$$a_y \sim N\left(0, \sigma^2{}_c\right)$$

where Chinook salmon length μ was a function of an intercept β_0, an effect β_1 of day of year X_1 an effect β_2 of tributary X_2, an interactive effect β_3 between day of year and tributary, and a random intercept a of year c. In plain terms, this model quantified how much larger Chinook salmon in Indian Creek were than in Little River, while accounting for seasonal growth that increasingly separated juvenile lengths between tributaries as winter progressed into summer as well as interannual differences in length among years due to factors not explicitly accounted for.

We also investigated effects of density dependence on Chinook salmon length within each tributary. These models were parameterized as:

$$\mu = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + a_c$$

$$a_c \sim N\left(0, \sigma^2{}_c\right)$$

where Chinook salmon length μ was a function of an intercept β_0, an effect β_1 of total annual Chinook salmon outmigrants X_1, an effect β_2 of day of year X_2, the interactive effect β_3 of total annual Chinook salmon outmigrants and the day of year, and random intercepts a for each year c. We used this model structure because we anticipated that Chinook salmon would be smaller in years with more conspecific migrants due to competition, that salmon would be larger later in the year, and that potential effects of competition on salmon size would be more apparent later in the year as salmon had experienced more time to grow. Ideally, we would also have examined for effects of density dependence on lengths of other salmonid species, but we decided against this because other species' longer rearing times complicated our ability to quantify competition. For coho salmon and steelhead, multiple age classes competed year-round while growth and mortality occurred prior to measurements at the traps, introducing much uncertainty in attempts to describe how many fish were present and how high their resource demands were during years prior. This challenge was less concerning in the case of Chinook salmon because nearly all juveniles outmigrated at age-0 before summer, making total annual counts more conducive to estimating competition.

Results

Indian Creek and Little River supported a diversity of abundances, outmigration timings, and ages across Chinook salmon, coho salmon, and steelhead (Figures 2–4). Salmonids outmigrated from January to November, mostly within late winter to early summer. Chinook salmon generally migrated earliest, followed by a relatively protracted

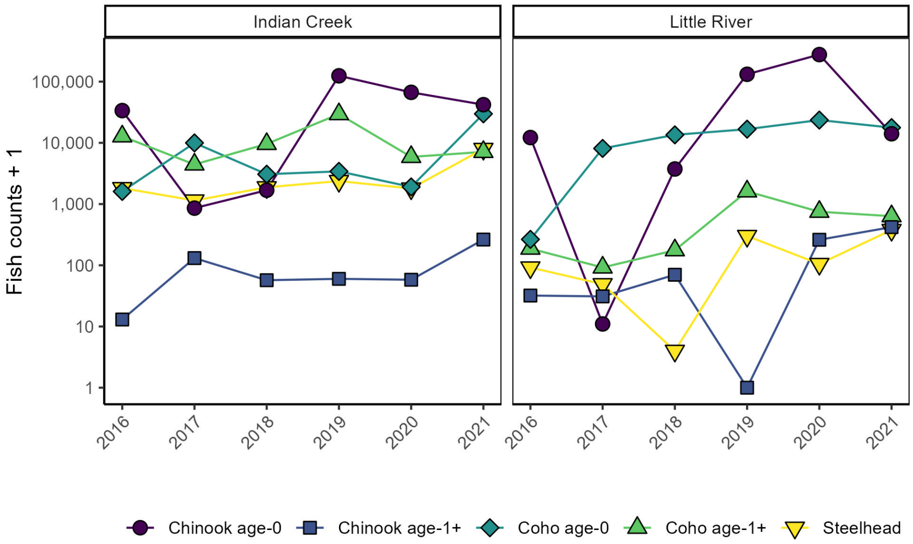

FIGURE 2
Assemblage composition compared between tributaries and among years. Y axes are log transformed to improve visibility of smaller counts.

outmigration of coho salmon that began before and ended after steelhead outmigrations. Abundance and composition also varied among years, with greater abundances in 2019–2021 than 2016–2018, coho salmon dominating the assemblage in 2017 and 2018, and Chinook salmon dominating the assemblage in 2016, 2019, and 2020. Juveniles were generally more abundant in Indian Creek than Little River, except in 2020 when juveniles were much more abundant in Little River and in 2018 when abundances were approximately equal between tributaries. Chinook salmon were dominated by small individuals presumably age-0 whereas coho salmon and steelhead included a wider range of sizes that presumably reflected multiple age classes. Overall, while distinct patterns in assemblages were present between tributaries (discussed below), there was also considerable variation among years, with each year and tributary supporting different assemblages. Altogether, this variation meant that the timing, shape, and number of migration peaks was markedly different among years and between tributaries.

Indian Creek and Little River supported distinct salmonid assemblages (Figures 2–5). Indian Creek supported greater abundances of coho salmon, especially age 1+ individuals, and steelhead. Indeed, age-1 coho salmon and steelhead were significantly more abundant in Indian Creek than Little River (Table 1, $p < 0.001$ [coho salmon], $p = 0.0021$ [steelhead]). Abundances of other salmonids did not significantly differ between tributaries (Table 1, $p \geq 0.44$). In both tributaries, age-0 Chinook salmon were numerically dominant.

The tributaries' assemblages differed significantly (Table 2, $p = 0.001$) but also shared significant temporal patterns (Figure 5, Table 2). Both tributaries' assemblage trajectories generally went up and right, then down, then left, then right in NMDS space from 2016–2021 (Figure 5). Perhaps the most striking variation shared by the tributaries over time was in Chinook salmon abundances, which were relatively high in 2016 and 2019–2021. In addition to this, steelhead abundances generally increased over time while coho salmon dominated assemblages in 2017 and 2018. Finally, both tributaries supported greater total salmonid abundances in each year of 2019–2021 than each year of 2016–2018.

Salmonids outmigrated ~23 days earlier from Indian Creek than Little River (Figure 6, Table 1, $p = 0.020$). Notably, monitoring in Indian Creek in some years appeared to begin after annual outmigrations had begun, suggesting the difference in median outmigration dates between the tributaries was likely an underestimate. For all species combined, the outmigration timing was also more protracted in Indian Creek compared to a more pulsed and shorter migration period in Little River, which was often due to its abundance of later-migrating coho salmon.

Age at outmigration also varied between tributaries. Both tributaries supported multiple outmigrant age classes, but Indian Creek supported proportionally older (or markedly larger—see Discussion) coho salmon and steelhead (Figure 7). Ages (or possibly only sizes, in the case of larger individuals) of coho salmon were especially different, with Little River supporting predominantly age-0 outmigrants whereas age-0 outmigrants comprised only ~50% of outmigrants in Indian Creek.

Some salmonid lengths differed between tributaries and were constrained by competition. Lengths of coho salmon (tributary parameter 95% CI posteriors: −0.57–0.55; Supplementary material) and steelhead (−0.83–0.71; Supplementary material) were not detectably different between tributaries. Notably, the complex age structure and multimodal length distributions of these species may have made differences between tributaries harder to detect. Chinook salmon, however, were significantly smaller in Little River than Indian Creek ($p < 0.001$; Table 1) and these differences widened as winter progressed through summer ($p < 0.001$; Table 1) (Figure 8).

The model detecting this relationship indicated that salmon were 6 mm smaller in Little River on April 5, the average day of year that Chinook salmon were measured. Effects of competition on salmon length (i.e., density dependence) were also evident in Chinook salmon. Specifically, Chinook salmon in both tributaries were smaller

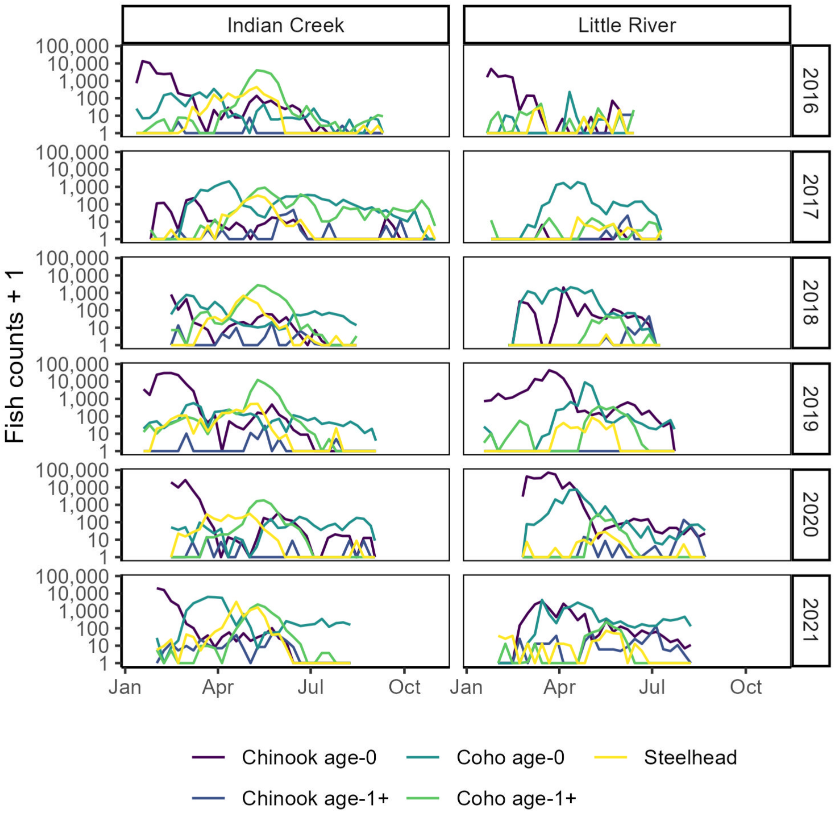

FIGURE 3
Timing and assemblage composition compared between tributaries and among years. Within-year counts are summed by week. Y axes are log transformed to improve visibility of smaller counts.

later in the year during years when tributaries' total Chinook outmigrants were greater (Figure 8, bottom). There was statistical evidence for density-dependent effects on growth in Indian Creek ($p < 0.001$; Table 1) and Little River ($p = 0.0021$; Table 1), with effect size being greater in Indian Creek than Little River (parameter estimate: −2.7 vs. −1.0; Table 1). Visual patterns suggested that density dependent effects on length were particularly apparent during May–July (Figure 8, bottom).

Chinook salmon redd counts generally increased across the study period, with especially high counts in 2018 and 2019 and greater counts in Indian Creek than Little River in 2016–2021 (Figure 9). For context, from 2014 to 2016, recruitment of Chinook salmon into Little River was impacted by the position of the river. During that time, the channel was on the west side of the valley and Little River flowed across a broad gravel bar, which restricted access to the relatively large Chinook salmon spawners. Notably, high Chinook salmon redd counts in 2018 and 2019 were followed by higher juvenile Chinook abundances in 2019 and 2020 (Figure 2).

Discussion

We quantified the demographics of juvenile salmonids outmigrating from a heterogeneous landscape made accessible by dam removal. The tributaries supported different species assemblages, outmigration timings, age structures, and population-level growth trajectories. Specifically, the warmer tributary produced salmonids that outmigrated ~23 days earlier, more age-1 coho salmon, more steelhead, some notably large or old coho salmon, and larger Chinook salmon given the date. Additionally, species composition and abundance varied substantially among years and between streams. Moreover, the colder, steeper tributary generally produced fewer juveniles, except in 2020 when abundances were dramatically higher in the colder, steeper tributary than in other years and in 2018 when abundances were approximately equal between tributaries. The patterns we observed were potentially due to multiple processes: (a) different stream gradients and temperature regimes favoring different species, (b) warmer temperature regimes accelerating incubation and growth, thus shifting seasonal outmigration timing forward, (c) stochastic, patchy adult recruitment and juvenile production during early phases of salmon repopulating the landscape, and (d) hatcheries sustaining baseline abundances of domesticated Chinook salmon that are not locally-adapted to the tributaries and happen to perform better in one than the other. Overall, restoring connectivity to tributaries with different characteristics rapidly enabled species to express diverse life histories. Such biological diversity is known to emerge from diverse habitat mosaics and promote resilience (e.g., Schindler et al., 2010; Lisi et al., 2013).

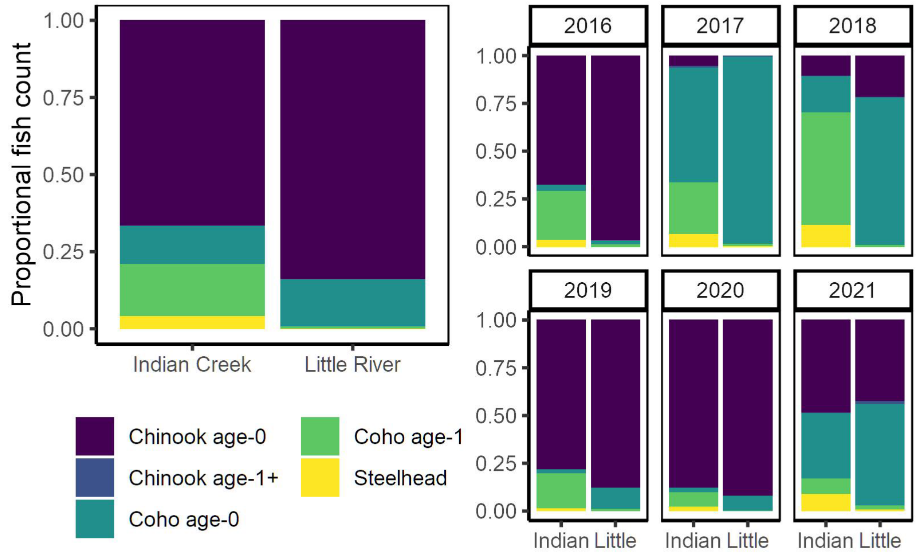

FIGURE 4
Proportional composition of salmonid assemblage compared between Indian Creek and Little River for all years (left) and individual years (right).

Temperature, stream gradient, and lake presence are fundamental to salmonid habitat mosaics, vary across landscapes, and likely drove some differences in demographics between the tributaries. High abundances of coho salmon being produced by a warmer, low-gradient tributary with lake access and ample beaver wetlands was consistent with this species' known habitat preferences (Bisson et al., 1988; Bugert and Bjornn, 1991). Additionally, temperature regimes vary across landscapes and influence all phases of salmonid life histories (e.g., Brett et al., 1969; Richter and Kolmes, 2005; Lisi et al., 2013; FitzGerald et al., 2021). Our estimate that salmonids outmigrate ~23 days earlier in the warmer tributary extends similar findings on coho fry (Liermann et al., 2017) to Chinook salmon in these systems. Warm or increasing temperatures can cue earlier migrations in juvenile salmonids (Spence and Dick, 2014 and references therein), which is consistent with our observations of earlier migrations in warmer Indian Creek. In warmer waters that accelerate metabolism, juveniles can incubate and – given sufficient food – grow faster, which may enable them to reach outmigration size thresholds earlier in warmer environments (Brett et al., 1969, Murray and McPhail, 1988, Peven et al., 1994, Cline et al., 2019). Put together, warmer waters and presumably sufficient prey may have enabled Chinook salmon inhabiting Indian Creek to grow faster, promoting earlier outmigration. Interestingly, salmonids in warmer Indian Creek included greater proportions of older (age-1+) coho salmon. Plausibly, threshold lengths may determine outmgiration timing more directly in individuals genetically predisposed to enter the sea at age-0 while migration timing in individuals predisposed to rear for a year depends less on individual length and thus temperature regime (unfortunately ago-1 coho were not abundant enough in both tributaries during the same years to robustly compare outmigration timings between them). Moreover, mosaics of habitat types, and the associated differences in the environmental conditions such as water temperature, depth, and velocity, can affect the life history diversity and age structure of coho salmon populations (Jones et al., 2021; Sethi et al., 2021). Coho salmon with access to lake environments (e.g., Lake Sutherland connected to Indian Creek) in higher latitude watersheds can utilize both lentic and lotic habitats, resulting in differences in life history, age structure, and freshwater migration patterns (Sethi et al., 2017, 2021, 2022). Conversely, there can be differences in life history and size at migration (yearling vs. parr, vs. fry migrants) and associated age structure (age 0 vs. age 1 – spring, summer, or fall/winter) in systems that have freshwater, estuarine, and ocean habitats connected or disconnected (Jones et al., 2021). Overall, the distinct environments in Indian Creek and Little River appear to have driven distinct life histories in juvenile salmonids.

We observed greater abundances of steelhead in Indian Creek than Little River, despite the latter's steeper, colder environment. While steelhead generally predominate among species in higher gradient habitats (McMillan et al., 2013), this may reflect their evolutionary ability to hold in faster currents (Bisson et al., 1988) and their comparatively broad spatial distribution within a watershed (McMillan et al., 2013) rather than a tendency to avoid warmer, lower gradient areas. Indeed, steelhead as a species can certainly tolerate rearing areas that are warm for salmonids (Richter and Kolmes 2005; Sloat and Osterback 2013) because they have evolved a scope for activity that is maximized at relatively warmer temperatures (Dickson and Kramer 1971). And, as outlined above, warmer streams within tolerable temperature ranges offer greater potential for growth, given adequate prey availability. Additionally, Indian Creek is larger and therefore presumably provides greater habitat capacity and its lake head dampens flow variation that can cause scour and flooding. For these reasons, Indian Creek's environment may be more conducive to steelhead production than Little River.

In addition to landscapes generating diversity, some assemblage patterns among years and between tributaries may be attributable to adult recruitment and hatchery processes. During this study's timeframe, salmonids were becoming more abundant and widely distributed across the landscape (Duda et al., 2021,

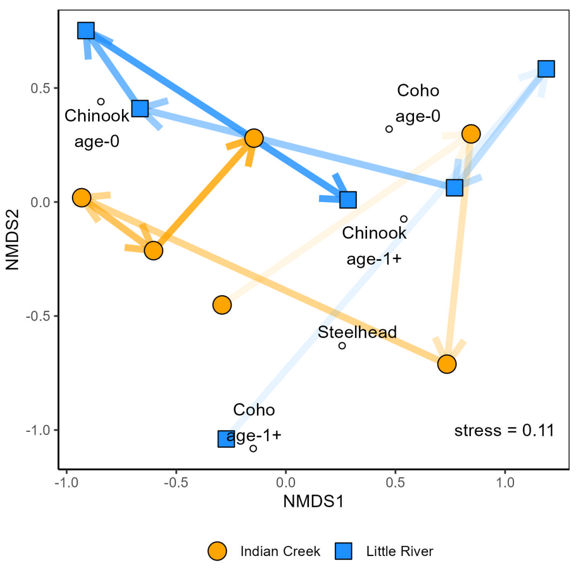

FIGURE 5
NMDS comparing salmonid assemblages between Indian Creek and Little River. Lines and arrows track the tributaries' changes from 2016–2021 and darken across time.

Pess et al., in review, this issue). Notably, Chinook salmon tend to spawn in mainstems unless high spawner abundances (and adequate flows) promote expansion into tributaries. This appeared to happen in 2018 and 2019, when Chinook salmon escapement was high (Pess et al., in review, this issue) and redd counts in Indian Creek and Little River were especially high, resulting in high juvenile abundances the following years. Indeed, some of the synchronized variation in juvenile assemblage composition between tributaries among years appeared to be attributable to variation in adult spawning the year prior. If Chinook salmon abundances continue to increase across the landscape, annual spawner distributions may more routinely expand into the tributaries, resulting in greater abundances the following years. However, an important nuance to understanding Chinook salmon in this system is that returning adults are, to date, overwhelmingly hatchery-origin and presumably descend from a hatchery lineage that originated in 1930 (Pess et al., in review, this issue). It therefore seems unlikely that juvenile Chinook salmon are locally adapted to Indian Creek or Little River. One interpretation of Chinook salmon outmigrating at smaller sizes from Little River may be that the current stock's genetically-determined traits happen to align more with niches in Indian Creek than Little River. Over decades as natural productivity has an opportunity to eclipse hatchery productivity, it remains to be seen whether natural selection will produce locally-adapted populations that exploit localized environments and opportunities, potentially driving more divergence in life histories between tributaries.

Competition also appeared to influence juvenile lengths and interact with the tributaries' different growth opportunities. Chinook salmon were smaller when conspecific abundances were higher, and such density dependent effects are common for salmonids in general (Grossman and Simon 2020). Notably, these effects were greater in Indian Creek, which appeared to support faster growth than Little River. That fish appeared to grow faster but experience greater density-dependent constraints on growth in Indian Creek is consistent with Indian Creek's warmer temperatures offering greater potential for growth, but possibly also greater potential for prey limitation by increasing salmonids' metabolic rates. Indeed, whether warmer waters within tolerable ranges promote growth depends on the interaction of temperature, prey availability, and competition (Crozier et al., 2010). While examining for the effects of competition on coho salmon and steelhead was beyond the scope of our study because of their more complex residence times, similar dynamics may influence growth in these species as well.

Many of the assemblage changes among years and between tributaries were unpredictable and yet appeared to offset one another, underscoring the concept that ecosystems are often stabilized by diverse options (Brennan et al., 2019; Munsch et al., 2022). Specifically, assemblages shifted back and forth among years from dominance by Chinook salmon to coho salmon and in 1 year. Little River produced a large abundance of steelhead smolts. Indeed, if the systems lacked Chinook salmon very few fish would have been present in 2016 and if they lacked coho salmon very few fish would have been present in 2017 and 2018. Because the dynamics of these three species were not synchronized among years, they generated portfolio effects whereby the abundance of the total assemblage was more stable than the more volatile abundances of individual species and age classes (Schindler et al., 2015). As is typically the case in ecology, our ability to predict or explain such fine-scale ecosystem changes will always be limited. However, we can count on stability to emerge from diverse systems on aggregate as their components spread risk and respond differentially to disturbances and opportunities (Schindler and Hilborn, 2015). Additionally, as alluded to above, this system remains in a recovery phase and its dynamics perhaps also reflect recruitment trends (i.e., generally increasing, but patchy abundances over time) and "trial and error" in natural selection contexts as populations attempt to inhabit and locally adapt to newly accessible areas. Overall, salmon production across the landscape may be stabilized by environmentally-distinct tributaries enabling salmon to stagger their life cycles across time and space, attributes that enable systems to spread risk and take advantage of unpredictable opportunities (Schindler et al., 2015).

Our findings are relevant to other attempts to increase salmonid diversity via habitat reintroduction. For example, preliminary observations suggest that the removal of San Clemente Dam (CA, United States) has enabled a diversity of steelhead (and perhaps rainbow trout) size classes to repopulate the landscape. Researchers attribute this biological diversity similarly as in our study to the diversity of newly-accessible habitats (Williams et al., 2018). Additionally, an upcoming project removing dams on the Klamath River will constitute the largest dam removal to date. This project will target the recovery of distinct Chinook salmon life histories that return in the spring and fall to different areas within the watershed (Oregon Department of Fish and Wildlife and the Klamath Tribes, 2021). The Klamath River watershed supports a remarkably heterogeneous landscape of stream temperatures and stream gradients

TABLE 1 Summary statistics of mixed effects models quantifying salmonid abundance, outmigrations timing, and length.

Model	Effect	Group	Term	Estimate	Std error	*P* value
Chinook age-0 count	fixed		Global intercept	9.7	1.2	<0.001
	fixed		Pop: Little River	−0.7	0.84	0.44
	random	year	sd(Random intercept)	2.6		
	random	residual	sd__Observation	1.4		
Chinook age-1 count	fixed		Global intercept	4.2	0.68	<0.001
	fixed		Pop: Little River	−0.41	0.84	0.65
	random	year	sd(Random intercept)	0.83		
	random	residual	sd__Observation	1.5		
Coho age-0 count	fixed		Global intercept	8.4	0.58	<0.001
	fixed		Pop: Little River	0.51	0.66	0.47
	random	year	sd(Random intercept)	0.86		
	random	residual	sd__Observation	1.1		
Coho age-1 count	fixed		Global intercept	9.1	0.37	<0.001
	fixed		Pop: Little River	−3.2	0.37	<0.001
	random	year	sd(Random intercept)	0.64		
	random	residual	sd__Observation	0.64		
Steelhead count	fixed		Global intercept	7.7	0.51	<0.001
	fixed		Pop: Little River	−3.4	0.58	0.0021
	random	year	sd(Random intercept)	0.75		
	random	residual	sd__Observation	1.0		
Median outmigration date	fixed		Global intercept	58	12	0.0032
	fixed		Pop: Little River	23	6.7	0.020
	random	year x species x age class	sd(Random intercept)	27		
	random	residual	sd__Observation	12		
Chinook length	fixed		Global intercept	53	1.3	<0.001
	fixed		Day of year	15	0.37	<0.001
	fixed		Pop: Little River	−6.0	0.48	<0.001
	fixed		Day of year x Pop: Little River	−1.6	0.46	<0.001
	random	year	sd(Random intercept)	3.3		
	random	residual	sd__Observation	8.3		
Chinook length DD: Indian Creek	fixed		Global intercept	50	2.1	<0.001
	fixed		Day of year	16	0.42	<0.001
	fixed		Annual Chinook migrants	−1.5	2.0	0.51
	fixed		Day of year x annual Chinook migrants	−2.7	0.44	<0.001
	random	year	sd(Random intercept)	4.6		
	random	residual	sd__Observation	8.7		
Chinook length DD: Little River	fixed		Global intercept	51	5.4	0.0010
	fixed		Day of year	14	0.33	<0.001
	fixed		Annual Chinook migrants	-3.9	4.7	0.45
	fixed		Day of year x annual Chinook migrants	−1.0	0.32	0.0021
	random	year	sd(Random intercept)	10		
	random	residual	sd__Observation	7.7		

DD: density dependence.

that could give rise to life history diversity similar to that observed in our study. Additionally, preliminary work has investigated the feasibility of reintroducing steelhead and early-migrating Chinook salmon to tributaries of the San Joaquin River and Eel River (CA, United States; Boughton et al., 2022; FitzGerald et al., 2022). Provided that the diversity of unlocked habitats in these systems are within the thermal tolerance of their salmonids' life stages, there is no obvious reason why diverse juvenile life histories would not emerge from these systems as happened in our study.

Similarly, we may expect the different environmental conditions that are distributed across the Elwha River system to generate juvenile life history beyond the tributaries we studied. The Elwha River system consists of hundreds of anadromous stream kilometers and thousands of overall kilometers that are nested across its environmentally heterogeneous landscape (Munn et al., 1999, Pess et al. in review, this issue). Its large elevation range, coupled with its variation in confined and alluvial valley bottoms, allows for considerable variation across space in conditions that determine habitat characteristics. Notably, high elevations experience quadruple the precipitation of lower elevations, experience a greater proportion of precipitation as snow, and are cooler (Munn et al., 1999). Furthermore, an array of habitat types such as high-gradient streams and floodplains are distributed across this template (Munn et al., 1999). Based on our observations in Indian Creek and Little River and a fundamental understanding that salmonid life history is linked to environmental conditions that vary across landscapes, we may expect life history diversity to be emerging across the diversity of many newly-accessible habitats in the Elwha River system.

TABLE 2 Summary statistics of PERMANOVA comparing salmonid assemblages between tributaries and among years.

Term	Df	Sum of squares	R^2	Pseudo-F	*p* value
Year 2017	1	0.65	0.23	9.7	0.001
Year 2018	1	0.54	0.19	8.1	0.001
Year 2019	1	0.28	0.10	4.2	0.012
Year 2020	1	0.35	0.13	5.2	0.005
Year 2021	1	0.17	0.062	2.6	0.073
Tributary	1	0.46	0.17	6.9	0.001
Residual	5	0.33	0.12		
Total	11	2.8	1		

Our mixture models that assigned fish to age classes include uncertainty that should be considered in the interpretation of our results. Our mixture models intended to parse out three age classes by leveraging *a priori* knowledge that these three age classes are often present in juvenile salmonid habitats, especially in the case of steelhead (Quinn, 2018), and will create three different length distributions after accounting for various covariates (i.e., day of year, tributary, or year). Importantly, age assignments were probabilistic, meaning we can make some of these assignments more confidently than others, but for simplicity we presented age composition based on the most likely outcome for each fish. Thus, the proportion of fish assigned to each age class includes uncertainty and more important than the absolute proportions of age classes is the qualitative pattern that Indian Creek was inhabited by proportionally more larger and older individuals, which is corroborated by visually comparing length at date values between tributaries (Figure 7). Additionally, the complex age structure of coho salmon and steelhead may impair model detection of differences in length at date of these species between Indian Creek and Little River, relative to the model used to examine Chinook salmon length. That is, coho salmon and steelhead may have differed in length at date between the two tributaries, but we may have been less able to detect these differences due to the more complicated data arising from their diverse age structure. Finally, without direct age sampling (e.g.,

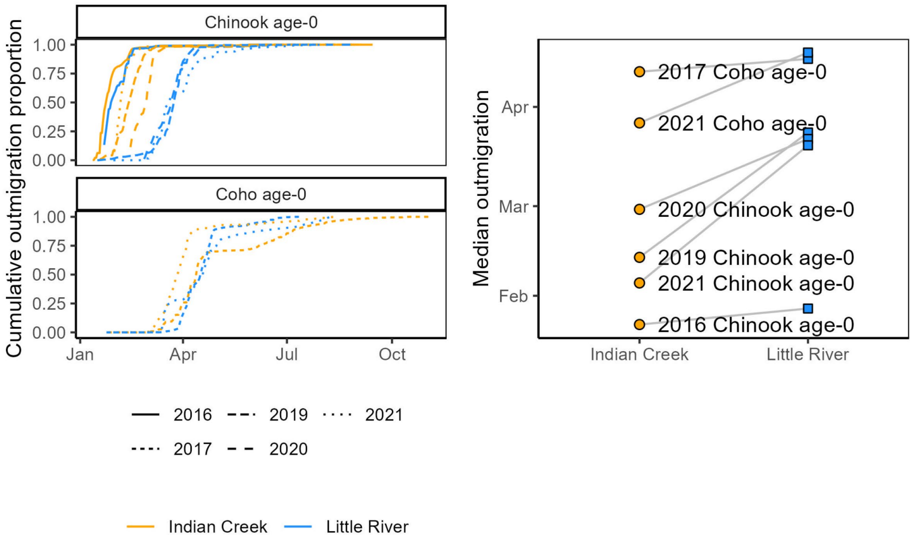

FIGURE 6
Salmonid outmigration timing compared between Indian Creek and Little River. Left: cumulative outmigrations as a proportion of total outmigrations. Right: median outmigration date, with dashed lines connecting observations of the same salmonid type and year.

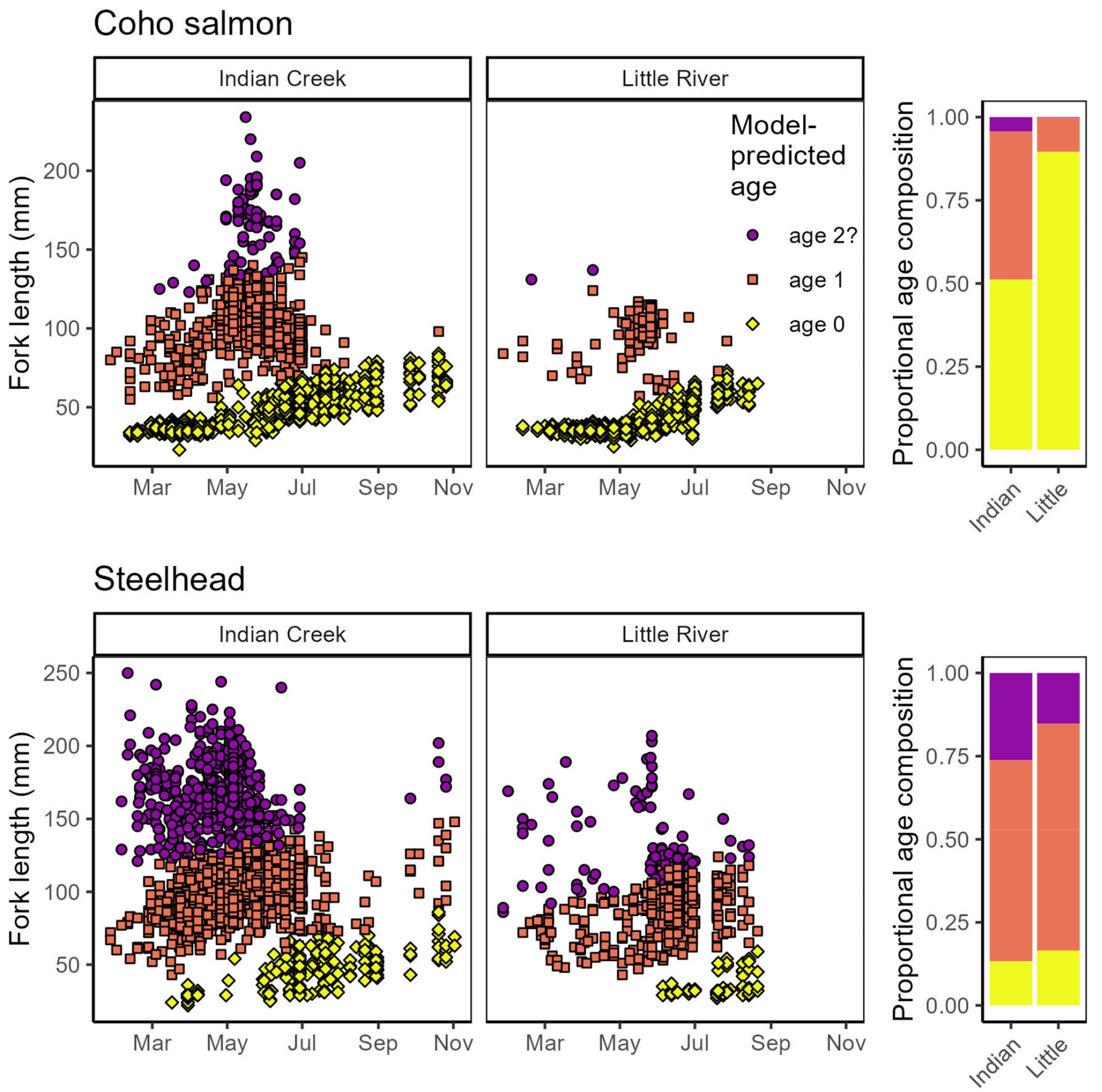

FIGURE 7
Model predicted ages of coho salmon and steelhead compared between tributaries. (Chinook salmon omitted because of their negligible juvenile age structure).

examining scales) and given that coho are not known to outmigrate at older ages as often do steelhead (Hodge et al., 2016; Quinn, 2018), we cannot confidently interpret whether the largest coho salmon in Indian Creek were age-2 or simply large age-1 individuals. Instead, we note that Indian Creek's coho salmon included many uniquely large individuals, which may reflect tributary-specific rearing durations or growth opportunities and contributed to differences in life histories between the two tributaries. Directly measuring the age of juveniles repopulating environmentally diverse tributaries following dam removal in this river system and others would be a natural extension of this study.

To conclude, diverse landscapes enable diverse life histories that promote resilience (Hilborn et al., 2003; Schindler et al., 2010; Hodge et al., 2016; Brennan et al., 2019), but human stressors that simplify and degrade landscapes suppress life history diversity and erode resilience (Munsch et al., 2022). Dams and other modes of habitat fragmentation contribute substantially to lost life history diversity (e.g., Yoshiyama et al., 1998), prompting efforts to restore diversity via dam removal. Our study—which addressed a knowledge gap regarding responses in juvenile life stages—and others (e.g., Quinn et al., 2017; Williams et al., 2018; Duda et al., 2021) demonstrate that dam removal can enable salmonids to repopulate heterogeneous landscapes and express local differences in their relative species abundance, outmigration timing, age classes, and growth rates, thus enabling landscapes' natural capacities to express diverse life histories. By actualizing diverse, complex systems that spread risk (Schindler et al., 2015), dam removal may promote resilience in salmonids and other species during an era of rapid and uncertain environmental change.

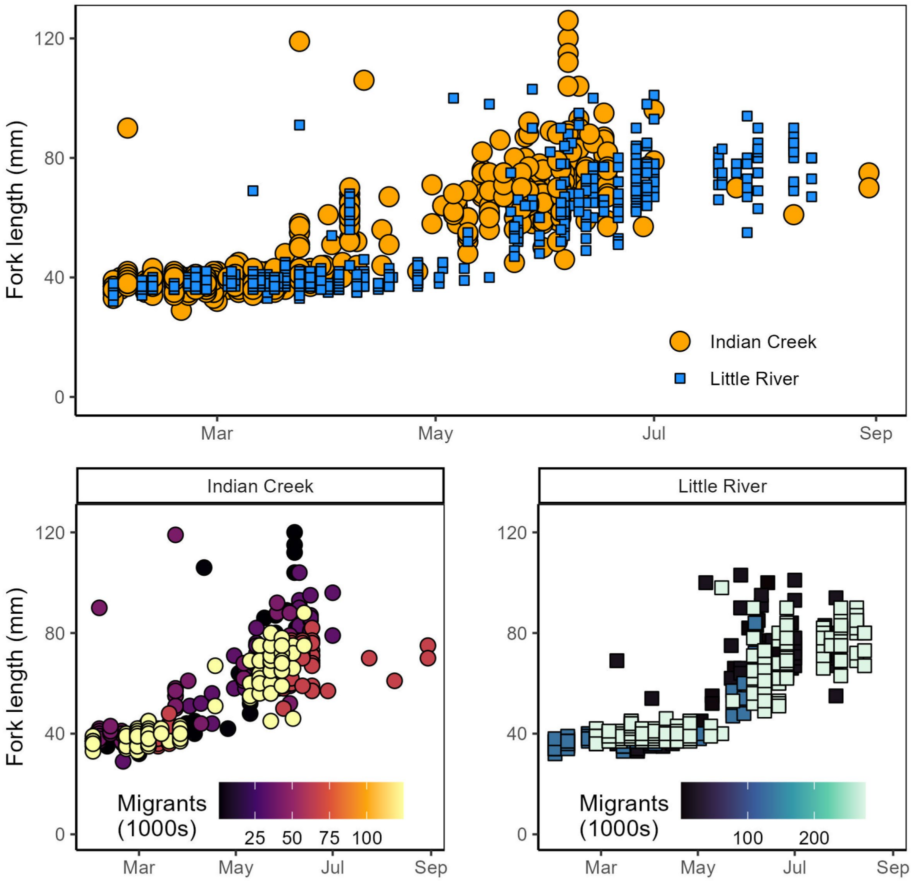

FIGURE 8
Top: Chinook salmon lengths compared between Indian Creek and Little River. Points describing Indian Creek fish lengths are larger and plotted behind Little River to improve visual comparison between tributaries. Bottom: Chinook salmon lengths compared within tributaries among years with different abundances of Chinook salmon outmigrants.

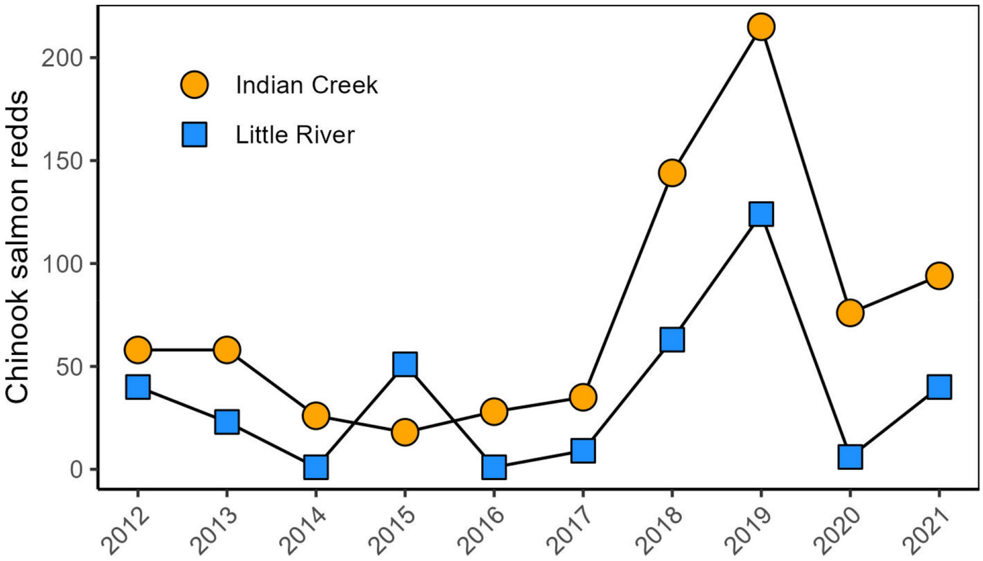

FIGURE 9
Annual Chinook salmon redd counts in Indian Creek and Little River.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Washington State (Washington State Scientific Collection Permit), National Park Service (Scientific Research and Collecting Permit), U.S. Fish and Wildlife Service (Native Threatened Specific-Recovery), and NOAA-NMFS (take permit).

Author contributions

SM: led writing, analyses, fieldwork, ideas, and revisions. MM and GP: design, fieldwork, project supervision, ideas, and revisions. ML: analyses, fieldwork, ideas, and revisions. TB: fieldwork, ideas, and revisions. JM: ideas and revisions. RM: design, fieldwork, ideas, and revisions. All authors contributed to the article and approved the submitted version.

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Conflict of interest

SM is employed by Ocean Associates Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1188921/full#supplementary-material

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Initial responses of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) to removal of two dams on the Elwha River, Washington State, U.S.A.

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Large dam removal is being used to restore river systems, but questions remain regarding their outcomes. We examine how the removal of two large dams in the Elwha River, coupled with hatchery production and fishing closures, affected population attributes of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). Initial responses by returning adult Chinook salmon and steelhead was an increase in the number and spatial extent of natural and hatchery origin fish. Although few naturally produced juvenile Chinook salmon and steelhead outmigrants were observed prior to and during dam removal, abundances increased three years after adult fish passage was restored, suggesting that impacts due to downstream sedimentation after dam removal were reduced. The Chinook salmon population demographics remain dominated by hatchery production, while increases in winter steelhead abundance included both hatchery and natural-origin spawners. The spatial expansion of winter steelhead upstream of former dam sites was predominantly by natural-origin spawners. We also observed a natural "reawakening" of summer steelhead that were in part derived from an up-river resident population that returned to the Upper Elwha. Our results showed that a combination of habitat, hatchery, and harvest actions can result in positive responses for salmonid populations.

KEYWORDS
dam removal, restoration, salmon, monitoring, salmon life-history diversity, hatcheries

1 Introduction

Dams are a major threat to the connectivity of river ecosystems across the world and have contributed to extinctions and imperiled status of migratory fishes (Pringle et al., 2000). However, many dams have now outlived their intended purposes and life spans, and consequently, over 1200 dams have been decommissioned and removed in the United States over the last two decades (O'Connor et al., 2015; Bellmore et al., 2016). Dam removal can lead to rapid ecosystem responses, such as downstream changes in spawning and rearing habitats, the re-emergence of river channels in former reservoirs, and restored fish passage (O'Connor et al., 2015; Tullos et al., 2016; Bellmore et al., 2019). Most removed dams to date have been small structures (< 8 m in height) (Bellmore et al., 2016), but removal of large dams (> 15 m) has gained momentum, particularly in the western United States (O'Connor et al., 2015).

Removing large dams that block the migration of anadromous salmon, trout, and char can reopen habitat and provide imperiled stocks an opportunity to increase their abundance and productivity as they expand their distribution and diversity across a reconnected watershed (Bellmore et al., 2019). This is a primary reason why dam removal is increasingly being considered and implemented to assist the recovery of depleted populations of Pacific salmonids (*Oncorhynchus* spp.) (Hare et al., 2019; Waldman and Quinn, 2022). Returning adult salmon can reoccupy either historically available or new habitats and increase their population size, even when initial abundance from donor populations is small (i.e., less than 100) or large (i.e., ~ 1 million) (Milner et al., 2007; Kiffney et al., 2009; Pess et al., 2012; Anderson et al., 2015). Salmon have generally responded favorably after removal of smaller dams (Hogg et al., 2015). However, large dams carry greater ecological tradeoffs. Large dam removals may provide access to a larger amount of habitat, but they also can store and potentially release more sediment that can exert a strong short-term impact on the productivity of affected downstream habitats and food webs (Morley et al., 2020). These sediment impacts can potentially impede the rate of movement into newly opened habitats upstream of former barriers and lead to short-term degraded conditions for fish occupying downstream habitats (Bellmore et al., 2019). While the long-term benefits to salmonids are expected to outweigh the short-term ecological costs, large dam removal is rare and consequently knowledge and peer-reviewed studies on the short- and long-term responses by Pacific salmon are scarce (e.g., Liermann et al., 2017).

In 1992, the Elwha River Ecosystem and Fisheries Restoration Act called for the "full restoration of the Elwha River ecosystem and native anadromous fisheries", setting the stage for one of the largest planned dam removals in history (Winter and Crain, 2008). The Act authorized the Department of the Interior to acquire and remove the Elwha and Glines Canyon dams on the Elwha River, Washington State (Figure 1). Both dams blocked access to most of the potential anadromous fish habitat for all five species of Pacific salmon, steelhead (*Oncorhynchus mykiss*), coastal cutthroat trout (*Oncorhynchus clarkii*), and bull trout (*Salvelinus confluentus*) (Ward et al., 2008). The concurrent removal of both dams started in September 2011 and was completed in October 2014. Approximately 30 million metric tonnes (Mt) of impounded sediment were ultimately exposed to fluvial erosion, and over 65% of the stored sediment has eroded since dam removal (as of 2016), of which only ~10% was deposited in the fluvial system (Ritchie et al., 2018). The remaining ~90% of the released sediment was transported to the coast, expanding the delta by ~60 ha (Ritchie et al., 2018), significantly diversifying and improving the estuarine and nearshore environment (Foley et al., 2017; Shaffer et al., 2017; Perry et al., 2023; Rubin et al., 2023).

The Elwha River provides a unique opportunity to understand the geomorphic evolution of a river system and the short-term responses of anadromous salmonids during and after removal of two large dams (East et al., 2015). In addition to intense sediment impacts, the initial movement of fish into riverine habitats between and upstream of the former dams could depend on several factors, such as the size and origin of the source populations, the potential for strays from other adjacent populations, the types and characteristics of the newly accessible habitat, and life history diversity (Pess et al., 2014). Further, the homing phenomenon displayed by salmon could be important because straying and movement can contribute to initial occurrence, but homing in future generations will be necessary to maintain the population gains and contribute to further growth and expansion. Lastly, dam removal can potentially improve resilience by increasing diversity (e.g., Schindler et al., 2010) if sufficiently unique habitats exist above the dams (e.g., Beechie et al., 2006; Waples et al., 2008) and the adaptive genetic diversity to express those life histories is retained by the fish (Thompson et al., 2019). Short-term, post dam removal response and diversification of life histories in coho salmon (*Oncorhynchus kisutch*) (Liermann et al., 2017), bull trout (Quinn et al., 2017; Brenkman et al., 2019), and Pacific lamprey (*Entosphenus tridentatus*) (Hess et al., 2021) has already been documented in the Elwha River since dam removal. Additionally, Duda et al. (2021) reported increases in spatial extent of Pacific salmon and bull trout upstream of the former dam sites. We present the first evaluation of interannual trends in juvenile and adult Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead abundances during and after dam removal, highlighting the relative contributions of hatchery and natural-origin individuals in the Elwha River.

Herein we focus on the short-term (i.e., less than 10 years) responses of hatchery and natural-origin Chinook salmon and steelhead populations during and after reconnection of the Elwha River. Leading up to the full removal of both dams, we expected an intense, short-term disturbance due to the large-scale increase and subsequent reduction in sediment supply, and eventual access to a large expanse of previously inaccessible pristine habitats. This combined with the current status (e.g., abundance), origin (i.e., hatchery or natural-origin), and diversity (i.e., resident and anadromous forms) of the populations prior to dam removal would exert a strong influence on Elwha River Chinook salmon and steelhead (Brenkman et al., 2008; Pess et al., 2008). A wide variety of monitoring approaches, ranging from SONAR to snorkel surveys, were implemented to evaluate these general hypotheses. Specific questions asked include:

1) What was the annual abundance and origin of returning adult Chinook salmon and winter steelhead during and after dam removal?

2) How many Chinook salmon migrants and steelhead smolts were produced and were annual estimates of juvenile abundance affected by potential streamflow and sediment impacts?

3) How far have Chinook salmon and steelhead expanded their spawning distribution?

4) Has dam removal given rise to the re-emergence of different life histories that were not present, or very rare, when migration into the Elwha River headwaters was blocked?

We used the data to compare and contrast the extent of reintroduction between the two species and in relation to prior research, review potential reasons underlying the responses, and discuss implications of our findings for other large dam removal projects.

2 Study area and salmonid populations of interest

The Elwha River is located on Washington State's Olympic Peninsula, originating in Olympic National Park (Figure 1). The Elwha drains 833 km^2 and flows 72 km from an elevation of 1,372 m at the headwaters to its mouth on the Strait of Juan de Fuca in the Pacific Ocean. The physical geography of the Elwha River system includes a series of alternating canyons and floodplains, which occur throughout the watershed (Pess et al., 2008). Two hydroelectric dams were built without fish passage facilities and eliminated upstream access to 95% of the Elwha River watershed (Brenkman et al., 2019), including Elwha Dam, which was constructed at river kilometer (rkm) 7.9 in 1912 and created Lake Aldwell reservoir, and Glines Canyon Dam, which was constructed at rkm 21.4 in 1927 and created Lake Mills reservoir (Figure 1). The 32-m-tall Elwha Dam was removed over an 8-month period from September 2011 to April 2012, while the Glines Canyon Dam (64 m in height) was removed over a 3-year period from 2011 to 2014 (Brenkman et al., 2019). In October 2014, shortly after the Glines Canyon Dam removal was complete, a large rockfall occurred in the canyon immediately downstream of the dam site near rkm 20.0 (Figure 1). The rockfall created a new barrier to upstream passage of

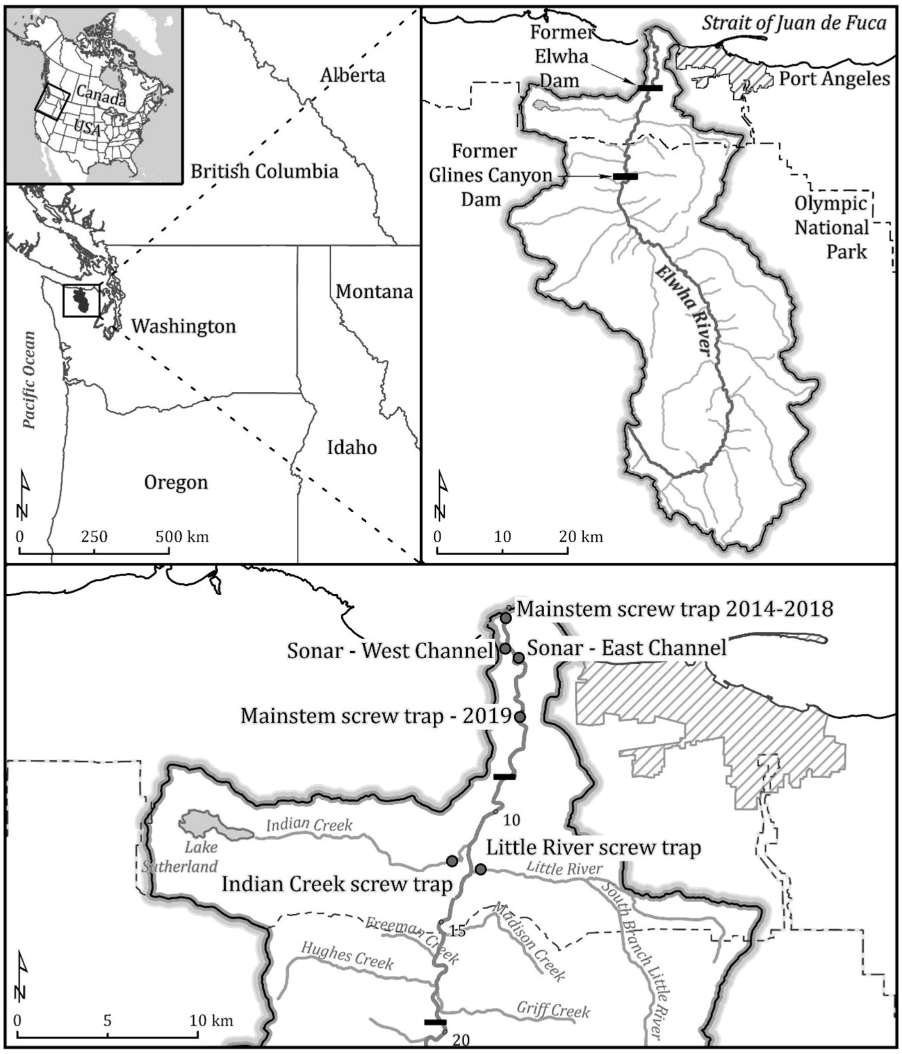

FIGURE 1
The Elwha River basin. Upper left is regional map of Elwha River, upper right is the entire Elwha River watershed. Lower map includes location of SONAR units and smolt screw traps. Map layer sources: National Park Service, Statistics Canada Census Program, United States Census Bureau's TIGER/Line, United States Geological Survey, Washington State Department of Ecology. Map projections: Lambert Conformal Conic, WGS 1984 Web Mercator.

adult salmonids, and consequently, removal of the boulders was initiated in October 2015, and completed in September 2016 (Brenkman et al., 2019; Ertle et al., 2019). Similar to previous Elwha publications, we refer to three main sections of the Elwha watershed (Figure 1**).** The Lower Elwha is downstream of the former Elwha Dam site to the river mouth (rkm 0.0–7.9). The Middle Elwha is between the two former dam sites, including the former Lake Aldwell Reservoir (rkm 7.9–21.7). Lastly, the Upper Elwha is upstream of the former Glines Canyon Dam, which included the former Mills Reservoir (rkm 21.7–61.6).

The Elwha River currently supports wild, natural-origin, hatchery, and nonnative fishes (Brenkman et al., 2019), including Chinook salmon, coho salmon, chum salmon (*O. keta*), pink salmon, sockeye salmon (*O. nerka*), rainbow trout, summer and winter steelhead (anadromous form of rainbow trout), coastal cutthroat trout, bull trout, and nonnative brook trout (*S. fontinalis*). Although two distinct runs of Chinook salmon were historically present in the Elwha River, a spring run and a summer/fall run, only the latter was thought to persist prior to dam removal (Brannon and Hershberger, 1984). Two juvenile life history strategies of Chinook salmon – stream type (1+ year old outmigrants) and ocean type (0+ year olds outmigrants) – also both currently exist in the Elwha River, with a large majority being ocean type. A dedicated Chinook salmon hatchery program was initiated in 1930 from Elwha River origin stock (Brannon and Hershberger, 1984), and in recent years, Chinook salmon releases have been large (annual average number released 1985 to 2014 = 2.5 million). The current Chinook salmon hatchery program was deemed necessary because the population has been dependent upon hatchery production for multiple decades and dam removal was predicted to reduce survival and production of Chinook salmon in the main stem Elwha River below the dams (NMFS, 2012). The Chinook salmon hatchery program played an important role in maintaining the persistence of the unique genetic lineage of Elwha Chinook salmon during the century that the dams were in place (NMFS, 2012). Releases of hatchery winter run steelhead have occurred since 1965, and out-of-basin summer steelhead were released from 1968 to 2008 (Duda et al., 2018). Native Elwha winter steelhead persisted in low abundance downstream of the dams prior to dam removal, but as with Chinook salmon, dam removal presented a potential threat to their short-term viability due to the expected elevated suspended sediment concentrations from stored sediment being released during and after dam removal. Managers developed a winter steelhead hatchery program using native broodstock that started releasing smolts in 2011 and stopped prior releases of hatchery steelhead derived from an out-of-basin stock (NMFS, 2012). The initial release goal for the winter steelhead program was 175,000 age-2 smolts (LEKT 2012), but that was adjusted to 30,000 in 2023 based on entry timing, increased abundance, adult-to-adult productivity, and distribution (Peters et al., 2024). Summer run steelhead existed only at very low numbers and may have been extirpated prior to dam removal, but they were expected to rebuild and reoccupy their former historical habitats upstream of both dams (Ward et al., 2008). A moratorium on commercial and recreational fishing for all species within the Elwha River watershed and terminal nearshore area was implemented in 2012 and continued through summer of 2023. A limited ceremonial and subsistence-fishing season for coho salmon occurred in the fall of 2023. The only other exception to the moratorium has been an ongoing recreational fishery targeting kokanee (non-anadromous form of the sockeye salmon) in Lake Sutherland, the headwaters of Indian Creek.

2.1 Chinook salmon and steelhead adult relocation

To help jumpstart salmonid reintroduction, adult Chinook salmon and winter run steelhead were relocated to habitats above the dam sites during and immediately after dam removal (Tables 1, 2). Relocated adults were obtained via natural recruitment into hatchery facilities (Chinook salmon and steelhead), and netting and trapping in the river (Chinook salmon only). In five of ten years during and after dam removal, adult Chinook salmon were relocated into five locations of the Middle Elwha upstream of the Elwha Dam site, with the greatest number of fish being relocated in 2018 and 2019 (Table 1). However, because only surplus hatchery fish were used for Chinook salmon relocation, males were numerically dominant in all years except 2019. From 2012 to 2014 and again in 2016, adult winter steelhead were captured at the Lower Elwha Klallam Tribe's (LEKT) hatchery trap and relocated into two Middle Elwha tributaries – Indian Creek and Little River (Figure 1; Table 2).

3 Methods

3.1 How do the questions link to the methods and results?

Multiple methods answered each of the four questions. Determining annual abundance of adult Chinook salmon and winter steelhead employed the use of SONAR units in the Lower Elwha. To determine the origin of returning adult Chinook salmon we evaluated carcasses of post-spawned fish for hatchery marks to estimate the proportion of hatchery-origin spawning Chinook salmon. For winter steelhead origin we utilized an adipose clip or coded-wire tag (CWT) (sometimes both could be present) to identify hatchery-origin adults. Individuals of both species were also captured during SONAR tangle netting in the Lower Elwha.

We utilized rotary screw traps to estimate the abundance of juvenile Chinook salmon and steelhead outmigrants. To determine if river conditions prior to, during, and following dam removal impacted production of juvenile Chinook salmon, we modeled the relationship between river discharge, sediment transport, and productivity of sub-yearling Chinook salmon (age-0 migrants/spawner), which includes data from both the SONAR and the smolt traps.

To determine the pattern of spawning distribution and expansion we conducted foot surveys to count spawning nests or "redds" to determine the distribution of spawning Chinook salmon and steelhead. We also conducted opportunistic snorkel surveys for

TABLE 1 Chinook salmon relocation by sex from the hatchery facilities in the Lower Elwha River to areas upstream of the former Elwha Dam site from 2011 to 2020.

Year	Indian Creek		Little River		Elwha River rkm 16.5		Elwha River rkm 20.5		Elwha River rkm 22.0	
	M	F	M	F	M	F	M	F	M	F
2011									7	3
2012	179									
2013			117							
2014										
2015										
2016										
2017										
2018							877	113		
2019					181	395				
2020										

Blanks indicate no relocation, jacks are excluded from the counts above.

adult summer steelhead because of our limited ability to enumerate them with other methods due to their apparent preference to immediately migrate upstream when returning to the Elwha between June and October. These surveys also gave us a relative indication of a unique life-history strategy that was not typically observed in the Lower Elwha prior to dam removal.

3.2 What is the annual abundance of returning adult Chinook salmon and winter steelhead during and after dam removal?

We used two methods to estimate the abundance of adult Chinook salmon and steelhead before and after dam removal (Figure 1). Prior to 2012 (before dam removal), adult abundance was estimated for both species by visually enumerating redds throughout the entire Lower Elwha and then multiplying the total count by an expansion factor (Chinook salmon 2.5 fish per redd, steelhead 1.8 fish per redd). For Chinook salmon redd-based estimates, the total number of visible redds was counted throughout the accessible river in weekly surveys during the spawning period as conditions permitted. The redd counts were then plotted against date and the area under the resulting curve was calculated. This area was divided by estimated redd life (21 days) and then multiplied by 2.5 to account for the sex ratio (English et al., 1992; Smith and Castle, 1994). For the redd-based steelhead estimates a similar sampling approach was used, but instead of using area under the curve, redds were individually flagged to avoid double counting, and the total number of unique redds was tallied at the end of the season and multiplied by 1.8 to account for the sex ratio.

TABLE 2 Steelhead relocation from the Lower Elwha River to Indian Creek and Little River upstream of the former Lower Elwha Dam site from 2012 to 2020.

Year	Indian Creek		Little River	
	Natural	Hatchery	Natural	Hatchery
2012	11		35	
2013			53	35
2014			1	58
2015				
2016	3	32		
2017				
2018				
2019				
2020				

From 2012 through 2020, during and after dam removal, adult Chinook salmon (starting in 2012) and steelhead (starting in 2014) were enumerated using two different multi-beam SONAR units, a DIDSON-LR (0.7/1.1 MHz) and an ARIS 1800 (1.1/1.8 MHz) (http://www.soundmetrics.com/Products, Sound Metrics Corp., Bellevue, WA). Multi-beam imaging SONARs acoustically ensonify the entire width and depth of a cross section of the river, producing movie-like imagery of fish swimming through the cross section. Two SONAR units were needed because the channel split near the mouth of the Elwha River (Figure 1). The SONAR units operated from late January or early February through September. The primary enumeration site was in the East Channel (EC) while a secondary site was in the West Channel (WC), with both sites located at rkm 0.8. SONAR site selection was based on four criteria: 1) almost all fish would pass the site; 2) the location was downstream of most spawning habitat; 3) the river channel was sufficiently narrow to accommodate the effective range of the SONAR; and 4) fish movement was primarily directed upstream with little milling (i.e., back and forth swimming) in the location of the SONAR. Depending on river discharge, the WC site was between 12 and 25 m wide and 1.3 m deep in the thalweg, while the EC site was 15 to 30 m wide and 2 m deep in the thalweg. We estimated that during Chinook salmon migration approximately 80% of the flow was in the EC, while the remaining 20% was in the WC. During the winter steelhead migration, the estimated proportion of flow was 60% EC and 40% WC. We did not account for or estimate fish spawning below the SONAR site.

3.2.1 Data analysis

We sub-sampled SONAR files to count returning adults and then modeled those data to estimate total annual abundance. For Chinook salmon, 20 minutes of each hour-long file was reviewed for fish passage at each SONAR site, which is on the upper end of the range of recommended subsampling regimes (Lilja et al., 2008). Due to relatively low spawner abundance during the steelhead season, the full hour was reviewed. Several variables were noted for each fish passage event, including the date, time, direction (upstream or downstream), distance from SONAR head, and body length (mm).

The net upstream fish passage count was tabulated by subtracting downstream passage events from upstream passage events (Xie et al., 2005). The method of estimation was slightly different for winter steelhead because we had to account for downstream migrating individuals that had migrated upstream and already spawned (kelts). Hence, we did not subtract downstream moving targets for any 24-hour period that had a net total downstream passage. This adjustment strikes a balance between accounting for kelts leaving the system that were not subtracted from the total escapement estimate versus subtracting downstream passage events due to milling or spawning behavior near the SONAR site. This adjustment increased the final escapement an average of 13% in any year. We were able to calculate this percentage because the Elwha River currently has a unimodal winter steelhead run timing with spawning concentrated in late-April through May.

To sum upstream and downstream passage events in each file, we also had to establish a minimum threshold length to distinguish adult Chinook salmon and winter steelhead from other species and life stages. We used field-measured lengths of fish captured during weekly or bi-weekly in-river tangle net sampling conducted at nine different sites within 1 km of the SONAR sites over the entire course of the SONAR season. The netting also allowed us to estimate the onset and completion of the Chinook salmon and steelhead run timing, and the proportion of each species present during the period when they overlapped. The size thresholds for adult Chinook salmon and winter steelhead were 550 mm and 500 mm, respectively. The 550 mm threshold effectively excluded Chinook salmon jacks (males that return after one year in the ocean and at smaller sizes than normal adults), smaller bodied bull trout, and pink salmon. For winter steelhead, we used 500 mm as the minimum size threshold, which excluded most bull trout. We then applied those length criteria to all SONAR measured targets so only adult steelhead and Chinook salmon were included in the simulation model. The 550 mm length cutoff for Chinook salmon included ~98% of all those field-measured each year. The 500 mm cutoff included ~95% of all field-measured steelhead.

3.2.2 Chinook salmon and winter steelhead

To estimate annual abundance, we used four-step (Chinook salmon) or three-step (winter steelhead) simulation models to adjust the total counts of the raw SONAR targets. In the first step, for Chinook salmon only, we expanded the 20-minute sub-sample counts to a full-hour (Lilja et al., 2008). Second, the raw targets exceeding the species-specific size thresholds were adjusted to species using a random draw from a binomial distribution populated by the number of target species in the tangle net sampling for that week and the total number of fish sampled that week. Third, we corrected the species-specific counts to account for observer error by using a linear regression analysis between the counting technician and a more experienced counter. Lastly, we filled in data gaps resulting from periods when the SONAR was not operating in order to expand the data to account for the entire run. The simulation also provided season- and year-specific coefficients of variation. Full methods utilized in this study including SONAR installation and simulation modelling are described in Supplementary Material Appendix A.

3.3 What is the proportion of hatchery-origin adult Chinook salmon and steelhead during and after dam removal?

We evaluated carcasses of post-spawned fish for hatchery marks to estimate the proportion of hatchery-origin spawning Chinook salmon. Chinook salmon carcasses were collected via stream surveys, a channel-spanning weir deployed from 2010–2013, and from the hatchery following spawning. We examined each carcass for four different hatchery marks, including a thermal otolith mark, fin clip, CWT, and scale analysis. The primary marking strategy employed in the Elwha with a marking-rate goal of 100% was a thermal otolith mark. A subset of hatchery Chinook salmon received adipose fin clips and CWT, which allowed us to detect Elwha-origin fish in (rare) cases where thermal otolith marks were not successfully applied, or to identify hatchery-origin fish from other watersheds. Finally, we classified a small number of fish as hatchery-origin based on scale analysis that indicated they had growth patterns indicative of hatchery rearing, despite not having other marks. We compared percent hatchery-origin Chinook salmon before and after dam removal using a binomial generalized linear model.

For winter steelhead, we used an adipose clip or CWT (sometimes both could be present) to identify hatchery-origin adults. Individuals were captured during SONAR tangle netting in the Lower Elwha River supplemented by limited sampling upstream of the former dam sites during 2014–2020. However, most winter steelhead were collected within 1 km of the LEKT hatchery (~rkm 2.4). Consequently, our samples were likely biased and therefore we only used those data to illustrate spatial differences in hatchery- and natural-origin proportions from 2014–2020. In 2019, a more intensive and spatially representative effort was undertaken to produce an unbiased estimate of basin-wide and reach-specific (Lower Elwha, Middle Elwha, and Upper Elwha) hatchery and natural proportions which considered spatial and temporal differences as well as differences in catch per unit effort (CPUEs) between sites (Peters et al., 2020).

3.4 How many Chinook salmon migrants and steelhead smolts were produced during and after dam removal?

We used rotary screw traps to estimate the abundance of juvenile Chinook salmon and steelhead outmigrants. Presumably, this effort could have also included some steelhead offspring destined to become summer run steelhead. Traps were in three locations – the Lower Elwha (rkm 0.3 and 3.3 in 2014–2018 and 4.0 in 2019–2020) and one each near the mouth of Little River (rkm 0.2) and Indian Creek (rkm 0.7). We report on two trap locations – the Lower Elwha and Indian Creek (Figure 1). The main stem trap was typically installed and operable by February 15th and removed by July 26th, although annual start and end dates varied due to river conditions and safety concerns. Indian Creek was installed and operable by January 27th and was completed by September 5th.

The trap in the main stem Lower Elwha was, on average, operational 73% (~118 days) of all potential days, compared to 95% (~211 days) of all potential days in Indian Creek. During the period of active dam removal and associated sediment transport (2012–2014), large amounts of sediment and organic debris (e.g., coarse wood) transported from the former reservoirs hindered the main stem trap operations. In 2013, no results were reported due to the trap being pulled or failing due to the amount and duration of debris effects. We report hatchery release numbers as a point of comparison for the abundance of natural-origin juvenile migrants, and for estimating smolt-to-adult return rate (SAR) of hatchery Chinook salmon.

3.4.1 Field methods

Smolt traps were inspected and cleaned daily or every other day. All captured fish were removed from the trap box using dip nets and transferred to plastic buckets so that each fish could be individually examined and identified. A weekly subsample of all species caught was measured and weighed throughout the outmigration period. Most hatchery Chinook salmon (0+) were not externally marked (only otolith marked) and thus difficult to distinguish from natural-origin fish without sacrificing them. However, most natural-origin Chinook salmon (0+) tended to migrate past the trap prior to the hatchery releases in June. Trap operations during hatchery releases typically ceased for several days because it was too difficult to sample such large numbers of fish. Starting in 2019, the trap was moved upstream of the Chinook salmon hatchery and all fish were assumed to be of natural origin. While errors in the hatchery vs. natural origin designation could have added variability to the Chinook salmon (0+) estimates, any error would be small relative to the observed increase in abundance in the most recent years. Winter steelhead produced in hatcheries were all adipose fin clipped post 2013 and therefore distinguished from naturally produced fish at the trap. See Supplementary Material Appendix B for details on determining the origin of smolts.

We estimated trap catch efficiency (i.e., proportion of total outmigrants captured) using multiple mark recapture tests across the trapping season at all three trap sites. In the smaller tributaries, weekly samples of 50 to 100 fish, representative of the species migrating at any given time (i.e., Chinook salmon subyearlings or smolts, coho salmon parr or smolts), were given a distinctive mark (Bismarck Brown) and released approximately 100 m upstream of the trap site. For the main stem trap, we used small-bodied (0+) Chinook salmon or chum salmon obtained from the LEKT and Washington Department of Fish and Wildlife (WDFW) fish hatcheries; these were also given a distinctive mark (Bismarck Brown) and then released approximately 1000 m upstream to test efficiency. For the small-bodied fish, we typically attempted multiple trials between late March and late May (~6 trials/year, Standard Deviation (S.D.) ± 3 trials/year) and averaged 16 days (S.D. ± 8 days) between trials. We estimated efficiency for 1+ fish (steelhead smolts) using 0+ trials in all years, because there were only three years with efficiency trials using 1+ fish at the main stem trap. This allowed for consistency across years. For the three years with trials based on 1+ fish, we generated a second estimate to allow for comparison. The 1+ efficiencies were generated using 1+ coho salmon that were captured and marked at the Indian Creek trap and recaptured in the main stem trap (2016, 2017 and 2019) and 1+ hatchery coho salmon that were marked and released from the LEKT hatchery and recaptured at the main stem trap (2017).

3.4.2 Data analysis

We combined daily catch data with efficiency trials to estimate total annual production. To incorporate uncertainty due to periods of missing data and expansion based on trap efficiency, we applied a flexible Bayesian model. Daily passage was assumed to follow a negative binomial distribution with a mean constrained to change smoothly with time – a random walk. Catch was modeled as a binomial distribution where the probability of capture was estimated from efficiency trials. Period-specific efficiencies were assumed to be independent due to observed temporal trends in efficiency for some traps. The estimates only incorporated passage during the trap operation. Therefore, if the trap was not in place during fish passage, these fish were not included in the estimate. We summarize the results with the median and 95% credible interval for total passage. We also include the coefficient of variation (CV) and the geometric CV, which is more appropriate for skewed distributions. See Supplementary Material Appendix B (section 3) for details of the smolt data analysis.

3.5 How productive were Chinook salmon during and after dam removal?

We used a combination of in-river abundance from SONAR estimates, hatchery mark rate, and age structure to estimate productivity as the total number of adult recruits produced by each cohort of Chinook salmon that spawned naturally in the Elwha River from 2004–2015. To estimate adult recruits, we first estimated the number of naturally produced Chinook salmon by multiplying the abundance of adults returning to the river by the proportion of natural-origin adults (1 − hatchery mark rate). We calculated separate estimates of proportion hatchery-origin in the hatchery broodstock and Chinook salmon spawning naturally in the river beginning in 2013, when we began consistently obtaining a representative sample of the fish spawning in the river. Next, natural-origin adult returns were then allocated to spawning cohorts using scale-derived age data for individuals collected from 2007 to 2020 (median = 572 individuals per year, range = 216–1,104). Because we sampled so few unmarked, natural-origin Chinook salmon (≤ 50 each year), we assumed no difference in the age structure between hatchery-origin and natural-origin fish. This allowed us to increase our age structure sample size, and implicitly prioritized capturing age variation among years rather than age variation between hatchery-origin and natural-origin salmon.

We report productivity as the ratio of adult salmon returning to the river relative to the number of spawners that produced them, with a value of 1.0 indicating replacement. We provide separate productivity estimates for fish spawned at the hatchery and those that spawn naturally in the river in order to compare them. Our approach did not distinguish between natural mortality and harvest mortality. To compare survival in the marine environment between natural-origin and hatchery-origin fish, we also estimated SAR. Here, we divided the number of natural-origin salmon returning from each cohort by the corresponding juvenile abundance estimate from the smolt trap, and the number of hatchery-origin salmon returning from each cohort by the number released from the hatchery. We note that these productivity and SAR estimates encompassed the period before and a small portion during dam removal.

3.6 How were annual estimates of Chinook salmon abundance affected by streamflow and sediment impacts?

To determine if river conditions prior to, during, and following dam removal impacted production of Chinook salmon, we modeled the relationship between river discharge, sediment transport, and productivity of sub-yearling Chinook salmon (age-0 migrants/spawner) from 2011–2018. We used daily discharge data (2011–2018) from the U.S. Geological Survey (USGS) (12045500 Elwha River at McDonald bridge near Port Angeles, WA) and estimates of suspended and bedload sediment discharge (tonnes per day) (Ritchie et al., 2018) as explanatory variables. As a response variable, we divided the total number of naturally spawning Chinook salmon (total escapement estimate minus hatchery take) by the number of Chinook salmon outmigrating subyearlings to calculate yearly estimates of Chinook salmon subyearlings per spawner.

To evaluate streamflow events, we developed a flow index for stream discharge (*annual flow index*) that includes the number of days above 56.6 m^3s^{-1}, which is the estimated bankfull discharge where bedload is mobilized (Ritchie et al., 2018), between October 1st and December 31st, which is the primary incubation and emergence period for Chinook salmon (Greene et al., 2005). We then summed the number of days above 56.6 m^3s^{-1} and multiplied that by the average discharge greater than 56.6 m^3s^{-1}. This allowed us to identify the overall duration and magnitude of events that could have affected egg-to-fry survival for the period of incubation.

$$annual\ \ flow\ \ index = \sum_{d=Oct\ \ 1st}^{Jan\ \ 1}\{\#days > 56.6\ \ m^3 \cdot s^{-1} \ast ave\ \ discharge > 56.6\ \ m^3 \cdot s^{-1}\} \tag{1}$$

Equation 1 assumes that the number of days and the amount of flow over the course of the entire incubation period would have the largest impact on egg-to-fry survival, a factor that can limit overall Chinook salmon productivity (Greene et al., 2005).

We developed a sediment transport index by summing the average total amount of sediment transport (*TST*) (tonnes) during the egg incubation and emergence period (Ritchie et al., 2018). Processed data were not available after September 30, 2016, so we estimated sediment transport from October 1, 2016, to December 31, 2016, using bedload data from bedload impact sensor plates located near rkm 4.9 available from the Bureau of Reclamation (Hilldale et al., 2015; Ritchie et al., 2018.). Based on prior years, the bedload sediment sensors quantified approximately 44% of the total estimated bedload transport. In addition, the daily bedload sediment ($S_{dailybed}$) is roughly 25% of the total sediment load (S_{total}) mobilized. We used those data to estimate the overall total sediment discharge for the October 1, 2016, to December 31, 2016, period with Equation 2:

$$TST = \sum_{d=Oct\ \ 1st}^{Jan\ \ 1} S_d\,(Daily\ \ measured\ \ sediment\ \ bedload\,\frac{\frac{tonnes}{day}}{0.44})/0.25 \tag{2}$$

Our comparison of prior year estimates to measured sediment discharge produced an r^2 of 0.89.

We calculated the flow-sediment index (Equation 3) for the egg incubation period (October 1st to December 31st) as the product of 1) the sum of annual flow index and 2) the total sediment transport during the same period:

$$FlowSedIndex = annual\ \ flow\ \ index\ \ \times\ \ \ TST \tag{3}$$

After calculating the annual index values, we then fit a linear model to the relationship between the log of the flow sediment index (*FlowSedIndex*) and the log of Chinook subyearlings per spawner for each year from 2011 to 2018 (Equation 4). This is equivalent to the power law model on the un-logged scale,

$$\frac{subyearlings}{spawners} = a \ast FlowSedIndex^b \tag{4}$$

where b is the slope of the log-log relationship. We used visual inspection of the relation on the log-log scale to confirm that the assumption of linearity was appropriate and that the variance was stable across the range of values.

3.7 How far have Chinook salmon and steelhead expanded their spawning distribution?

We conducted foot surveys to count redds to determine the distribution of spawning Chinook salmon and steelhead. We use the term steelhead here because we could not determine which portion, if any, of the redds were from summer run steelhead. To estimate each species' spatial expansion, we delineated the Elwha River into three sections based on the presence of the former dams. Each individual redd was geolocated (latitude and longitude) with GPS (Garmin model GPSmap 60CSx). It is important to note that Elwha River Chinook salmon redd surveys are more readily apparent and feasibly surveyed than steelhead redd surveys in the roadless area above former Mills reservoir due to their seasonal low flow timing (i.e., late summer/early fall) compared to steelhead which spawn during higher winter and spring flows.

3.7.1 Chinook salmon redd counts

Each year in mid-September from 2012–2018, we conducted one- to five-day long peak redd counts in the main stem Elwha River, its larger floodplain channels, and several major tributaries. Survey timing was based on the estimated historical date of peak spawning activity for Elwha River Chinook salmon, approximately September 15th–September 25th. The Lower Elwha and Middle Elwha were surveyed in all years, while the Upper Elwha was surveyed in 2016–2018. Limited supplemental surveys were conducted in the Upper Elwha beginning in 2014 in the former Mills Reservoir area from the former Glines Canyon Dam (rkm 22) upstream to the entrance of Rica Canyon (rkm 25.7). Surveys did not cover major canyon areas of the Elwha River during peak surveys except for Rica Canyon in 2014 and 2015 (Duda et al., 2008; Brenkman et al., 2012). Additionally, no comprehensive surveys have occurred in larger tributaries to the Upper Elwha except Long Creek in 2018. Finally, river discharge and turbidity levels were greatest in 2012, and as a result, surveys were limited to above the Elwha Dam site where turbidity levels were much lower. In 2013, water clarity of the river improved enough to allow surveys below the former Elwha Dam, and 2014 conditions allowed for a full survey from the mouth to just above the former Glines Canyon Dam. Since 2015, turbidity has not been a factor during surveys in any reach, and during this period, we consider redd data reflective of the spatial distribution of spawning.

3.7.2 Steelhead redd counts

Between 2012 and 2018, we conducted weekly to bi-weekly redd counts from February through June or early July to determine the location and timing of adult steelhead spawning (Gallagher et al., 2007). Resident rainbow trout were the only other spring spawning salmonid and their redds were distinguished from steelhead redds based on size and substrate (McMillan et al., 2015). Most redd counts occurred in tributaries where water clarity was unaffected by dam removal and their small size allowed for surveys to safely occur. Surveys were completed in four Upper Elwha tributaries with the following percentages of potential steelhead spawning habitat surveyed: Cat Creek (100%), Long Creek (90%), Hurricane Creek (100%), and Boulder Creek (100%) and six Middle Elwha tributaries: Little River (50%), Indian Creek (25%), Griff (100%), Madison (100%), Campground (100%), and Hughes Creeks (100%). Surveys of the main stem were conducted as conditions allowed, but due to the timing of their spawning visual counts were severely limited by reduced water clarity that often made it impossible to identify and count redds. Steelhead redd data were used to document spawning in previously unavailable locations but may not accurately reflect the spatial distribution of redds due to difficulties surveying the main stem. Except for surveys in 2010 and 2013, when main stem water clarity was good (see section 3.2), we do not use steelhead redd survey data to estimate total spawners.

3.8 Has dam removal given rise to the re-emergence of different life histories that were not present, or very rare, when migration into the Elwha River headwaters was blocked?

3.8.1 Snorkel surveys

We conducted opportunistic snorkel surveys for adult Chinook salmon and adult summer steelhead in 2013 and 2016 in shorter sections of the Middle and Upper Elwha, followed by annual snorkel surveys from 2017–2020 in the Middle and Upper Elwha. The annual surveys covered most of the Middle and Upper Elwha except for canyons (see Brenkman et al., 2012). Snorkel counts were conducted in early- to mid-September to ensure the majority of adult summer steelhead had entered freshwater. Once in the water, divers moved downstream and would enumerate fish in each habitat unit and then relay those numbers to a bank recorder. Generally, the process consisted of two divers swimming downstream side-by-side, with some up river reaches covered with a single diver. Summer steelhead were distinguished from resident rainbow trout by their larger size, silvery coloration, presence of a strong sea line, and few spots below the lateral line. Divers also classified each adult steelhead as hatchery, wild, or unknown, depending on the presence of an adipose fin. For more details on the snorkel survey methods please refer to Brenkman et al. (2012) and Duda et al. (2021). We only surveyed a portion of the watershed therefore our resulting counts represent a lower bound on total abundance.

4 Results

4.1 What is the annual abundance of returning adult Chinook salmon and winter steelhead during and after dam removal?

Prior to dam removal (1986–2010), expanded redd count data showed an average annual return ± 1 SD of 2,827 (± 1,778) adult Chinook salmon in the Elwha River (Figure 2A). During (2011–2014) and following (2015–2020) dam removal, SONAR data showed average annual returns of 3,444 (± 1,125) and 4,734 (± 2,409) Chinook salmon respectively. We estimated the average number of naturally spawning Chinook salmon before, during, and after dam removal as 1,393 (± 1,218), 1,930 (± 747), and 3,523 fish (± 1,949), respectively (Figure 2A). The proportion of total returning adult Chinook salmon taken for hatchery breeding purposes before dam removal was 53% (± 15%), compared to 45% (± 6%) during dam removal and 31% (± 8%) following dam removal. Based on SONAR, the estimated number of returning adult winter steelhead to the Elwha River from 2014 to 2020 ranged between 890 and 1,985 fish (average 1,400 ± 350) (Figure 2B). Starting in 2016, the population has been increasing at approximately 10% annually except for a 10% decrease in 2019 (Figure 2B).

4.2 How many Chinook salmon migrants and steelhead smolts were produced during and after dam removal?

The number of subyearling and yearling Chinook salmon released from the hatchery prior to dam removal averaged 2,596,545 (± 801,861), which was higher than the 1,953,609 (± 808,897) released during and after dam removal. The number of natural-origin subyearling Chinook salmon from the Elwha River averaged 43,828 (± 47,932), 46,973 (± 39,798), and 323,764 (± 407,976), before, during, and after dam removal, respectively (Figure 3A). A dramatic increase in the estimated number of natural-origin subyearling Chinook salmon occurred when over 500,000 and almost 1 million subyearlings were produced in 2019 and 2020 (Figure 3A), respectively. The estimates for 2016, 2017, and 2020 yearlings were one to two orders of magnitude less than the subyearlings, the only years when trap efficiency was sufficient to allow estimates of yearling outmigrants (Table 3).

The average hatchery releases of steelhead smolts during and after dam removal was approximately 122,596 (± 53,514) fish. The

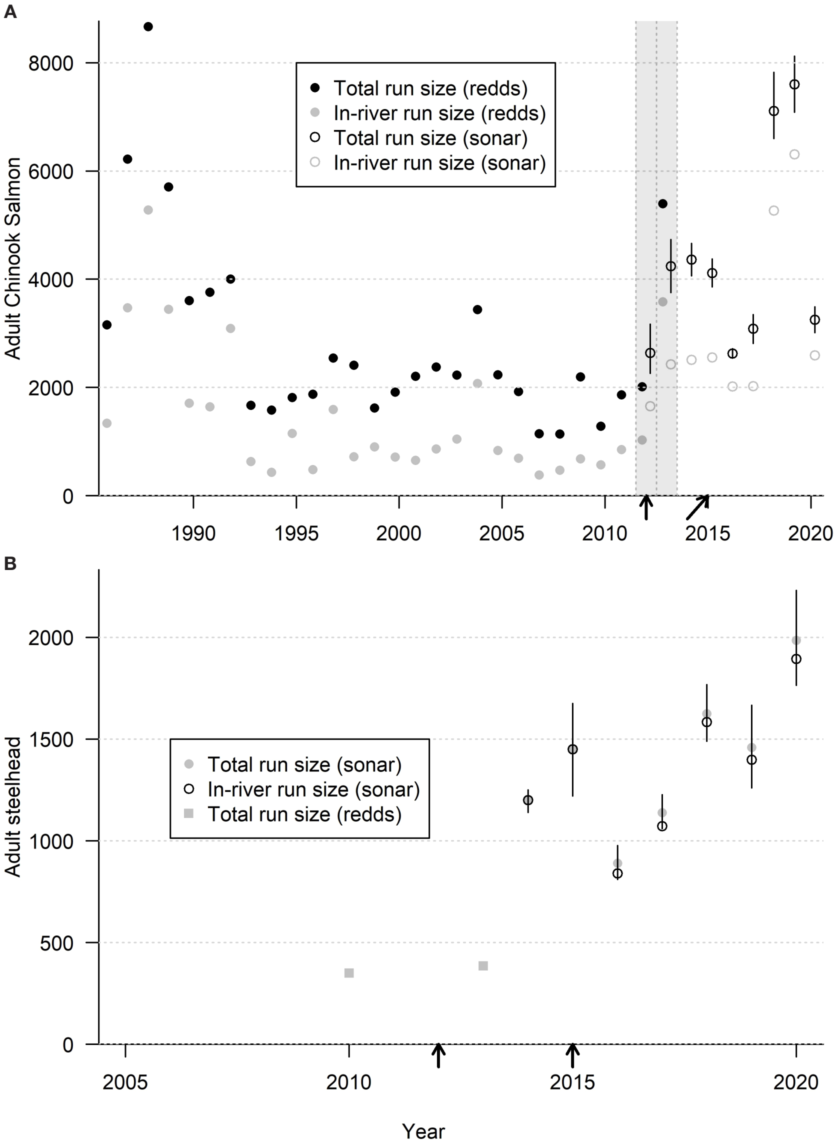

FIGURE 2
Interannual trends in abundance of **(A)** adult Chinook salmon and **(B)** adult steelhead in the Elwha River before, during, and after dam removal based on redd surveys and SONAR. Shaded areas denote estimates of Chinook salmon during years of simultaneous redd surveys and SONAR. Dark solid lines denote 95% confidence intervals. Arrows (straight and angled) denote the removal of the Elwha and Glines Canyon dams and associated rockfall blockages in Glines Canyon. Removals for hatchery broodstock account for the difference between total run size and in-river run size.

average annual estimate of natural-origin steelhead smolts during and after dam removal was 8,884 (± 5,380), but unlike Chinook salmon they did not display the same large increase in natural production in 2019 and 2020 (Figure 3B). Between 2013 and 2020, outmigrating subyearling Chinook salmon from Indian Creek, a tributary located at rkm 12.1 not impacted by the sediment supply changes from the dam removal, ranged between 1,188 and 129,759 and averaged 53,396. Between 2013 and 2020, the annual average number of steelhead smolts from Indian Creek was 1,523 fish with a low of 146 in 2014 and a high of 2,550 in 2019.

4.3 What is the proportion of hatchery-origin adult Chinook salmon and steelhead during and after dam removal?

Across return years 2009–2020, the median proportion of hatchery-origin returning adult Chinook salmon from all collection sources was 95.9% (range = 92.0–98.0%, Figure 4A). In 2016–2020, when some returning salmon might have been produced from parents that spawned upstream of the Elwha Dam site, the proportion of hatchery-origin Chinook salmon was not

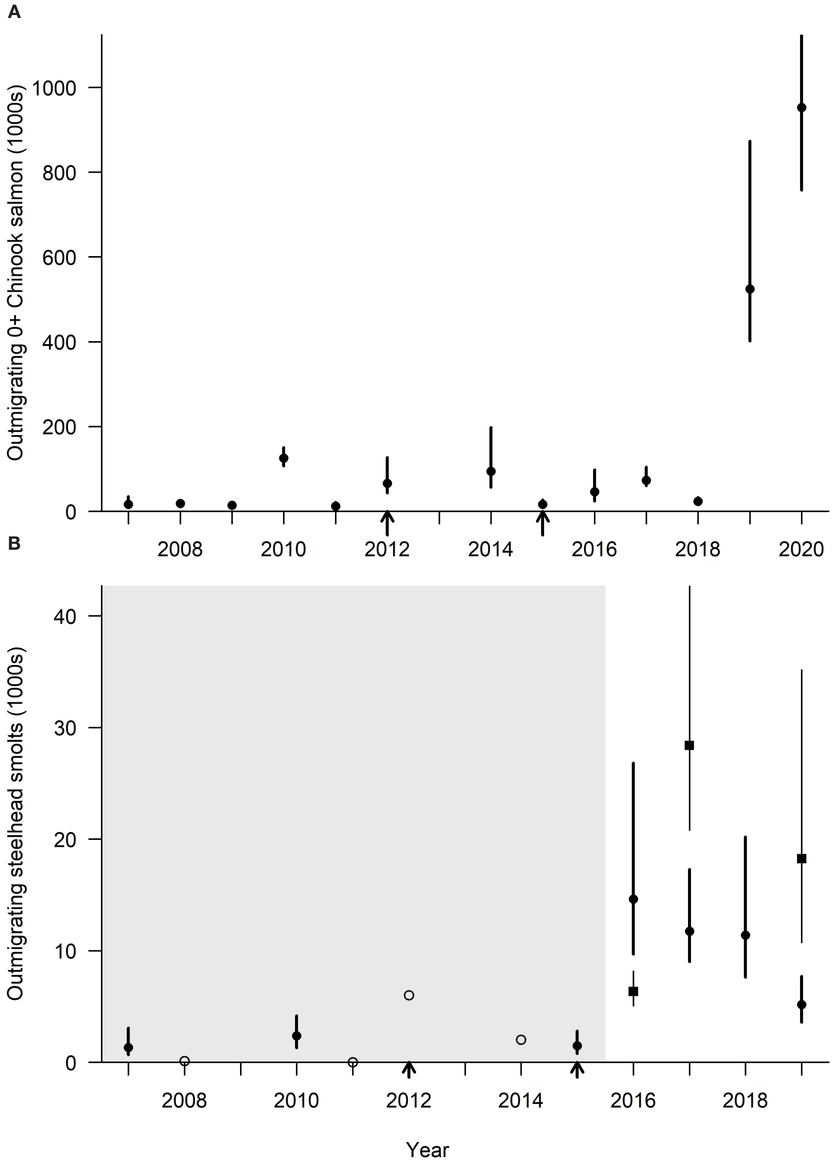

FIGURE 3
Interannual trends in abundance of outmigrating natural-origin subyearling juvenile Chinook salmon and natural-origin steelhead smolts from 2008 to 2020 in the Elwha River. **(A)** Outmigrating subyearling juvenile Chinook salmon estimated at the screw trap in the main stem Elwha River (rkm 0.3 and 3.3 in 2014–2018 and 4.0 in 2019–2020). The filled circles and vertical bars represent the median estimate and 95% credible interval. Arrows denote the removal of the Elwha and Glines Canyon dams and associated rockfall blockages in Glines Canyon. **(B)** Steelhead smolts estimated at the main stem screw trap (rkm 0.3 and 3.3 in 2014–2018 and 4.0 in 2019–2020). The open circles without credible intervals represent years in which the catch was less than 10. The black filled rectangles represent the separate estimates based on the independent large-bodied fish efficiency estimates. The gray region represents years in which the outmigrant estimates are believed to be under-estimated due to expansions based on 0+ salmon for this period.

TABLE 3 Elwha River smolt trap catch data and abundance estimates for yearling Chinook salmon from 2014 to 2020.

Year	Raw catch	Trap efficiency	Abundance estimate
2014	71	NA	NA
2015	25	NA	NA
2016	86	0.076	1374 (960–3672)
2017	47	0.134	593 (389–1098)
2018	21	NA	NA
2019	4	NA	NA
2020	142	0.023	4301 (4031–7248)

Efficiency estimates for 1+ Chinook salmon were only available in some years.

significantly different from 2009–2015, based on a binomial general linear model (p > 0.10, Figure 4A). However, restricting the analysis to only Chinook salmon spawning naturally in the Elwha River yielded a slightly lower proportion hatchery-origin in 2016–2020 (median = 93.8%) compared to 2009–2015 (median = 95.5%, glm $p< 0.05$). The proportion of hatchery winter steelhead caught during sampling from 2014–2018 was 0.85, but 0.54 in 2019 (Table 4). However, the proportion of hatchery winter steelhead caught upstream of former Elwha Dam was lower than that downstream of the dam during both periods (Table 4).

4.4 How productive were Chinook salmon during and after dam removal?

Estimates of naturally spawning Chinook salmon productivity (adult to adult) from 2004–2015 were ≤ 0.40 in all years and ≤ 0.20 in eight of 12 years, which is below the 1.0 replacement value (Figure 4B). Adult-to-adult productivity of Chinook salmon spawned in the hatchery was greater than that of naturally spawning salmon in all years, exceeding replacement in nine of 12 years (Figure 4B). However, SAR of natural-origin Chinook salmon was consistently greater than hatchery-origin Chinook salmon in the Elwha River (Figure 4C). Median SAR increased from the period prior to dam removal (brood years 2005–2010) to the period during dam removal (brood years 2011–2015), for both hatchery-origin (before = 0.13%; during = 0.19%) and natural-origin (before = 0.26%; during = 0.75%) Chinook salmon. However, the SAR were highly variable and one of the lowest values for both hatchery- and natural-origin Chinook salmon was observed during dam removal (Figure 4C).

4.5 How were annual estimates of Chinook salmon abundance affected by streamflow and sediment impacts?

Plotting values of subyearling Chinook salmon migrants per spawner against the flow-sediment index between 2011 and 2018 suggests an inverse relationship (Figure 5). This was supported by an estimated negative slope for the log-log linear fit ($b = -0.44$, 95%CI [−0.67,−0.20], $R^2 = 0.78$). During and after dam removal, the years 2014, 2015, and 2017 had the highest flow-sediment index, and the lowest estimated Chinook salmon freshwater productivity (Figure 5).

4.6 How far have Chinook salmon and steelhead expanded their spawning distribution?

Although the spatial extent of our Chinook salmon redd counts varied and was limited in the main stem Elwha due to poor visibility, our surveys were able to document several patterns. First, we observed adult Chinook salmon in the Middle Elwha immediately after removal of the Elwha Dam (rkm 7.9) in April of 2012. Second, following that initial observation, from 2012–2018 the density of Chinook salmon redds in the Middle Elwha was similar or greater than the densities in the Lower Elwha (Figure 6). Third, following removal of the rockfall blockage in 2015 and 2016, Chinook salmon redds have been consistently observed above the former Glines Canyon Dam (rkm 22), with the former Lake Mills Reservoir (rkm 22–25) being the most intensively used spawning area in the Upper Elwha. Fourth, as a result of the expanding spatial distribution, the overall extent of redds (difference between furthest upstream and downstream) has ranged between 45 and 55 km upstream.

Although based on surveys in tributaries rather than the main stem (due to poor visibility), we observed a similar pattern for steelhead redds. For example, following removal of the former Elwha Dam in 2011, spawning winter steelhead were immediately observed in two tributaries – Little River and Indian Creek – to the Middle Elwha that were unaffected by sediment from dam removal. Since that time, numerous steelhead have moved into and spawned in Little River, which contained the greatest cumulative number of redds among all tributaries for all years from 2012–2018 (Figure 7). Indian Creek, located immediately west of Little River, has also consistently supported spawning winter steelhead. Since 2014/2015, Hughes Creek, another tributary to the Middle Elwha, has been used by spawning steelhead and has supported the highest annual number of redds among tributaries in some of those years (Figure 7). Like Chinook salmon, once the rockfall blockage in Glines Canyon was removed, steelhead were immediately observed spawning in tributaries draining areas upstream of the former Glines Canyon Dam, with Boulder Creek generally containing the greatest number of redds (Figure 7). Overall, for Chinook salmon and steelhead, the spatial distribution of redds shifted from the Lower Elwha prior to dam removal to the Middle Elwha during and after dam removal.

4.7 Has dam removal given rise to the re-emergence of different life histories that were not present, or very rare, when migration into the Elwha River headwaters was blocked?

Adult summer steelhead were first observed by snorkelers in 2013 (one adult) and 2016 (six adults) during two relatively short surveys of the Lower and Middle Elwha (rkm 5–18). Once surveys were expanded

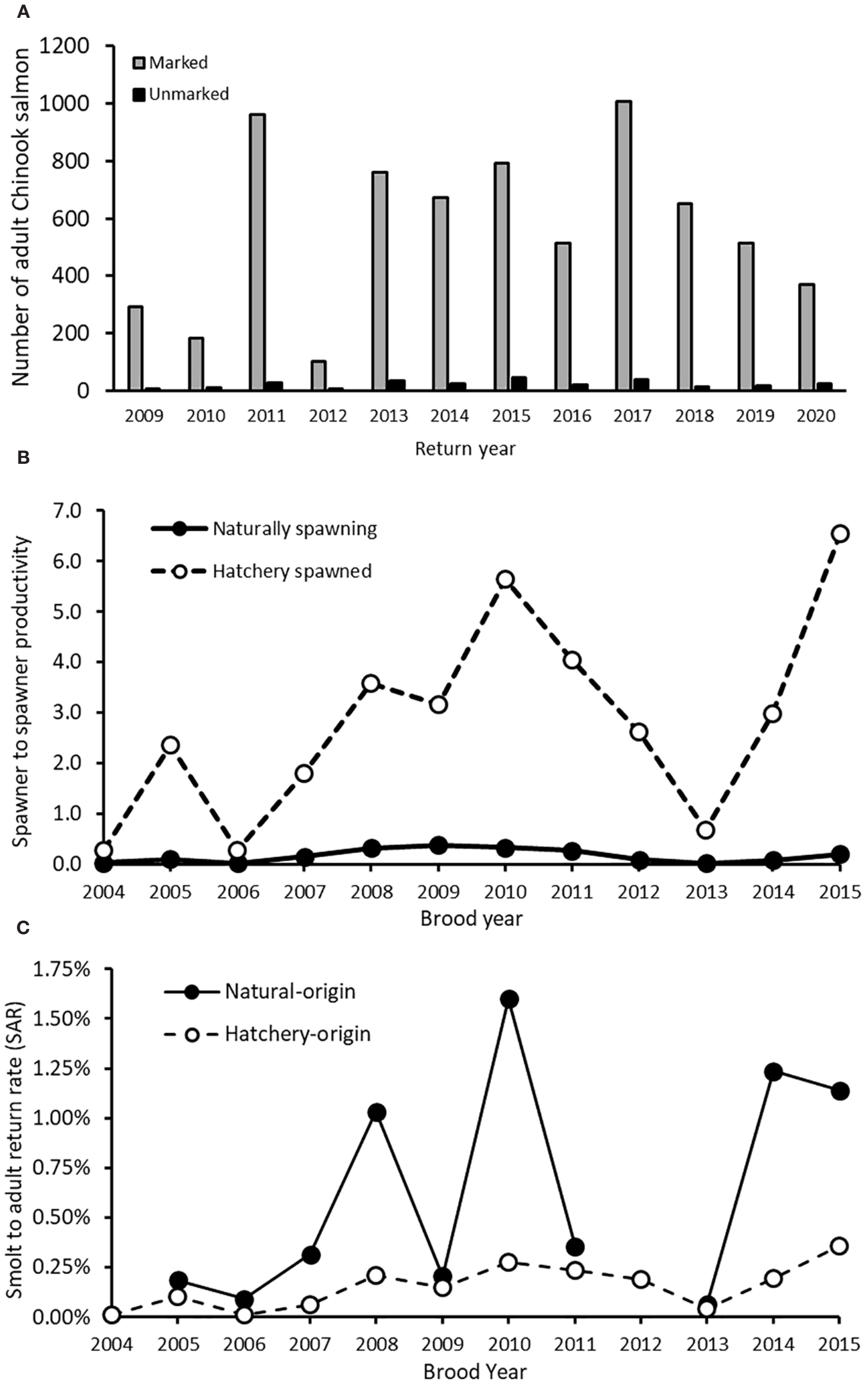

FIGURE 4
Elwha River Chinook salmon natural- and hatchery-origin metrics. **(A)** Number of hatchery marked and unmarked adults, **(B)** spawner-to-spawner productivity, and **(C)** Smolt-to-adult return rate (SAR) estimates for Elwha River Chinook salmon. In **(C)**, for each brood year (BY), hatchery-origin juveniles include subyearling (BY + 1) and yearling (BY + 2) releases.

to systematically cover the same length of habitat each year, the number of adult summer steelhead observed during snorkel surveys in the Middle and Upper Elwha ranged between 74 and 318 between 2017 and 2020 (Table 5). The number of steelhead increased from 2017–2019, and then declined in 2020. Less than 1% of the summer steelhead counted via snorkel survey in the Middle and Upper Elwha were identified as hatchery steelhead via a clipped adipose fin.

5 Discussion

Dam removal can help recover and increase the abundance, productivity, spatial distribution, and diversity of imperiled populations of anadromous salmonids by restoring access to formerly productive habitats. However, removal of large dams is a relatively new conservation action and consequently, data on the

TABLE 4 Numbers and proportion of natural and hatchery origin adult winter steelhead observed during sampling in the Elwha River with 95% credible intervals from 2014 to 2019.

Years	River section	Hatchery origin	Natural origin	Proportion hatchery origin
2014–2018	Downstream of Elwha Dam	235	42	0.85 (0.80, 0.89)
2014–2018	Upstream of Elwha Dam	6	18	0.25 (0.12, 0.45)
2019	Downstream of Elwha Dam	40	34	0.54 (0.45, 0.65)
2019	Upstream of Elwha Dam	0	24	0.00 (0.00, 0.14)

We calculated Bayesian 95% credible intervals for the proportion of hatchery origin adult steelhead by assuming a binomial distribution and using a beta prior with α=β=1.

potential benefits are scarce. We used multiple lines of evidence over an approximately 10-year period (2011–2020) to evaluate the short-term responses of Chinook salmon and steelhead to the removal of two large dams in the Elwha River. We found several results that are important to fish populations on the Elwha, as well as to future dam removal actions scheduled in other watersheds. First, estimates from spawning surveys or redd counts prior to dam removal and SONAR during and after dam removal indicate the number of returning Chinook salmon and winter steelhead has improved since the dams were removed. This was driven by increased SAR of hatchery Chinook salmon and increased abundance of hatchery- and natural-origin winter steelhead. Second, smolt trap data showed that the number of subyearling Chinook salmon migrants and steelhead smolts has also increased since dam removal. The increased production of natural-origin subyearling migrant Chinook salmon appears related to improved river conditions in recent years, based on a strong negative relationship between dam-removal induced sediment impacts (i.e., our flow-sediment index) and the abundance of natural-origin subyearling migrants during and immediately following dam removal when conditions in the main stem Elwha River were unfavorable for survival. Third, redd counts indicate the spatial distribution of spawning Chinook salmon and steelhead has expanded – including above both former dam sites – after dam removal. Last, snorkel surveys revealed the initial re-establishment of summer run steelhead, a life history that was only rarely observed in the years leading up to dam deconstruction (Duda et al., 2021). The combined results suggest dam removal and the associated management actions has already improved viable salmon population parameters for two ESA-listed species in the short term, and recent increases in productivity associated with stabilization of the main stem Elwha River below the dams offer hope for continued rebuilding of natural-origin populations over the long term.

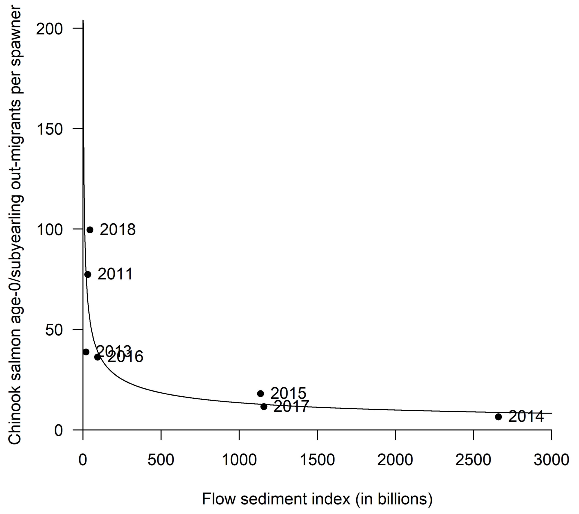

FIGURE 5
The relationship between the sum of the discharge of the number of days where flow is above bankfull discharge (56.6 cms) multiplied by the total sediment volume (tonnes) during incubation (September to December) vs. the number of subyearling juvenile Chinook salmon per spawner – 2011 to 2018.

5.1 Responses of Chinook salmon and winter steelhead to dam removal

One of the primary goals of dam removal was to increase the long-term abundance and resilience of natural-origin Chinook salmon and winter steelhead in the Elwha River, both of which were highly depleted and protected under the ESA (Brenkman et al., 2008; Pess et al., 2008; Ward et al., 2008). The rate of dam removal was designed to be fast enough to affect only up to four brood years of salmonids, but slow enough that erosion and redistribution of the sediment stored in the former reservoirs would keep pace with dam removal and maintain conditions suitable to meet municipal water needs (Randle et al., 2015). Nonetheless, there was a great deal of uncertainty about how salmonids would respond because of the magnitude and rate of reservoir sediment erosion associated with dam removal.

We found the abundance of returning adult Chinook salmon generally increased, rather than declined, since the dams were removed, including some of the largest returns in the past several decades. However, the Chinook salmon population is demographically dominated by hatchery-origin fish (≥ 92% in all years, Figure 4A), and natural reproduction is well below replacement (Figure 4B). Nonetheless, the distribution of spawning adults has expanded into newly opened habitats, which is a common result of barrier removals (Kiffney et al., 2009; Pess et al., 2014; Anderson et al., 2015). Chinook salmon population stray rates range from less than 5% to up to 34%, averaging ~15% (Westley et al., 2013; Keefer and Caudill, 2014; Pearsons and O'Connor, 2020), so some of the initial occupiers may have originated from other river systems. Based on CWT information

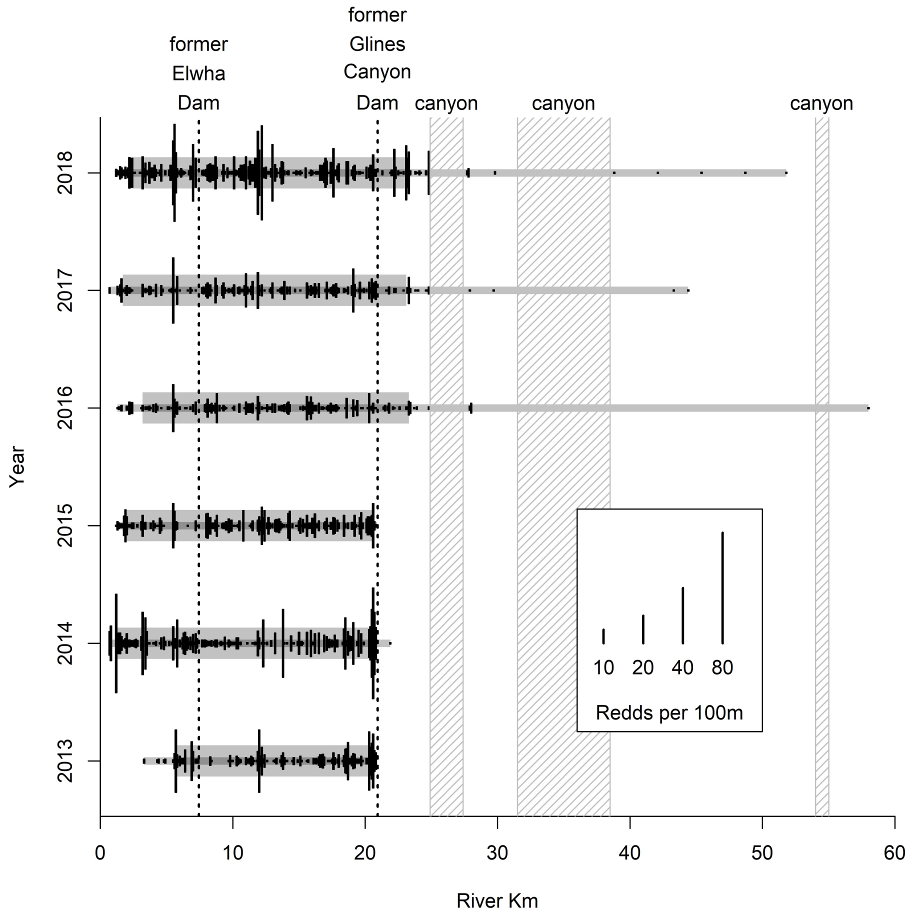

FIGURE 6
Number of Chinook salmon redds observed downstream, in-between, and upstream of former dam sites in the Elwha River from 2013 to 2018. Solid black lines denote Chinook salmon redd densities/100 m. Narrow grey lines denote the total extent of Chinook salmon redd distribution. Thicker grey line denotes the central 90% of Chinook salmon redd distribution.

from the Elwha approximately 8.5% (23 out of 275) of the fish collected in 2017 were from nearby streams (Weinheimer et al., 2018). Regardless, our results indicate most Chinook salmon are hatchery-origin and that adult abundance fluctuations during and after dam removal are, in large part, due to hatchery production and survival of hatchery-reared juveniles.

Returns of winter steelhead have also increased since dam removal, from hundreds of fish in 2013 to almost 2,000 adults in 2020. Hatchery-origin steelhead derived from native Elwha River broodstock have significantly contributed to the overall increased abundance of winter steelhead, and they are particularly common in the Lower Elwha. Our observations of adults in the Middle and Upper Elwha suggest that expansion of the spatial distribution of winter steelhead is largely being driven by natural-origin fish. Although we did not genetically determine the origin of returning adults in this study, stray rates for steelhead range from less than 5% to 14% (Keefer and Caudill, 2014; Pess et al., 2014; Pearsons and O'Connor, 2020), though winter steelhead recipient stray rates are typically greater than donor stray rates (~29%) (Pearsons and O'Connor, 2020). However, a large contribution from strays seems unlikely, considering the immediately adjacent watersheds contain only small populations of steelhead and other, larger populations in Puget Sound overall are greatly depleted, with most having fewer returning adults than we documented in the Elwha River (Cram et al., 2018).

The limited spatial, numerical and life-history expansion of Chinook salmon compared to steelhead could be partly related to sediment impacts associated with differences in the temporal and spatial distribution of spawning adults and their associated redds. Although Chinook salmon and steelhead have moved upstream of both dams, most Chinook salmon spawn in the fall in the main stem Elwha River between or below the former dam sites. Sediment concentrations in those sections was consistently high during the Chinook salmon egg-to-fry incubation period from October through December of 2012–2015, due to the considerable increase in sediment supply mobilized via dam removal (Ritchie et al., 2018). Sediment transported from the former Mills Reservoir aggraded the streambed in the Middle Elwha by over 1.0 m and the Lower Elwha by 0.5 m after October of 2012 (Ritchie et al., 2018). High stream flow events in 2014 and 2015 created further aggradation and degradation (+/− 0.3 m), and as a result, over 3 Mt and 1.5 Mt of sediment was mobilized in 2014 and 2015, respectively (Ritchie et al., 2018).

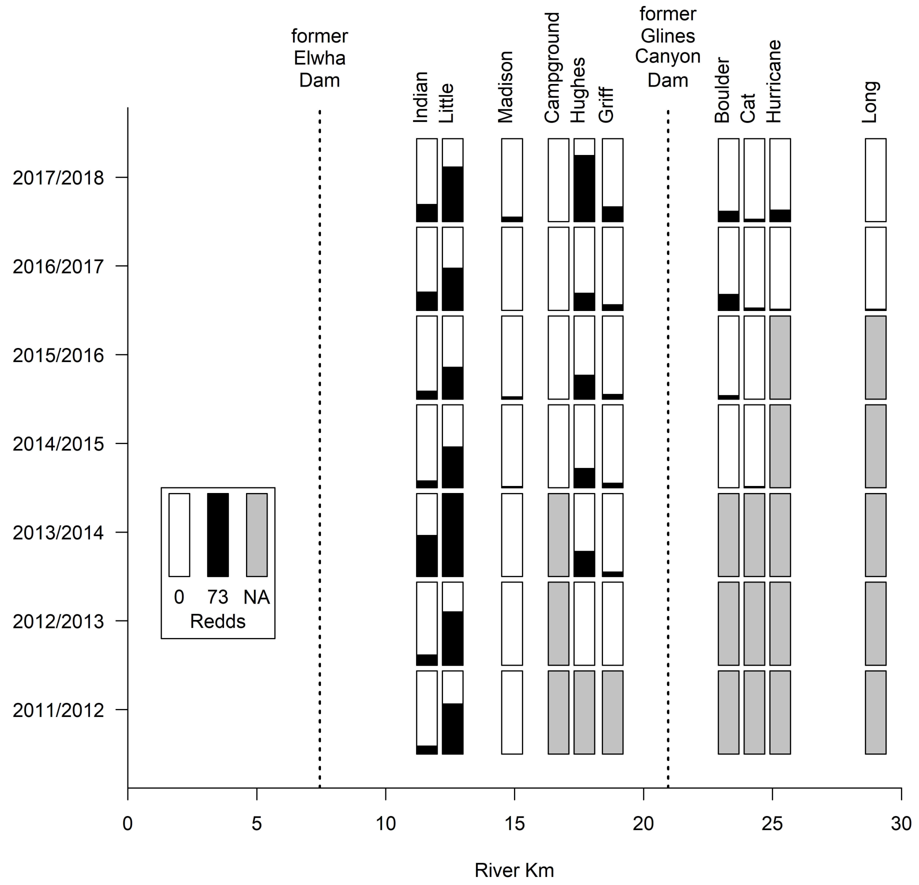

FIGURE 7
The number of steelhead redds in surveyed tributaries in the Middle and Upper Elwha River from 2011 to 2018. "NA" indicates no survey conducted. The black filled bars indicate the relative number of steelhead redds to the total maximum steelhead redds counted during this time period (73 in Little River in 2013/2014).

Our model using annual flow-sediment index suggests the natural production of subyearling Chinook salmon migrants was strongly negatively impacted in years with high streamflow and sediment loads. Salmon survival during egg incubation and through emergence partly depends on egg burial depths exceeding the depth of streambed scour during the incubation period (Montgomery et al., 1996; DeVries, 1997). Salmonid egg burial depths can range from 0.03 m to 0.5 m depending upon the species, size of the female, substrate size, and other factors (DeVries, 1997). During and immediately following the dam removal years, aggradation and degradation in the main stem Middle and Lower Elwha River approached or exceeded these egg burial depths. We hypothesize streambed scour and fill associated with changes in sediment initially impacted egg-to-fry survival of naturally spawning Chinook salmon.

We did not see a similar pattern for natural steelhead smolt production. Although winter steelhead also spawned in the main stem, they did so in spring. The later spawn timing means their eggs and emergent juveniles, unlike Chinook salmon, were not exposed to peak flow events that occurred in fall and winter. Additionally, steelhead have also more frequently spawned in habitats that were not directly impacted by increased sediment, such as tributaries like Little River and Hughes Creek and the main stem Middle and Upper Elwha. Therefore, the timing and location of steelhead

TABLE 5 Number of adult summer steelhead observed upstream of former dam sites in the Elwha River from 2017 to 2020 based on snorkel surveys.

Year	Rkm location	Total rkm surveyed	Snorkel survey month	Adult summer steelhead observed
2017	35.0–58.0	23	September	74
2018	35.0–58.0	23	September	216
2019	35.0–58.0	23	September	318
2020	35.0–58.0	23	September	92

Less than 1% of all steelhead counted were identified as hatchery steelhead.

spawning and emergence likely reduced their vulnerability to potential sediment impacts from dam removal. Accordingly, as annual sediment loads stabilize to background levels (Ritchie et al., 2018), and conditions in the main stem become more favorable for spawning and egg incubation, we predict that the productivity of naturally spawning Chinook salmon will increase and become more similar to what we observed in 2018 and 2019.

Other factors may also have shaped the early response of natural-origin Chinook salmon and steelhead. Differences between the hatcheries, the status of each population prior to dam removal, and the presence of resident *O. mykiss* life histories between and above the dams may have contributed to the observed patterns. Major dam removal projects present tradeoffs, such as whether to use hatcheries or rely on natural-origin fish for reintroduction (Anderson et al., 2014). Hatcheries on the Elwha River were used to reduce the risk of population extinction during a period of heightened environmental impacts (largely from sediment) immediately following dam removal and to increase the abundance of Chinook salmon and steelhead populations (Ward et al., 2008; Peters et al., 2014). The original start time of Elwha hatchery operations varies with each species. The Elwha River Chinook salmon hatchery program was initiated in 1930 (Brannon and Hershberger, 1984) and almost all Chinook salmon production before dam removal was due to hatchery production. Thus, considering the long duration of Chinook salmon hatchery production, the associated potential risk of domestication selection for traits advantageous to the hatchery environment, and loss of fitness in the wild (Pess et al., 2014; Araki et al., 2008), are greater for Chinook salmon than steelhead in the Elwha. Some level of re-adaptation to the natural environment may be necessary for Chinook salmon to achieve sustained natural population growth and meet demographic thresholds linked to recovery (NMFS, 2012; Peters et al., 2014). Under this hypothesis, the naturally spawning population must have a level of reproductive isolation from the hatchery to observe any such readaptation, and reduced hatchery production could help achieve this goal. Whether the population retains suitable genetic material for re-wilding and the degree of reproductive isolation needed to achieve it are open questions.

Elwha steelhead had a much different hatchery history than Chinook salmon. Steelhead hatchery stocks released into the Elwha prior to 2011 were intended to be segregated from, rather than integrated with, the wild steelhead population in the Elwha River (*sensu* Mobrand et al., 2005). When these releases were terminated, a small but resilient population of wild steelhead remained more than 100 years after Elwha Dam was constructed. Beginning in 2011, releases from a new hatchery program derived from native Elwha steelhead was designed to increase abundance of fish harboring native genetic diversity using captive brood techniques (NMFS, 2012). Thus, the current steelhead program has a much shorter history than the Chinook salmon hatchery program.

The origin of the Chinook salmon and steelhead may also have affected the spatial distribution of spawning adults, which has implications for reintroduction success because it can influence productivity, habitat use and overall viability (Pess et al., 2012). For instance, hatchery Chinook salmon (Hoffnagle et al., 2008) and steelhead (Hayes et al., 2004; Feeken et al., 2019) may disproportionally return to areas near their release sites, resulting in a more downstream distribution compared to natural-origin fish (Hughes and Murdoch, 2017). These hatchery-influenced patterns are presumably related to the strong homing ability displayed by salmonids (Quinn, 1993). Thus, homing may help explain, in part, why the distribution of Chinook salmon and their redds was skewed towards the Lower and Middle Elwha, and why hatchery-origin winter steelhead were more common in the Lower Elwha, while natural-origin steelhead seem to be driving spatial expansion into the Middle and Upper Elwha. This behavioral tendency could limit access to lesser used, but higher quality habitats further upstream that were not impacted by dam removal. For example, the estimated numbers of recruits per spawner were two times greater for spawning pink salmon in the Fraser River above the former Hell's Gate rockfall than below it during the peak time of reintroduction (Pess et al., 2014). Therefore, population productivity and growth rates of natural-origin Chinook salmon may also partly depend on their ability to expand their spatial distribution into habitats where they would have less competition and better conditions for spawning and egg incubation.

5.2 Re-emergence of summer run steelhead into headwaters of Elwha River

Finally, the response of steelhead, particularly the re-emergence of a summer run, has likely benefited from the abundant population of native resident rainbow trout present upstream of the former dams. Resident rainbow trout can produce anadromous offspring (Kendall et al., 2014) and represent a source of anadromous individuals, particularly when anadromous adult abundances are low (Losee et al., 2020). Populations isolated above barriers often retain both the genetic (Clemento et al., 2008) and physiological (Holecek et al., 2012) traits of anadromy. Residents can also mate with (McMillan et al., 2007) and contribute genes to their anadromous counterparts (Christie et al., 2011). Resident rainbow trout upstream of Glines Canyon Dam were producing migrants that were seawater tolerant and apparently capable of an anadromous life history as late as the early 1990's (Hiss and Wunderlich, 1994). It thus appears dam removal not only opened up additional freshwater habitat for anadromous steelhead, but also provided access to the ocean and potential interbreeding between steelhead and resident trout, both of which can increase the number of breeders and genetic variation within a reconnected population (Weigel, 2013).

Increased life history diversity was a predicted response to the removal of the Elwha River dams (Brenkman et al., 2008; Pess et al., 2008). Adaptive management guidelines explicitly recognized the importance of life history diversification to the recovery of Chinook salmon and steelhead in the basin (Peters et al., 2014). Although spring Chinook salmon and summer steelhead life history types historically occurred in the Elwha River before the dams were constructed, thus far only summer steelhead have re-emerged after dam removal. Summer steelhead were rarely seen prior to dam removal (Duda et al., 2021), but rapidly increased their observed numbers from 2017 to 2020 (Table 5). This is likely due to reconnection with the favorable cold-water temperature regime and alternating canyon and floodplain geomorphology of the

Elwha River basin upstream of the dams (Beechie et al., 2006; Brenkman et al., 2008; Pess et al., 2008). Additionally, there have not been any releases of hatchery summer steelhead during or after dam removal, with preliminary genetic analyses indicating that the summer run fish harbor alleles for early run timing and a large portion of the resident rainbow trout above the former dams harbor those alleles as well (Fraik et al., 2021). A similar response of increased anadromy, in addition to larger body size, was documented in Elwha River bull trout, which were common between and above the dams prior to removal (Brenkman et al., 2019; Duda et al., 2021). The "reawakening" of the summer steelhead life history strategy and increased abundance and condition of bull trout in the Elwha River further suggests salmonids can retain the ability to express anadromy after decades of isolation from the sea and highlights how species with sources of resident fish can respond to re-connectivity of a watershed (Thrower et al., 2004).

5.3 Implications for other dam removal projects

The management and monitoring of how salmonids respond to dam removal in the Elwha River has several implications for future dam removal projects. First, sediment impacts and large-scale changes to the river can occur from dam removal during and immediately following deconstruction (Ritchie et al., 2018). Given substantial sediment impacts from dam removal, reduced invertebrate prey availability for salmon can force them to temporarily adjust their foraging and diets (Morley et al., 2020). Although impacted sections of river can become productive for salmon relatively quickly, depending on discharge and sediment transport, species that most heavily rely on habitats impacted by dam removal, such as Chinook salmon in the main stem Elwha River, will likely struggle to maintain natural production until sediment levels return to a more natural level and regime.

Second, hatchery production was important for Chinook salmon and steelhead to persist through the most disruptive phase of dam removal. However, reintroduction into upstream areas has included hatchery, transplantation, and natural approaches. Chinook salmon, for example, have been almost entirely reliant on releases of large numbers of hatchery smolts. Reintroduction for other species, such as coho salmon, was jumpstarted by temporary relocation of hatchery adults to two tributaries to the Middle Elwha during the highest sediment impact periods before natural spawning started to occur, as well as consistent coho salmon hatchery production post dam removal (Liermann et al., 2017; Denton et al., 2022). Hatchery production was not used for bull trout (Quinn et al., 2017; Brenkman et al., 2019), Pacific lamprey (Hess et al., 2021), or summer steelhead (Fraik et al., 2021). These studies of other species, in combination with our results, suggest hatchery production may be particularly beneficial for species with an extensive history of hatchery operation that also are expected to rely heavily on the most impacted habitats. However, hatchery production may not be as needed for species with a long history of natural production, resident life histories, and the ability to access and spawn in unimpacted habitats.

Third, attempts to re-establish self-sustaining populations through barrier removals may be assisted by reducing or eliminating harvest. A fishing moratorium was enacted in the Elwha River watershed to protect fish and reduce the risk of extinction during dam removal and help to increase immediate abundance (Pess et al., 2012; Anderson et al., 2014; Bellmore et al., 2019). There was no commercial or recreational in-river Elwha River Chinook salmon fishery for decades prior to dam removal. There was a steelhead recreational and commercial fishery that varied in season length over the years up until 2012. Terminal harvest of Chinook salmon varies substantially across Puget Sound as a whole, but some populations experienced rates up to approximately 30% (PSIT and WDFW, 2022); avoiding this level of terminal harvest mortality has resulted in thousands of additional Chinook salmon spawners, equivalent to approximately an additional year of adult Chinook salmon returns following dam removal. Similarly, using the average steelhead harvest rate in Puget Sound for the same period of 7% (S.D. 6%) (Cram et al., 2018), would result in an additional 493 (+/−35) additional spawners in the Elwha since 2011. A similar approach of fishing closures may benefit susceptible species and stocks in watersheds where survival maybe dramatically impacted by dam removal.

Last, large dam removal can be disruptive, rendering many traditional monitoring approaches unviable, particularly in larger watersheds with multiple species of interest. High turbidity levels for extended periods of time forced a shift from redd counts to SONAR, which allowed annual estimates of Chinook salmon and steelhead abundance and associated run timing. Foot and boat surveys during peak spawning allowed us to continue tracking the spatial distribution of spawning adults in areas and years where river conditions allowed. Smolt trapping was also impacted by changes to the river throughout the study period (but in particular during and after dam removal) requiring adjustments to the mainstem trap location and operations. Together these adaptations to fish sampling approaches allowed us to capture important aspects of reintroduction that otherwise would not have been possible.

5.4 Conclusions

Fish reintroduction in larger watersheds can take up to 20 years or more (DOI, 1996; Milner et al., 2008; Pess et al., 2012), while smaller watersheds can establish self-sustaining salmon populations in five years or less (Bryant et al., 1999; Glen, 2002). It is too early to conclude that recovery of Chinook salmon and steelhead populations due to dam removal in the Elwha River has been successful. Nonetheless, in the short period since dam removal we observed several promising results, ranging from increased abundance and spatial distribution to the re-emergence of a unique life history, and were able to evaluate the effects of streamflow and sedimentation on the production of natural-origin juvenile Chinook salmon.

While these results are encouraging, it is also important to remember that many challenges remain, particularly for Chinook salmon that are mostly hatchery-origin and have not distributed themselves as broadly, to this point, as expected. Whether dam removal in the Elwha River results in salmon, trout, and char populations that are more abundant, diverse, and resilient than prior to dam removal will be determined over the course of the next several decades. Although we cannot answer that question yet, the project has taught us many lessons about monitoring and managing salmonids and their habitat during and after dam removal (see also Peters et al., 2024). The response of Chinook salmon and steelhead to the removal of the Elwha River dams is not just about dam removal; rather, it is about a suite of cumulative management actions including use of hatchery production, and an in-river fishing and terminal nearshore moratorium. Succinctly characterizing this complexity during a period of extreme changes was challenging, which is why we relied on several different methods, such as SONAR to count fish and estimate run timing in river conditions that did not allow for visual surveys, and smolt traps to enumerate outmigrating juveniles. We complimented those stationary-point sampling methods with a spatial component that included systematic and opportunistic on-the-ground foot and snorkel surveys when and where visibility allowed. By being adaptive with our monitoring, we were thus able to use multiple methods and lines of evidence to track the short-term response of Chinook salmon and steelhead. Our findings improve existing knowledge about potential short-term salmonid responses to dam removal and offers insight into the complexity for those tasked with trying to quantify reintroduction of multiple species across remote watersheds with varying degrees of hatchery- and natural-origin salmon and steelhead populations.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

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

GP: conceptualization, methodology, formal analysis, investigation, resources, data curation, original draft, review and editing, visualization, supervision, project administration, funding acquisition. MM: conceptualization, methodology, investigation, resources, data curation, original draft, review and editing, supervision, project administration, funding acquisition. KD: methodology, formal analysis, investigation, resources, data curation, original draft, review and editing, visualization, supervision, project administration. JA: conceptualization, methodology, formal analysis, investigation, resources, data curation, original draft, review and editing, visualization, supervision, project administration, funding acquisition. ML: conceptualization, methodology, formal analysis, resources, data curation, original draft, review and editing, visualization. RP: conceptualization, methodology, investigation, resources, data curation, review and editing, supervision, project administration, funding acquisition. JM: conceptualization, methodology, formal analysis, investigation, resources, data curation, original draft, review & editing, visualization, supervision, project administration, funding acquisition. SB: conceptualization, methodology, investigation, resources, data curation, review and editing, supervision, project administration, funding acquisition. TB: conceptualization, methodology, formal analysis, investigation, resources, data curation, original draft, review and editing, visualization, supervision, project administration, funding acquisition. JD: conceptualization, investigation, resources, data curation, review and editing. KH: review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Author KD was employed by the company K. Denton and Associates LLC.

The remaining authors declare that the research 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.2024.1241028/full#supplementary-material

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Seven dam challenges for migratory fish: insights from the Penobscot River

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More than a century of impoundments in the Penobscot River, Maine, USA, has contributed to population declines in migratory fish in the system. A decade of change, research, and monitoring has revealed direct and indirect ways that dams have influenced the river habitat, connectivity for migratory fish, and the food web. The removal of two main-stem dams (in 2012 and 2013) and bolstering of fish passage have been part of coordinated restoration efforts in the watershed. Integral to this undertaking was support for short- and long-term monitoring and research that included physical habitat, fish passage, and broad scale ecological assessments. Herein we discuss the seven interconnected and complex ways that dams have affected the Penobscot River ecosystem, particularly for migratory fish. These include familiar influences ascribed to dams: i) impaired access to habitat, ii) injury and mortality, and iii) delays of migration. Other ecological influences are less studied and more subtle: iv) facilitation of predation, v) community shifts, and vi) demographic shifts. Lastly, dams result in vii) a loss of ecosystem services that would otherwise be intact in an unimpounded system. We draw on both direct examples from the Penobscot River and broader information to characterize how impoundments have transformed this ecosystem for more than a century. Recent dam removals and mitigation efforts have reestablished some of these ecological functions.

KEYWORDS
fish passage, dam, river, restoration, migration, anadromous, catadromous

Introduction

Human cultures are inextricably linked to river systems and people have shaped landscapes worldwide through damming. In the United States, there are more than 91,000 documented dams that serve significant functions for communities, including sources of water, navigation, and power generation (Roy et al., 2018). In the State of Maine alone, there are nearly 600 active dams (USACE, 2023) and many other uncatalogued impoundments. Biophysical processes have long been recognized to be fundamentally affected by dams and the impoundments they create. Rivers flows, thermal regimes, and sediment transport may all be affected (Poff et al., 1997; Petts et al., 2006). These endogenous factors influence river channel conditions that govern precipitation runoff and routing within the watershed's hydrologic system in a manner that systematically modifies the river hydrograph. While evidence of changes to river flows caused by climate change has also been documented in Maine (Dudley and Hodgkins, 2002; Gerard, 2018), large scale land cover changes (from tree clearing, road construction, and dam construction) have been the most pervasive disturbances in the Penobscot River watershed over the past two centuries (Opperman et al., 2011).

The ecological result of dam-related perturbations has both human costs and ecological ramifications. The decisions made in management of coastal river systems result in socioeconomic tradeoffs that directly affect fish populations (Roy et al., 2018) and have a long and well-documented history of being in direct conflict with the livelihoods and life-ways of Indigenous Peoples, especially in New England (Bennett, 2017). While dams provide societal functions to meet human needs, their operation often conflicts with migratory fish conservation goals (Song et al., 2019). Many migratory species' populations have declined due to dams (together with habitat destruction, overexploitation, and climate change; Wilcove, 2010) and now persist at greatly diminished levels (Greene et al., 2009; Limburg and Waldman, 2009; Waldman and Quinn, 2022). Mitigative steps such as operational guidance or fish passage may be implemented through the Federal Energy Regulatory Commission (FERC) in the United States but these multi-decade licenses may constrain both industrial and conservation potential (Vogel and Jansujwicz, 2022).

Conservation actions in the Penobscot River

Lessons learned after dam removals have been critical in understanding the subtle and synergistic ecological influences of damming. Those lessons complement a wealth of literature that is unequivocal as to the effects of dams. Dam removals may have immediate effects on river ecosystems (e.g., Catalano et al., 2007; Burroughs et al., 2010; Hitt et al., 2012; Poulos et al., 2014). These effects have been demonstrated in a tributary of the Penobscot River watershed (Gardner et al., 2013; Hogg et al., 2015) but recent changes to the main-stem of the River after dam removal have been extraordinary in scope. This river has been the focus of restoration efforts over the last several decades making its study a significant contributor to the advancement of river restoration ecology.

Central to the ancestral and current homelands of the Penobscot Nation, the Penobscot River is the second largest watershed in the New England states of the northeast USA, and the largest entirely within the State of Maine (approximately 22,300 km^2). The river has five major tributaries, hundreds of smaller streams, and its basin includes approximately 330 km^2 of lakes and ponds. This diversity in physical habitat continues to support runs of the full assemblage of native sea-run fish populations. Atlantic and shortnose sturgeons (*Acipenser oxyrinchus* and *A. brevirostrum*), striped bass (*Morone saxatilis*), rainbow smelt (*Osmerus mordax*), and tomcod (*Microgadus tomcod*) migrations are generally in the main-stem and estuary. Other sea-run species have longer migrations that often necessitate upstream and downstream passage at existing dams (Saunders et al., 2006). River herring (alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis*), American eel (*Anguilla rostrata*), American shad (*Alosa sapidissima*), Atlantic salmon (*Salmo salar*), and sea lamprey (*Petromyzon marinus*) all have large amounts of required habitat located upstream of current dams (Trinko Lake et al., 2012). For many of these species, historic estimates (based in part on commercial catch data dating back to the 1800s) range into the millions of individuals per year with unknown levels prior to colonization. For alosine fishes, historic populations are estimated to be at least two orders of magnitude greater than they are today (Hall et al., 2011). The construction of main-stem dams initiated in the 1800s limited the upstream extent of migration (Saunders et al., 2006) and notably impacted harvest (Foster and Atkins, 1867).

Fisheries restoration efforts in the Penobscot River, which began in the mid-1800s (Moring et al., 1995), initially concentrated on the Atlantic Salmon, a culturally and economically iconic species (Schmitt, 2016). Despite the precarious status of this and many other diadromous species, present numbers of salmon in the Penobscot River are large relative to other northeastern USA rivers. In addition, relative to other large northeastern rivers, the Penobscot River watershed has less urban development and relatively fewer dams (Opperman et al., 2011). As a result, this river represents, and has represented for decades, a high priority for restoration of diadromous fish and associated ecological processes (e.g., Everhart and Cutting, 1968; Martin and Apse, 2011).

The Penobscot River Restoration Project

To resolve longstanding conflict over the licensing of hydropower operations on the Penobscot River, a multiparty settlement agreement was signed in June 2004 (Opperman et al., 2011). Parties included dam owners, federal and State of Maine partners, the Penobscot Indian Nation, several non-governmental organizations, and the Penobscot River Restoration Trust (PRRT; a non-profit organization established to implement the restoration project). The agreement filed with the FERC, outlined a plan (the Penobscot River Restoration Project; PRRP) to restore native sea-run fish through the i) purchase and removal of the two most seaward dams (Veazie and Great Works); ii) purchase, decommissioning, and construction of a nature-like bypass channel around a third dam (Howland); iii) maintenance of current energy generation through increased power generation at six existing dams (Gilman Fall, Stillwater, Orono, Weldon, West Enfield, and Milford); and iv) efforts to improve fish passage at four dams (Figure 1).

In 2012, the Great Works Dam was removed, followed by the Veazie Dam in 2013. Howland Dam was not removed but was instead decommissioned and a nature-like fish bypass built in 2016. Milford Dam (as of 2013 was the lowermost dam on the river) received a new fish lift to aid in fish passage, as well as two new turbines to offset energy production losses at other dams. We note that the PRRP resulted in minimal upstream passage at the Stillwater Branch (Figure 1), depending on a small fish lift and active trucking (Opperman et al., 2011).

While the PPRP has improved connectivity in the Penobscot River watershed, the physical influence of the dam removals is localized to the Veazie and Great Works Dam remnants, roughly 15 km of main-stem river access. It is important to note that while the project is often described as having “Opened up 2,000 miles of rivers and streams to sea-run fish” (NRCM, 2023), the more precise description frames it as “improved access” to 2,000 miles of habitat (or to 500 miles, as reported by Day, 2006) through both dam removals and efforts to improve fish passage. Recognizing a lack of monitoring associated with other dam removals, and congruent with calls for assessment (e.g., Hart et al., 2002), the PRRT began discussions about science and monitoring as early as 2004. This work critically informed the funding and course of research efforts, the results of which provide a unique opportunity to assess the effects of both dam removals as well as the persistent influences of those dams that remain.

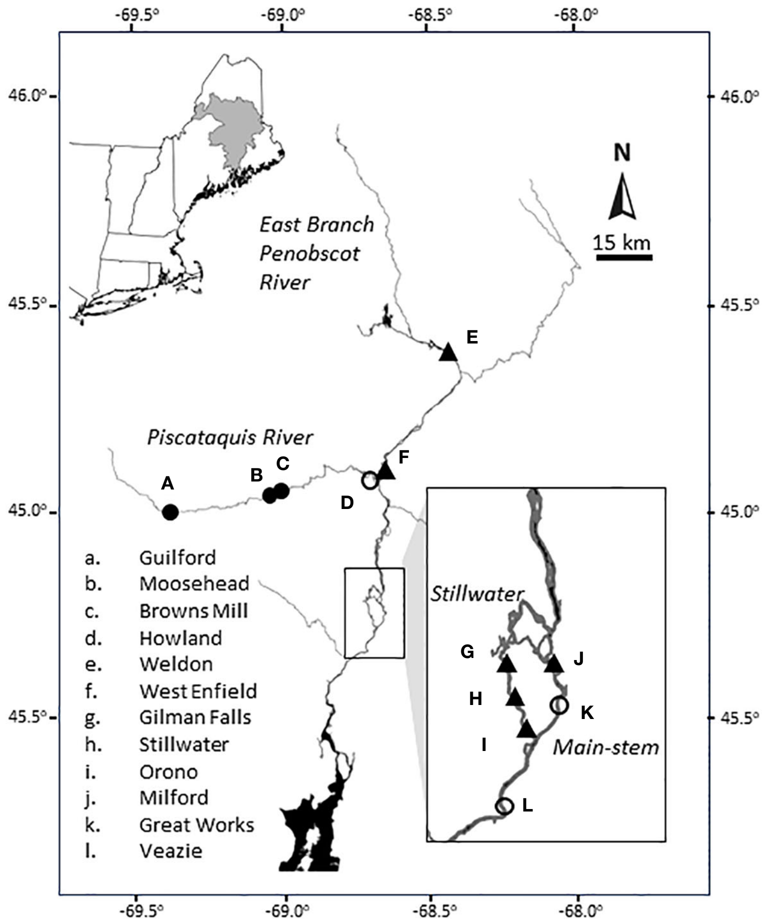

FIGURE 1
Map of the Penobscot River, Maine, USA with main-stem dams (others omitted for clarity). Upper left insert shows the New England region of the USA with the shaded area indicating the Penobscot River watershed for reference. Actions of the Penobscot River Restoration Project (PRRP) include the removal of the two most seaward dams (Veazie and Great Works) and decommissioning and construction of a nature-like fish way at a third dam (Howland) indicated by open circles. Energy generation (or water ponding) was increased at six existing dams (Weldon, West Enfield, Milford, Gilman Falls, Stillwater and Orono) shown by filled triangles. Dams not included in the PRRP are indicated by filled circles. Dam names are indicted by lower case letters “a” through “l”.

Seven influences of dams on migratory fish

Herein we describe seven influences of dams on migratory fish and their ecosystems. The ecological outcomes we identify from dams and their impoundments are linked to one another, thereby producing a suite of effects that are synergistic in nature. Decades of study in the Penobscot River, and subsequent restorative actions through dam removal or mitigation, have helped to characterize both the obvious and subtle ways that dams influence the ecology of migratory fishes (Figure 2). We draw on specific examples of migratory fish in the Penobscot River, bolstered by literature, to identify the suite of ecological outcomes associated with the construction of dams in a riverine system: i) impaired access to habitat, ii) injury and mortality, iii) delay of migration, iv) facilitation of predation, v) community shifts, vi) demographic shifts, and vii) loss of ecosystem services.

We attempt to highlight the complexity and interconnected nature of these ecological influences as they present a critical challenge for managers and dam operators who wish to minimize and mitigate the influences of these structures. We would be remiss if we did not acknowledge that undammed rivers are neither homogenous nor universally passable to all fish. Migratory fish interact with many natural features in rivers that are partial or complete barriers to movement. These features (e.g., rapids, waterfalls, or natural lakes) may impose some (or all) of the influences we ascribe to anthropogenic structures. However, there are two fundamental distinctions between the influences of natural impediments and human created dams. Firstly, the construction of dams in North America has occurred in the last several hundred years, exerting selective pressures over abbreviated evolutionary time scales (Zarri et al., 2022). Secondly, the abundance of human-built structures on many coastal rivers is far greater than patterns of natural fragmentation in rivers (Freeman et al., 2003).

First: impaired access to habitat

Perhaps the most obvious effect of dams follows directly from their function of storing and controlling water. Dams divide free-flowing, continuous habitats into distinct, discontinuous fragments and create impounded waters. Riverine ecosystems rely upon basin-scale storage and transport of resources (Vannote et al., 1980) and the proliferation of damming has disrupted these processes by altering flow regimes and restricting the movement of aquatic fauna (Ward and Stanford, 1987). Habitat fragmentation may lead to local extirpation (Kiffney et al., 2009; Carvajal-Quintero et al., 2017), population declines (Limburg and Waldman, 2009), or extinction (Ricciardi and Rasmussen, 1999; Carvajal-Quintero et al., 2017).

Many of the Penobscot River's migratory species are among those most vulnerable to the effects of damming globally, including alosines, lampreys, and eels (Liermann et al., 2012). Dams are migration barriers that exclude these species from important upstream habitats and caused some populations (e.g., Atlantic salmon, and American shad) to decline into single-digit abundances (Opperman et al., 2011; DMR, 2022). The depletion of Maine's diadromous community mirrors the trend for these fishes across North America and globally (Waldman and Quinn,

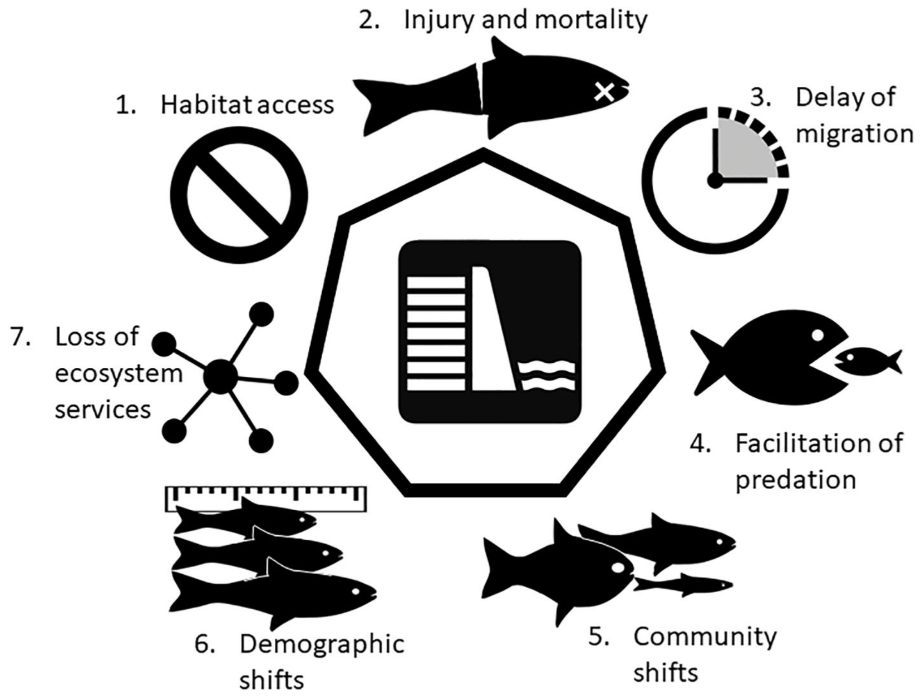

FIGURE 2
The seven direct and indirect impacts of dams on migratory fish and their ecosystems.

2022). Three Penobscot River species have garnered federal protection (Atlantic sturgeon, shortnose sturgeon, and Atlantic salmon) under the Endangered Species Act (USFWS, 1967; NMFS, 2010; USFWS and NMFS, 2018) with rainbow smelt having been listed as a federal Species of Concern (Enterline et al., 2012). Dams are cited as a primary threat to these protected species within the Penobscot River (Atlantic and shortnose sturgeons; Fernandes et al., 2010; rainbow smelt, Enterline et al., 2012; Atlantic salmon, Rubenstein et al., 2023).

The removals of main-stem dams as part of the PRRP has revealed the direct relation between dams and restricted access to habitat. The PRRP and associated efforts have dramatically increased the abundance of diadromous fishes within the Penobscot River (Scherelis et al., 2020; DMR, 2022; Whittum et al., 2023). Before dam removal, the American shad population was of unknown size and limited to habitat downstream of Veazie Dam. Only 16 adults had passed through the fishway from 1978 to 2012 (Grote et al., 2014a; Grote et al., 2014b). Annual counts at Milford Dam have now surpassed 10,000 (in 2022) and the population has supported a growing recreational fishery (DMR, 2022). From a combination of passage improvements and adult stocking into spawning lakes, the 2023 river herring run has approached 6 million individuals, increased from tens of thousands of fish before dam removals (DMR, 2022; Figure 3). Shortnose sturgeon have been tracked moving upstream of the former Veazie Dam (Johnston et al., 2019) and several have been encountered at the Milford Dam fish lift. Atlantic salmon permeability through the region with the two dam remnants was greatly improved from critically poor passage (Holbrook et al., 2009) to that of an open river (Izzo et al., 2016). At a smaller scale, dam removal on a tributary of the Penobscot River, the Sedgeunkedunk Stream led to a rapid recolonization (within one year) by sea lamprey (Hogg et al., 2013) and other migratory fish (Hogg et al., 2015).

However, many species have not recovered to target abundances (Opperman et al., 2011). Penobscot River runs of Atlantic salmon remain low (only 589 individuals were counted in 2021). River herring runs, although greatly improved, are likely still an order of magnitude less than runs pre-1600s (e.g., Hall et al., 2012). Despite dam removals, the Penobscot River remains a heavily impounded system. The two main-stem dam removals, while significant, had the limited influence of opening 15 km of river. Aspirational projections for Atlantic salmon (12,000), and American shad (2 million) are fully dependent on restoring connectivity between the ocean and important habitats in northern headwaters (Opperman et al., 2011). Fishways are often used to allow access to habitat that is otherwise constrained (Waldman and Quinn, 2022), and this is the case in the Penobscot River.

Most hydropower dams in the Penobscot River now have at least one form of fish passage that serves the general fish community, and several have also installed eel-specific bypasses (Opperman et al., 2011; Mensinger et al., 2021a; Molina-Moctezuma et al., 2021; Peterson, 2022). Overall upstream passage for adult Atlantic salmon at Milford Dam (now the lowermost dam), was relatively high (92%) over a span of six years (Izzo et al., 2016; Peterson, 2022), though with significant passage delays (days to weeks). Surviving downstream passage remains challenging for migrating juvenile Atlantic salmon (smolts) at Milford and other dams (Holbrook et al., 2011; Stich et al., 2014; Stich et al., 2015a). Downstream passage (for both juveniles and adults) is demonstrably critical for population persistence (e.g., American shad; Stich et al., 2019). In general, however, adult and non-salmonid juvenile downstream passage

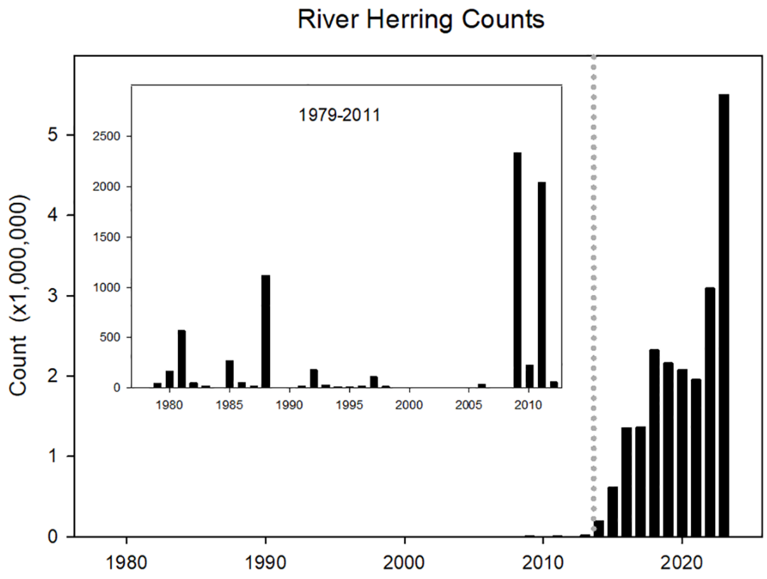

FIGURE 3
Estimated returns of river herring (*Alosa pseudoharengus* and *A. aestivalis*) to the main-stem of the Penobscot River, Maine, USA at Veazie Dam from 1979 to 2013, and aggregate at Milford Dam and Orono Dam thereafter post dam removal (indicated with vertical dotted grey line). The data show a rapid increase in river herring coincident with dam removal and coordinated upstream stocking (DMR, 2022).

performance remains poorly characterized making such assessments important directions of future study.

Overall, however, fishway mediated access to upstream habitat falls far short of the capacity of unimpeded river systems (Zydlewski et al., 2021). Most fishways fail to effectively restore connectivity for all native species (Bunt et al., 2012; Noonan et al., 2012; Algera et al., 2020; Hershey, 2021). It is also common for fishways to be designed and evaluated for passage of salmonids (Noonan et al., 2012) and salmonids typically have the highest passage success through these structures (Noonan et al., 2012; Hershey, 2021). Importantly, migratory fish populations passing dams incur mortality, injury, and delay (Roscoe et al., 2011). Even the nature-like fishway at Howland Dam, while providing greatly improved passage (compared to when it was a functioning hydropower facility) remains distinguishable from free-flowing river reaches in terms of both passage delays and survival of Atlantic salmon smolts (Molina-Moctezuma et al., 2021).

Second: injury and mortality

Dams prevent access of some migrants to upstream habitat, but those that attempt to reach that habitat may face risk of injury or mortality. Upstream migrants must navigate fishways (or other paths) to move upstream. Passage attempts may lead to sub-lethal injuries (Castro-Santos et al., 2009) or mortality (Roscoe et al., 2011) due to engineered conditions or operational failures. While the run of American shad remains low in the Penobscot River, dozens to hundreds of dead adult American shad are removed from the fishway structure annually. Similar incidental losses for river herring and other migrants occur (Jason Valliere, Maine Department of Marine Resources, personal communication, August 31, 2023). Delays in passage may increase injury risk (McLaughlin et al., 2013) however it is difficult to assess what occurs within the fishway versus during searches for the fishway entrance.

Because dams are not freely permeable to movements in both directions, fish passage risks may be compounded by extensive searching periods. Migrating Atlantic salmon adults (Izzo et al., 2016; Maynard et al., 2017) and American shad (Grote et al., 2014b; Peterson, 2022) in the Penobscot River make wide-ranging upstream and downstream directional movements. Alewife are also known to "oscillate" in this way in other systems (McCartin et al., 2019). Such behaviors may put an individual at a great disadvantage even after successful upstream dam passage. These fish may suffer high mortality while moving back downstream (Castro-Santos and Letcher, 2010) being caught in an ecological trap that is confounded by the energetic cost of delay (Rubenstein et al., 2023). For iteroparous species, whether searching or not, fish that make it successfully past a dam must survive at least one downstream passage event.

Atlantic salmon are known to experience high mortality after completing spawning, but if successful in navigating dams moving downstream, they return to the sea (Maynard et al., 2018) either in the fall or following spring (Ruggles, 1980; Maynard et al., 2017). The population cost of losing these larger, multi-year fish may be significant due to their increased reproductive potential. Female Atlantic salmon may invest up to 25% of their body mass into egg production (Fleming, 1996). The loss of "big old fat female fish" may have significant population effects (*sensu* Hixon et al., 2014). Though Atlantic salmon restoration has focused on upstream passage more than multiyear spawning (USFWS and NMFS, 2018), the biological importance of these fish is clear (Fleming, 1996; Hixon et al., 2014).

Recruitment of juvenile anadromous fish spawned upstream of dams is entirely dependent upon the successful emigration downstream. Downstream migrating Atlantic salmon smolts have been extensively studied in the Penobscot River and river sections with dams are consistently identified as areas of high mortality (Holbrook et al., 2011; Stich et al., 2014; Stich et al., 2015a; Molina-Moctezuma et al., 2021; Molina-Moctezuma et al., 2022). As we explore later, sub-lethal injuries may partly explain why Atlantic salmon smolt mortality in the estuary is elevated both through delay and predation (Stich et al., 2015b; Stich et al., 2015c; Molina-Moctezuma et al., 2022).

For American eel, downstream migration is the culmination of up to decades of growth in fresh water before initiating fall migration. Migrants must locate a passage route and some individuals spend days searching, drawing on energy stores (Carr and Whoriskey, 2008; Piper et al., 2015; Eyler et al., 2016). Like other downstream migrating fish, adults risk impingement and impact-related injuries, as well as lethal and sub-lethal strikes by turbine blades in power generating stations (Piper et al., 2015; Eyler et al., 2016). In the Penobscot River, eel mortality rates are elevated at the two extant main-stem dams (West Enfield and Milford) but is indistinguishable from background mortality in reaches where Veazie and Great Works Dams were removed (Mensinger et al., 2021a). Injuries consistent with turbine blade strikes are commonly observed downstream of dams (Figure 4) supporting the

FIGURE 4
Injured American eels (*Anguilla rostrata*) are frequently encountered in the main stem of the Penobscot River, Maine, USA indicating that these downstream migrants pass through dam turbines and suffer injury. Severely injured fish may still be alive and may travel long distances (kilometers) from the site of injury, suggesting telemetry assessments may underestimate direct mortalities. (Photo credit, Zydlewski Laboratory, University of Maine).

assumption that entrainment through the turbines occurs – with negative outcomes for survival.

Challenges of downstream passage are a partial driver of the decision to not pass sturgeon upstream of Milford Dam. The few shortnose sturgeon that entering the Milford fish lift annually are moved back downstream based on uncertainty in their historical range (assumed to be at the Milford Falls, although unclear [see Knight, 1985; Petersen and Sanger, 1986]) and resulting need to also move back downstream as adults or juveniles if spawning occurred (Jeff Murphy, NOAA's National Marine Fisheries Service, personal communication). There mortality and injury have been demonstrated during downstream movements of sturgeon encountering dams during in other rivers systems (McDougall et al., 2013; McDougall et al., 2014; Jones and Cotel, 2023).

Changing conditions may also affect passage and survival at dams. At Milford Dam, water attraction conditions on the west shore of the Penobscot River tend to attract upstream migrants that are frequently left stranded in pools as river and operational conditions change (Jason Valliere, Maine Department of Marine Resources, personal communication, August 31, 2023). When noticed, this has led to concerted efforts to capture and move upstream migrating Atlantic salmon (Figure 5). Other species without federal protection, however, are not prioritized for such interventions. During the fall migration it is common to see stranded alosines that succumbed to low oxygen conditions (Figure 5).

Third: delays of migration

Rivers are the highways for migratory fish, and they are critical corridors for rapid movement. As we have discussed, dams restrict access to habitat. Engineering solutions (fishways) may facilitate movements and partly mitigate habitat fragmentation. Success, however, depends on three steps: attraction to the fishway entrance, entry, and successful transit. In the Penobscot River, the speed of movements and fish passage for both upstream and downstream migrating animals are slowed by dams in the system. This influence is obviated by the aggregations of migrating fish that may be observed below dams (Figure 6), but telemetry studies performed in the Penobscot River have provided more quantitative estimates of delay.

Prior to the removal of Veazie and Great Works dams, upstream migrating Atlantic salmon adults were denied access to, or delayed in, reaching upstream habitat in the Penobscot River (Holbrook et al., 2009; Sigourney et al., 2015). For adult Atlantic salmon, completion of the dam removals as part of the PRRP allowed rapid passage through the reaches with the dam remnants. However, adults now experience substantial delays (often several weeks) at Milford Dam, a facility that operates with a fish elevator (Izzo et al., 2016) compared with the original Denil style fishway (a series of closely-spaced U-shaped baffles; Holbrook et al., 2009). Similarly, American shad adults approached Veazie Dam prior to the dam removals but did not pass in large numbers (Grote et al., 2014a). While passage of American shad at Milford Dam has increased (to more than 10,000 annually; DMR, 2022), telemetry assessment suggests that passage remains hampered by delays (Peterson, 2022). In contrast, sea lamprey adults now reach Milford Dam and are relatively successful in passing the dam (70–82%) with little delay (Peterson et al., 2023). While mean delay times for passage were low for successful fish (<48h), others experienced substantial delays (9–11 days) before abandoning upstream movements altogether.

Delays at dams are commonly observed in many impounded river systems. American shad (e.g., Castro-Santos et al., 2017; Weaver et al., 2019) and river herring (Haro et al., 1999; Noonan et al., 2012) have been demonstrated to have difficulty passing dams. Sea lamprey face delays and repeated failures to move through the fishways in the Connecticut River (Castro-Santos et al., 2017). Delays for salmonids have been documented in many river systems (Raymond, 1979; Wertheimer and Evans, 2005; Scruton et al., 2008; Keefer et al., 2012; Caudill et al., 2013; Nyqvist et al., 2017; Hagelin et al., 2021; Ohms et al., 2022). These delays may be biologically relevant (e.g., impacting ontogenic synchrony with nature) or even deadly. When fish are delayed by dams, they may be subjected to temperatures that reach lethal or near-lethal levels (Marschall et al., 2011). As discussed above, flows or water

FIGURE 5
Changing environmental conditions in conjunction with operational changed may leave fish stranded as upstream or downstream migrants in the Penobscot River, Maine, USA. On the left, an endangered Atlantic salmon is rescued from a pool below Milford Dam that became isolated from the river while searching for an upstream route. On right, hundreds of alewife juvenile were stranded below a low-head dam as flows decreased. (Photo credits, Maine Department of Marine Resources).

FIGURE 6
River herring are seen congregating below a dam on the Penobscot River, Maine, USA indicating the incomplete access provided to upstream habitat. (Photo credit, Zydlewski Laboratory).

regulation decisions may also trap fish in areas where they are unable to escape or are susceptible to predation from natural or human predators (Figure 5). The longer they remain in the area, the more protracted the risk.

For adult upstream migrants, even modest delays may be energetically costly. Rubenstein et al. (2023) found that Atlantic salmon were delayed an average of 16–23 days at Milford Dam prior to passing and had lost 11–22% of initial fat reserves. These losses may be compounded by high water temperatures if thermal refugia are not available (Holbrook et al., 2009). Such delay-mediated energy losses are likely to be important during a migration (Thorstad et al., 2008). Returning adults cease consumption upon freshwater entry (Kadri et al., 1995) so that energy stores are the sole fuel for survival, migration, and spawning success.

For iteroparous species (e.g., Atlantic salmon, American shad, and river herring) protecting energy stores may contribute to post-spawn survival. Glebe and Leggett (1981) suggested that loss of more than 60% of energy reserves may serve as a constraint to iteroparity. For American shad, empirical evidence suggests that the threshold for post-spawn survival may be as low as 30–40% (Leonard and McCormick, 1999). Risks of both direct and indirect mortality through delay-mediated energy depletion are heightened when fish must pass multiple dams. This heightened mortality is consistent with the observed declines of American shad repeat spawners in the Connecticut River (New England) that fell from 49% (Walburg and Nichols, 1967; Carscadden and Leggett, 1975; Limburg et al., 2003), to 5% in 60 years after accessing habitat upstream of impoundments (Atlantic States Marine Fisheries Commission [ASMFC], 2020). This pattern of "*forced semelparity*" (Zydlewski et al., 2021) has obvious implications for population demographics. For semelparous species such as the sea lamprey, adult delays may likewise result in added energy losses that impair survival, migration, and spawning. For upstream migrating juvenile American eel, delays may functionally restrict their access to rearing habitat (Verdon and Desrochers, 2002) and may have differential individual effects based on variation in motivation (Mensinger et al., 2021b).

Delays are also observed at dams as fish migrate downstream. In the Penobscot River, Atlantic salmon smolts displayed slower movement rates in areas where dams were located (Spicer et al., 1995; Stich et al., 2015b). Studies also found that smolts arriving during the day experienced longer delays than those that arrived at night (Holbrook et al., 2011). Delays are directly associated with lower survival in the Penobscot River (Molina-Moctezuma et al., 2022) and elsewhere (Castro-Santos and Haro, 2003; Marschall et al., 2011; Nyqvist et al., 2017). This pattern is not held at all dams in the Penobscot River, however, as Browns Mill Dam (on the Piscataquis River, Maine, USA) had the lowest mortality (indistinguishable from in-river mortality) but the highest delays (up to 10 days; Molina-Moctezuma et al., 2021). Delays for downstream migrating smolts were reduced after construction of the nature-like fishway at Howland Dam in 2016, however, only about one third of the smolts used the bypass. Downstream delays from dams on the Penobscot River were also found to occur for adult American eels (Mensinger et al., 2021a), which may have a significant impact on spawning and population success as these are old, semelparous individuals.

Flow conditions strongly influenced the delays incurred by fish moving up or downstream at dams. Downstream migrating adult American eels were slowed at West Enfield and Milford dams, but this lag was erased individuals by higher flows during the migratory season (Mensinger et al., 2021a). Similarly, the Penobscot River experienced exceptionally high spring flows in 2017, 2018 and 2019. Atlantic salmon smolts tracked during these three years had greatly reduced delays and higher survival relative to lower flow years total cumulative survival of greater than 75% versus less than 50% in previous years (Molina-Moctezuma et al., 2022).

Delays may influence migrants through a disassociation of ontogenic processes with environmental windows of opportunity. Many migratory species develop physiological characteristics associated with anticipated shifts in habitat at the time of migration (Zydlewski and Wilkie, 2012). Smoltification in salmonids is an adaptive developmental stage that synchronizes the physiological capacity to osmoregulate in seawater with migratory behavior (Zydlewski and Wilkie, 2012; Stich et al., 2015c) and has been described as a window of opportunity to match physiological capacity with environmental conditions (McCormick et al., 2009). Delays may disrupt the match between migration and development. Consequently, fish may enter the ocean in suboptimal conditions (McCormick et al., 1998; Zydlewski et al., 2005; Marschall et al., 2011). All other factors being equal, salmonids migrating later in the season likely face greater physiological challenges than early migrants (McCormick et al., 1999). Overall, this can create greater physiological challenges, affect sensitivity to starvation, and adversely influence ocean survival (McCormick et al., 1999; Zydlewski et al., 2003; Wilson et al., 2022).

In contrast to the ontogenic development of seawater tolerance in migratory salmon, American shad develop tolerance to full strength seawater about three months in advance of their downstream migration (Zydlewski and McCormick, 1997a).

However, juveniles lose their ability to regulate ions in fresh water, a change influenced by declining autumnal temperatures (Zydlewski and McCormick, 1997b). These developmental changes mean that entry into seawater late in the migratory season is physiologically challenging (Zydlewski et al., 2003) which may ultimately reduce survival of juvenile shad (Shrimpton et al., 2001). Whether migrating as a juvenile or as an adult, delays at dams consume critical energy for migration, cause a mismatch between developmental stages and the environment, and expose fish to unfavorable environmental conditions. We have shown how delays may lead to diminished survival and reduce biological fitness. Delays are also intimately intertwined with other risks, such as predation.

Fourth: facilitation of predation

Dam and fishway construction have been shown to create habitat suitable for opportunistic or ambush predators (Rieman and Beasmesderfer, 1991; Pasha et al., 1997). Fish that are aggregated near dams, delayed in passage, or disoriented by flow and turbulence, are increasingly vulnerable to predation (Ruggerone, 1986; Rieman and Beasmesderfer, 1991; Isaak and Bjornn, 1996; Blackwell and Juanes, 1998; Agostinho et al., 2012). Predator vulnerability of fish delayed near dams is obviated by seasonal diet shifts of predators incorporating more migrant prey species in their diets (Blackwell and Krohn, 1997; Fritts and Pearsons, 2006). This dietary shift has been observed in the Penobscot River where river herring have become an important seasonal prey item of smallmouth bass (*Micropterus dolomieu*) in the lower river (Watson et al., 2019).

Bald eagles (*Haliaeetus leucocephalus*), osprey (*Pandion haliaetus*) and double-crested cormorants (*Phalacrocorax auritus*) are known predators of diadromous species near impoundments (Ross and Follen, 1988; Call, 2015). In the Penobscot River, cormorants have been known to select seasonal foraging areas adjacent to dams to feed on migrating Atlantic salmon smolts in addition to other anadromous species such as rainbow smelt or river herring (Blackwell and Krohn, 1997). Prior to the PRRP, most avian predator diets in the upper Penobscot River were freshwater in source, although bald eagles were likely foraging on stocked Atlantic salmon smolts (Call, 2015). Presumably, avian predators now exploit the increased alosine forage base upstream of Milford Dam. Even large upstream migrants are vulnerable to avian predation. One of three adult salmon that passed Browns Mill Dam in 2020 was captured by a bald eagle while delayed in the 1 km head pond between dams Browns Mill and Moosehead Dams on the Piscataquis River (Peterson, 2022).

The role of in river predation for Atlantic salmon smolts has been of growing conservation concern. While marine mortality has been identified as being a critical source of loss for the species, freshwater and estuarine mortality may exceed coastal mortality for Atlantic salmon smolts (Kocik et al., 2009; Hawkes et al., 2019). In the Penobscot River, mortality rates for smolts are relatively low in free-flowing stretches of river but elevated near dams (Holbrook et al., 2011; Stich et al., 2015a; Molina-Moctezuma et al., 2022). Therefore, resolving the causal agent of mortality at dams is important for exploring possible mitigative actions. The development of acoustic predation tags provides a new tool for determining the disposition of tagged fish (Halfyard et al., 2017; Schultz et al., 2017). Recent acoustic telemetry data with predation sensors in the Penobscot River suggests that predation risk is 5-fold greater through impounded reaches (Mensinger et al., in press).

Atlantic salmon smolt mortalities in the estuary are also linked to their dam passage experiences (Stich et al., 2015a) likely because of increased delays (Molina-Moctezuma et al., 2022). Observed delays in transit rates at dams (Holbrook et al., 2011; Norrgård et al., 2013; Stich et al., 2015b) may result in loss of physiological smolt characteristics (McCormick et al., 1999; Budy et al., 2002; Ferguson, 2006) thereby reducing performance (Handeland et al., 1996). Thus, the asynchrony between the development of osmotic tolerance and timing of arrival in the estuary may contribute to mortality in the Penobscot estuary (Stich et al., 2015c). Such changes in salinity tolerance are exacerbated by descaling injuries as might occur at dams (Zydlewski et al., 2010) and may increase susceptibility to predation. Observations that predation risk in the estuary is nearly twice that of impounded areas (and 9-fold greater than in free-flowing river; Mensinger et al., in press) suggest a causal relation between dam delays and predation mortalities.

The slow rate of travel faced by downstream migrants in impoundments exposes migrants to fish, avian and mammalian predators. Weldon Dam's impoundment is approximately 5 km long and is a reach of exceptionally high mortality risk for Atlantic salmon smolts (as high as 25%; Stich et al., 2015a; Molina-Moctezuma et al., 2022). It is notable that the gauntlet of predators in the impounded regions differs from the natural river. The changed lentic community favors predatory species including smallmouth bass, largemouth bass (*Micropterus salmoides*) and chain pickerel (*Esox niger*). While all these predators may be found throughout the Penobscot River, smallmouth bass are exceptionally widespread (Kramer, 2006; Kiraly et al., 2014). Smallmouth bass are a generalist and piscivorous fish that has been widely introduced (Loppnow et al., 2013) and implicated in declines of salmonids and other taxa (Magoulick, 2004; Fritts and Pearsons, 2006; Middaugh et al., 2016). As these predatory species are abundant in impoundments (Whittum et al., 2023), dam removal may notably reduce predation risk to juveniles by both reducing predator density and increasing speed of migration (Pasha et al., 1997).

The presence of predation in and near river impoundments is widely observed. In Pacific Northwest, migrating salmon (*Oncorhynchus* spp) are a key prey item for smallmouth bass near dams (Tabor et al., 1993; Fritts and Pearsons, 2004). Adult Atlantic salmon are preyed upon by the European catfish (*Silurus glanis*) near fishways in France (Boulêtreau et al., 2018) and in Brazil, redeye piranha (*Serrasalmus rhombeus*) prey on neotropical fish near fishway entrances (Agostinho et al., 2012). We note the presence of humans as another predator that are drawn to the aggregations of fish below dams (Jackson and Davies, 1988; Carey et al., 2011). Migratory fish in the Penobscot River are vulnerable enough near dams to warrant closure to "*That area within 150 feet of any part of the Medway, West Enfield and Milford Dams, including fishways*" (MDIFW, 2023). Milford Dam is highlighted as a place to fish for striped bass as their prey are congregated (Holyoke, 2021). Such angling pressure for striped bass and American shad results in the hooking of endangered adult Atlantic salmon (Jason Valliere, Maine Department of Marine Resources, personal observation, August 31, 2023).

Fifth: community shifts

Dams fundamentally change local biophysical conditions. Impoundments warm quickly, and shift from a lotic to lentic habitat. These changed conditions may disadvantage native species, providing a permissive environment for non-native species (Baxter, 1977; Ward and Stanford, 1987; Pess et al., 2008). Non-native fishes may find themselves well-positioned to outcompete or prey upon native salmonids and other fishes adapted to cold, free-flowing habitats. Impoundments may also tend to favor non-native minnow species (e.g., Whittum et al., 2023), which often arrive as bait-bucket introductions (Ludwig and Leitch, 1996). Dam-influenced fish assemblages are therefore not necessarily less *diverse* than those assemblages in free-flowing rivers (e.g., Burroughs et al., 2010; Hogg et al., 2015), but they are generally depleted in native species and enriched with non-native species. The Penobscot River is predominantly inhabited by macrohabitat generalist species (e.g., smallmouth bass) and riverine species (e.g., white sucker), and these species dominate the biomass in the main-stem Penobscot River.

Dam removals have been observed to result in rapid and often profound changes to riverine fish communities (Catalano et al., 2007; Burroughs et al., 2010; Hitt et al., 2012; Poulos et al., 2014). These changes have been demonstrated in the Sedgeunkedunk Stream, a tributary of the Penobscot River where persistent changes were observed within weeks of dam removal (Gardner et al., 2013; Hogg et al., 2015). In coastal systems, recolonization of diadromous fishes in newly available habitat represents a major shift (Hitt et al., 2012; Weigel et al., 2013; Hogg et al., 2015). Similarly, the fish community in the Penobscot River was substantially modified by the increased presence of migratory fish, but this influence diminishes with the number of dams that must be passed (Kiraly et al., 2014; Watson et al., 2018; Whittum et al., 2023).

The Penobscot River remains a heavily impounded system with improved, but demonstrably imperfect fish passage. Although upgraded passage has allowed migratory species to attain greater upstream ranges, much of the community structure above the lowermost dam has remained similar to pre-dam removal conditions (Whittum et al., 2023). Upriver, the East Branch of the Penobscot River currently has had little to no presence of alosines, suggesting poor combined passage through Milford, West Enfield, and Weldon dams. Weldon Dam is a significant barrier (13.7 m; USACE, 2023) compared to downstream dams. Fish passage at Weldon Dam (pool and weir) and West Enfield Dam (vertical slot) are likely more selective than the fish elevator system at Milford Dam (Bunt et al., 2012).

In the Piscataquis River, the Howland nature-like fishway allows for fish passage (to and from the Penobscot River) without changing the impoundment. The solution of a nature-like fishway is desirable when there is high social or cultural value attached to the impoundment. Like other fishways, this structure leaves the habitat upstream of Howland Dam with little change after construction (Kiraly et al., 2014; Watson et al., 2018; Whittum et al., 2023). As might be anticipated, the extant impounded riverine reaches within the Penobscot River continue to favor cyprinid species and higher relative abundance of top predators, such as chain pickerel, smallmouth bass, and largemouth bass. As a result, any juvenile migrants above these dams may encounter an enhanced local density of piscivores when moving downriver. Migration delays at impounded locations may provide additional opportunity for predation from these reservoir species (Molina-Moctezuma et al., 2021). The risk is multiplied if passing several dams.

We would be remiss if we did not note that dam removal may also have unintended (and undesired) outcomes for the native fish community by facilitating the movement of non-native species. The expansion of some non-native fish such as the white catfish (*Ameriuris catus*) are likely the result of increased movement permeability in the system (Whittum, 2022). When contemplating the use of dam removal as a conservation approach, managers may benefit from considering how enhanced passage might influence non-native species (Cooper et al., 2021). Indeed, fears of the expansion of angler transported (and non-native) northern pike (*Esox lucius*) have prompted state proposed legislation to modify fishways on tributaries of the Penobscot River to exclude "invasives" (LD 1049, *131st Maine Legislature, An Act to Protect Maine's Inland Fisheries from Invasive Fish*). In principle, fishway modification may allow for differential passage (and therefore connectivity) for different species based on species-specific fishway passage performance (Noonan et al., 2012). This approach would, however, make fish passage more difficult for all species.

Sixth: demographic shifts

Dams have the potential to cause demographic shifts in populations due to a suite of influences on distinct ontogenetic stages and variable life histories within species. These influences may include shifts that result from selective pressures such as size selection in fish passage and mismatches between upstream access and downstream survival through dams for migrants. At the population level, shifts may manifest as changes in size and age structure, reductions in rates of iteroparity, or loss of life-history complexity and variability. While demographic shifts are increasingly well documented, the degree to which selective pressures influence local adaptation is poorly understood for many species.

Size selection in fish passage may limit access to spawning and rearing habitat by individuals of specific sizes, which alters average size of individuals while reducing variability in size. For anadromous species, selectivity in fish passage directly imposes selection on the component of adult spawners that access spawning habitat. This selection may operate on physiology, anatomy, or behavior (Mensinger et al., 2021b). Size-selective passage of Atlantic salmon has been observed in the Penobscot River (Sigourney et al., 2015; Maynard et al., 2017), whereby larger fish were less successful in passing dams to reach spawning habitat. Exclusion of the largest females from spawning grounds may affect both underlying phenotypes of spawners and survival in other life stages for a population. Trucking spawning fish around fishways, combined with conservation hatchery practices, may partly alleviate this selective pressure (Sigourney et al., 2015; Maynard et al., 2017).

Mensinger et al., 2021b observed that larger juvenile (glass) eels climbed faster than smaller ones. For catadromous species this size selection in passage may lead to differences in individual growth opportunities in freshwater habitats, or even skew sex ratios based on physiological limitations of habitat downstream of dams (Mensinger et al., 2021b). Size selection at challenging passage structures (anthropogenic or natural) may impose energetic limitations on rates of growth, maturation, and migration that have not been extensively studied. It may simply make some upstream habitat functionally inaccessible (Verdon and Desrochers, 2002).

Dams may also cause shifts in size structure and life history traits through mortality during downstream passage. If downstream survival of adult and juvenile fish through dams is not sufficiently high, upstream fish passage may become an ecological trap (Ohms et al., 2022). Because life history traits such as size, age at maturity, and iteroparity are co-inherited (Aykanat et al., 2019), downstream survival through dams may influence multiple population demographics simultaneously. Low survival through dams during downstream migration by post-spawn adults was associated with reduced iteroparity of Atlantic salmon in the Penobscot River (Maynard et al., 2018) and steelhead trout (*Oncorhynchus mykiss*) in the Snake and Columbia rivers in the northwestern USA (Wertheimer and Evans, 2005; Keefer et al., 2008). When adult downstream survival rates through dams were less than perfect (i.e., 100%), American shad age structures were predicted to be truncated through loss of older fish and repeat spawning rates were predicted to be reduced with increasing upstream fish passage (Castro-Santos and Letcher, 2010; Stich et al., 2019). Additive mortality incurred by passing multiple dams is compounded at the watershed scale with respect to changes in demographics such as abundance, size structure, and iteroparity (Castro-Santos and Letcher, 2010; Stich et al., 2019; Zydlewski et al., 2021).

The degree to which demographic shifts are realized may vary with damming intensity and upstream fish passage, environmental conditions, and life history variation. Abundance of American shad, for example, varies as a function of upstream passage, number of dams, configuration of spawning and rearing habitat relative to dams, as well as latitudinal clines in growth, maturation, fecundity, and iteroparity (Zydlewski et al., 2021). In the Penobscot River, where only 16 adults passed the lowermost dam from 1978 through 2012, fish exhibited repeat spawning rates as high as 75–95% (Grote et al., 2014b), though the population persisted at low abundance (Grote et al., 2014a) prior to the removal of Veazie Dam. Fish reached smaller maximum sizes and reached older ages despite elevated natural mortality estimates in the Penobscot River compared to other rivers in the northeastern part of their range (Gilligan-Lunda et al., 2021). In the Connecticut River, maximum age and repeat spawning rates have been reduced since implementation of upstream fish passage and despite closure of commercial fisheries and stable spawner abundances (ASMFC, 2020). These reductions in maximum age and repeat spawning have occurred even though Connecticut River American shad reached larger sizes and experienced lower mortality rates than in the Penobscot River (Gilligan-Lunda et al., 2021).

In species or populations with variable life histories, dams may influence population demographics through elimination of life history complexity, thereby reducing evolutionary stability of populations in variable environments. For example, coastal cutthroat trout (*Oncorhynchus clarkii*; Trotter, 1989) and steelhead trout (Thorpe et al., 1998; Satterthwaite et al., 2009; Hodge et al., 2016) exhibit high diversity in anadromous and freshwater resident life histories, in addition to variability in iteroparity. This diversity of life histories presumably reduces risk to extirpation through a portfolio effect (Moore et al., 2014) and includes genotypic and plastic responses (Satterthwaite et al., 2009; Whiteley et al., 2010). Whereas population structuring has been observed in steelhead trout upstream and downstream of barriers in the Elwha River, this structuring rapidly degraded following dam removal. Data suggest that overall genetic diversity was preserved within isolated freshwater and anadromous populations, indicating strong potential for recovery (Fraik et al., 2021). Similarly, a large body of research has demonstrated rapid adaptation of freshwater life histories in alewife following dam construction and land locking independently among many populations in Connecticut, USA (Palkovacs et al., 2008). Both phenotypic and genotypic responses in alewife populations are postulated to create eco-evolutionary feedbacks that drive rapid changes in populations (Palkovacs and Post, 2008). Recent evidence suggests that many of the underlying genomic changes can also be reversed through introgression with anadromous individuals following implementation of fish passage or dam removal (Reid and Goodman, 2020).

Finally, American shad exhibit parity on a continuum across their native range, with semelparous populations in southern rivers (south of 35° latitude) and increasingly high rates of iteroparity in northern rivers (Leggett and Carscadden, 1978) that correlate to differences in maturation (ASMFC, 2020), growth, and longevity (Gilligan-Lunda et al., 2021) and regional population structuring (Hasselman et al., 2010). Within the central range (35–41° latitude) of American shad, intermediate rates of iteroparity prevail, with multiple life histories present in some rivers (ASMFC, 2020). It remains unknown to what degree these life histories vary longitudinally within rivers. Work in undammed rivers (e.g., Delaware River, mid-Atlantic region of the USA) may aid in differentiating between the influence of migratory distance and damming.

Seventh: loss of ecosystem services

The six influences of dams discussed above are directly tied to interactions with migratory fishes. The ecological influences of dams, however, include changes in ecosystem function and human use that are indirectly linked to migrating fishes through ecosystem functions. We broadly identify these changes as "ecosystem services". Inclusion of connections between migratory fishes and broader ecosystem function in this paper is consistent with shifts towards more holistic approaches to ecosystem and multispecies management (Larkin, 1996; Eriksson et al., 2011; Andersen et al., 2015). Ecosystem services have supported human well-being through history in both expected and unanticipated ways (Limburg and Waldman, 2009; Hall et al., 2012).

Dams have been the primary cause of migratory fish population declines across North America (Limburg and Waldman, 2009) and Europe (Wilson and Venerata, 2019). The direct loss of fisheries potential in the Penobscot watershed has been documented (Saunders et al., 2006). Hall et al. (2011) calculated that by 1850, river herring spawning habitat in Maine had been reduced to less than 5% of available habitat because of dam construction on small rivers, and to 1% of habitat by 1887 when the largest rivers were spanned by dams (Atkins, 1887). Impoundment of the Penobscot River has reduced American shad production potential nearly 90% (Stich et al., 2019), contributing to a dam-related coast-wide loss of 39% based on habitat access alone (Zydlewski et al., 2021). The loss of recreational angling for sea run fish also affects the region's economy (Pinfold, 2011) and culture (Schmitt, 2016). The loss of fisheries has been particularly detrimental to indigenous communities.

The connection of Wabanaki people on the Penobscot River to once abundant sea run-fish species has been important for both sustenance and cultural connection (Speck, 1940; Harper and Ranco, 2009). The Penobscot Nation, *penawahpkekeyak*, are the *people of the place of the white rocks*, referring to a reach of river that bears their name. Similar connections are reinforced through stories and folklore (Kolodny, 2007). This federally recognized tribe has more than 2,400 enrolled members and is considered one of the oldest continuous governments in the world (Charlie Loring, Jr., Director, Department of Natural Resources, Penobscot Indian Nation, personal communication, August 31, 2023). Dam-mediated losses of sea run fish are viewed as a critical threat to the Penobscot Nation's formative connection to the river, and the PRRP has been viewed as integral to the *"reclamation of their cultural identity and sovereignty"* (Frederick, 2006).

Dam-mediated losses of migratory fish runs may have effects beyond their local geography, either through trophic connections (as predator or prey) or range-wide population resilience. For the semelparous, panmictic American eel, adult downstream migrations are limited by access to upstream juvenile rearing habitat. Dam related loss of production from any river means that the entire population is diminished, particularly as adults from northern regions tend to be female (Wang and Tzeng, 1998; Jessop, 2010). Ames and Lichter (2013) assert that large, stable concentrations of young-of-the-year alosines influenced where resident and migrating gadid (cod) groups were located. The dam-associated loss of river herring and shad resulted in a loss of forage for ground fish such as Atlantic cod (*Gadus morhua*) haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and white hake (*Urophyscus tenuis*). These important northern coastal shelf fisheries collapsed coincident with the damming of rivers in the region (Lotze and Milewski, 2004). Striped bass also prey on blueback herring, alewife, and American shad, thereby benefiting from their abundance (Trent and Hassler, 1966; Nelson et al., 2003; Walter and Austin, 2003; Savoy and Crecco, 2004).

As dams alter fish assemblages, other interactions may directly or indirectly occur (Hanson and Curry, 2005; Kiffney et al., 2009). The presence of alewife and blueback herring in high numbers may benefit other species through substitution. As river herring populations rebound in the Penobscot River, it has been suggested that they may serve as a prey buffer for species such as the endangered Atlantic salmon (Saunders et al., 2006; Oke et al., 2020; Hare et al., 2021). These species are likely to become more important as a forage base as populations increase both in river and along the coast (Ames and Lichter, 2013). Mammalian predators such as the harbor seal (*Phoca vitulina*) and birds (e.g., bald eagles, osprey, double-crested cormorants) would also likely be limited by dam-mediated population losses (Able and Fahay, 2010; Call, 2015).

Predation pathways contribute important linkages among freshwater, marine, and terrestrial ecosystems by transference of energy and nutrients (e.g., Durbin et al., 1979; Petticrew et al., 2011; Willis et al., 2017; Barber et al., 2018). Anadromous species transfer freshwater-derived nutrients to marine environments during juvenile seaward migration (Willis et al., 2017; Barber et al., 2018). Then adults, which obtain a high proportion of their mass while feeding in marine environments, transfer "marine-derived nutrients" (hereafter MDN) to freshwater ecosystems during the spawning season through direct consumption, the release of gametes, excretion of metabolic wastes, and carcasses decay (e.g., Durbin et al., 1979; Twining et al., 2017; Barber et al., 2018). The pathways of MDN transference from anadromous fish to streams vary among their life history. While carcass decay is the principal input from semelparous species, excretion is the principal input from some iteroparous species such as alosines (Schindler et al., 2003; Post and Walters, 2009; Figure 7). Additionally, carcasses of anadromous fishes may be transferred to terrestrial ecosystems by water movement and terrestrial predators, thereby transferring MDN to riparian food webs (Hocking and Reynolds, 2011; Quinn et al., 2018). Catadromous species can generate the same transference of energy and nutrients in an opposite pathway (Saboret et al., 2021).

Pulsed subsidies of MDN from anadromous fish increase the primary productivity of freshwater ecosystems through the bottom-up pathway of nutrient incorporation. In temperate regions, where freshwater ecosystems are less productive than marine ecosystems, MDN from anadromous species transfers nutrients to freshwater ecosystems increasing their primary productivity (Wipfli et al., 2010; Weaver et al., 2016; Weaver et al., 2018a). In the Penobscot River basin, both bottom-up and top-down pathways of MDN incorporation in freshwater ecosystems have been studied experimentally through carcass addition and theoretically through modeling (Guyette et al., 2013; Guyette et al., 2014; Weaver et al.,

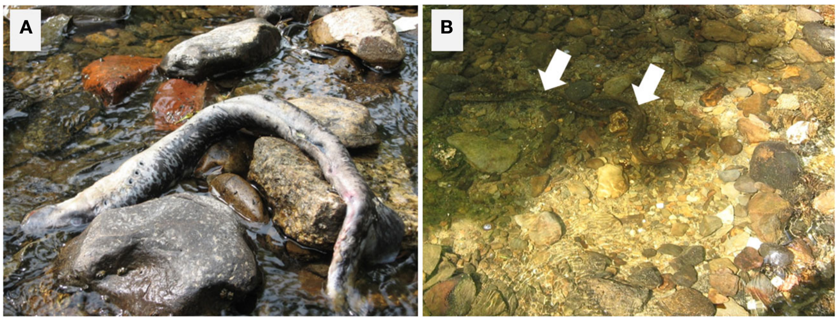

FIGURE 7
Migrating fish impact their ecosystems in complex ways. Sea lamprey (Petromyzon marinus) are native to the Penobscot River, Maine, USA. **(A)** As a semelparous species, lamprey carcasses provide nitrogen and phosphorous into deprived streams. **(B)** These fish have been shown to condition stream beds in ways that benefit other vertebrate and invertebrate taxa (lamprey are indicated with arrows, the nest that has been dug is in the center). (Photo credits, Zydlewski Laboratory, University of Maine).

2015; Weaver et al., 2016; Weaver et al., 2018b; Weaver et al., 2018c; Zydlewski et al., 2021). Both producers and consumers incorporate MDN from anadromous fish subsidies (Guyette et al., 2013; Guyette et al., 2014; Weaver et al., 2016; Weaver et al., 2018b). Direct or indirect assimilation of carcass material may increase growth of young Atlantic salmon thereby bolstering survival (Guyette et al., 2013). Sea lamprey larvae assimilated nutrients found from the carcasses of their post-spawn adult conspecifics, which may improve their growth and enhance earlier metamorphosis (Weaver et al., 2018c).

Consumption of MDN from anadromous fish subsidies may also transfer beneficial biomolecules to in-stream consumers. Anadromous fishes accumulate high contents of vital dietary biomolecules such as ω-3 highly unsaturated fatty acids (hereafter ω-3 HUFAs) in their tissues while feeding in marine food webs; therefore, they transfer them from ω-3 HUFAs-rich (marine) to ω-3 HUFAs-poor food webs (freshwater) through their subsidies (Fuiman et al., 2015; Figueroa-Muñoz et al., 2022; Závorka et al., 2023). Evidence of transference of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) to in-stream consumers following the consumption of anadromous fish subsidies (i.e., carcasses and eggs) has been documented both experimentally and in natural systems (Heintz et al., 2004; Landsman et al., 2018; Figueroa-Muñoz et al., 2022). Indeed, pulsed subsidies of MDN from anadromous fishes, especially eggs, can constitute an important source of ω-3 HUFAs to predators in the Penobscot River.

The absence of migratory fish from habitat in the Penobscot River has deprived the ecosystem of other services as well. Atlantic salmon and sea lamprey are considered "*ecosystem engineers*": they physically change benthic habitats during their nest construction, thereby affecting other organisms in streams (Moore, 2006; Hogg et al., 2014). Spawning sea lamprey generate changes in the streambed during nest construction, making it more complex and benefitting benthic invertebrates (Hogg et al., 2014; Weaver et al., 2018b; Figure 7). Furthermore, nest construction may benefit drift-feeding species (e.g., brook trout and Atlantic salmon) by providing them with energetically profitable foraging habitats (Fausch and Northcote, 1992) or by improved spawning habitat through removal of fine sediments (Saunders et al., 2006; Hogg et al., 2014).

The interruption of migratory fishes by dams also interrupts the life cycle of a myriad of parasitic organisms. While impacts on some species may not initially be recognized as a lost opportunity cost for society (e.g., a host for freshwater copepods; Powell et al., 1999), other interactions are readily recognized as valuable from the human perspective. Freshwater mussels are one of the most imperiled groups of animals in North America (Master et al., 1998) with many species federally listed or extinct (Bogan, 1998). As a result, two species – the yellow lamp mussel (*Lampsilis cariosa*) and tidewater mucket (*Leptodea ochracea*) – were listed as Threatened under the Maine Endangered Species Act in 1997. Within watersheds, dams constrain fish movement and limit freshwater mussel dispersal through their fish-host dependent life history. Glochidia – the parasitic larval stage of freshwater mussels – generally require a vertebrate host to complete development (Kat, 1984; Kneeland and Rhymer, 2008). It is easy to see, therefore, how limitations in fish movement also may limit distribution patterns of mussels. Such examples demonstrate how the loss of migratory fish on one system may influence local and regional ecosystems in complex ways.

Summary

Both the removals of dams and the continued operations of other dams in the Penobscot River have allowed us to better understand the direct and indirect ways that these structures fundamentally alter the river ecosystem. The ecological influences imposed by dams on migratory fishes are both complex and interconnected. Fish populations are affected by direct exclusion, injury, and delay. We have also highlighted less obvious effects such as predation, community changes, demographic shifts, and loss of ecosystem services. The loss of ecosystem services is a diminution of the ecological links native fish species have with the physical, biological, and cultural aspects of the watershed. This complexity makes comprehensive assessment of these seven factors challenging to assess, especially in isolation from one another.

Because dams are constructed and operated to serve human needs, their presence represents a tradeoff with their influence on ecological function (Roy et al., 2018; Song et al., 2019; Roy et al., 2020). In some cases, direct comparisons of alternative approaches may be instructive in weighing costs and benefits of hydropower (Sharma and Waldman, 2021). Such analysis is hampered, however, by the inherent challenges in quantifying the value of an intact river (WWF, 2022), leading conventional economic analyses to chronically undervalue natural resources (Odum, 2007).

Data from the Penobscot River and elsewhere demonstrate that fishways are consistently incomplete in restoring habitat connectivity (Hershey, 2021), and likely fall short in the capacity for restoring populations to the levels possible in intact rivers (Zydlewski et al., 2021). However, fishways are frequently seen as the de-facto "solution" for fragmentation (Waldman and Quinn, 2022) despite their generally poor performance (Noonan et al., 2012). Where socioeconomic tradeoffs are possible, complete removal of dams has been repeatedly demonstrated as an effective tool for restoring the ecological functions that have been diminished (Magilligan et al., 2016; Waldman and Quinn, 2022). The removal of the Edwards Dam in Kennebec River in Maine (1999) was one of the first targeted dam removals for migratory fish restoration (Crane, 2009). Decades later migratory fish have returned to that river, in the millions for some species (Wippelhauser, 2021). Within the Penobscot River, dam removals have allowed the full suite of native fishes to recolonize parts of their historic ranges (Trinko Lake et al., 2012; Hogg et al., 2013; Izzo et al., 2016; Johnston et al., 2019; Whittum et al., 2023), with populations of some species also numbering in the millions now. The Penobscot River remains heavily impounded and ecological processes are impaired, but rehabilitation has brought a suite of migratory fish back to waters that been without them for generations.

Author contributions

JZ: Writing – original draft, Writing – review & editing. SC: Writing – original draft. CD: Writing – original draft, Writing – review & editing. GF-M: Writing – original draft, Writing – review & editing. CM: Writing – original draft, Writing – review & editing. SS: Writing – original draft. RS: Writing – original draft, Writing – review & editing. DS: Writing – original draft, Writing – review & editing. SV: Writing – original draft, Writing – review & editing. KW: Writing – original draft, Writing – review & editing. GZ: Writing – review & editing.

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Conflict of interest

The authors declare that the research 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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Isotopic niches of diadromous fishes inform on interspecific competition in an obstructed catchment

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Competition arises when species share a limited resource, but this can be avoided through niche partitioning. Despite the large body of literature on diadromous fishes, very few studies have focused on niche partitioning when competing for resources. Diadromous fishes are suffering a global decline throughout their range in part due to their peculiar life history traits as they migrate from the sea to freshwater to spawn or the reverse. They are particularly sensitive to river fragmentation induced by barriers. Dams for instance are expected to alter the spatial distribution and resource exploitation of diadromous fishes as well as other organisms. Here, we studied the ecological niche of six taxa of diadromous fishes, temporally co-occurring in the same land–sea continuum obstructed by two river dams. We used Bayesian mixing models run on C and N isotopes to infer the various habitats used and the origin of the trophic carbon in muscle and scale tissues of diadromous fishes. Results showed that the sub-adults of *Anguilla anguilla*, juveniles of *Petromyzon marinus*, and *Salmo trutta* exploit mainly the freshwater, or marine part for adults of *Lampetra fluviatilis*, whereas juveniles of *Platichthys flesus* and Mugilidae use all the habitats of the land–sea continuum. In the freshwater habitat, the microphytobenthos and biofilm are the main sources of carbon used, while in the marine habitat, the basal carbon sources are more diverse. The analyses of niche overlaps between diadromous fishes demonstrate that the widest isotopic niches, observed for *A. anguilla* and *P. flesus*, also have more impact within the community. Results are discussed in terms of intra- and interspecific competition between these diadromous fishes and their generalist/specialist strategies in an obstructed catchment.

KEYWORDS

diadromous fishes, stable isotopes, trophic niche, competition, dam, catchment

1 Introduction

Species, populations, or individuals that co-exist locally potentially compete with each other for resources, notably when limited (Hutchinson, 1957; Chase, 2011). In this sense, resources can include any ecological features and their interactions such as diet and habitat (Chase, 2011). One way to limit intra- and interspecific competition is niche partitioning (Chase, 2011). Niche partitioning can occur spatially and/or temporally, following the variability of resource distribution through space and time. Specialization/generalization strategies theoretically respond to several environmental forces, including population size (Sargent and Otto, 2006, reviewed in Sexton et al., 2017), resource abundance, diversity, and accessibility (MacArthur and Pianka, 1966; Charnov, 1976; Svanbäck and Bolnick, 2007). In the context of interspecific competition and considering population size, models predict that specialization is expected to be promoted in locally rare populations/species, while generalization will be favoured when population/species are locally abundant (Sargent and Otto, 2006, reviewed in Sexton et al., 2017). Specialists are also expected to maximize their fitness in one environment, while generalist fitness will be maximized in multiple ones (Sexton et al., 2017). According to the niche theory, the smaller the local community (individuals and species), the greater the community will be impacted by stochastic ecological processes (Chase, 2003; Fukami, 2004). This is the case for instance when the type and abundance of preys vary in heterogeneous environments. In an environment where resources are patchily distributed, the optimal foraging theory predicts that the niche width of a consumer depends on habitat and prey availabilities as well as their distribution (MacArthur and Pianka, 1966; Charnov, 1976; Svanbäck and Bolnick, 2007). The range of preys is expected to be greater in generalist consumers than in specialist consumers. Therefore, determining niche width can reveal spatial and temporal patterns in resource use and interspecific resource competition (Bolnick et al., 2011), which is particularly important for species conservation. This conceptual framework is particularly relevant for diadromous species sharing common life history traits and resources, whose populations have declined worldwide for many reasons including the fragmentation of freshwater habitats (e.g., Costa-Dias et al., 2009; Lassalle et al., 2009; Duarte et al., 2021; Waldman and Quinn, 2022).

The diadromous fishes have peculiar life history traits as they migrate from the sea to freshwater to spawn (anadromous) or the reverse (catadromous) (Myers, 1949; Harden-Jones, 1968). Many temperate watersheds host multiple diadromous species with varied life histories both within and between species. In France, the potential richness in diadromous taxa is higher in the largest rivers, with, for instance, a maximum of seven taxa observed for the French Atlantic and the English Channel River systems (Seine, Loire, Adour, Dordogne, and Garonne) (Merg et al., 2020). They all share a life history that makes them particularly sensitive to river fragmentation induced by the construction of dams, weirs, and sluices (Pringle et al., 2000; Limburg and Waldman, 2009; Waldman and Quinn, 2022). In Europe, there are more than one million river barriers (Belletti et al., 2020). For diadromous fish, river barriers hamper connectivity and can lead to the confinement of populations and accumulation of individuals down to the barriers (Katano et al., 2006; Drouineau et al., 2018; Forget et al., 2018; Trancart et al., 2020; Verhelst et al., 2021; Teichert et al., 2022a). Over-density can increase intra- and interspecific competition, which in turn can hamper species diversity and individual growth, survival, and/or reproduction (Laffaille et al., 2003; Machut et al., 2007; Costa et al., 2008). Dams have been shown to decrease diadromous species diversity (Merg et al., 2020) and alter growth and resident/migrant strategies in the white-spotted char (*Salvelinus leucomaenis*) (Morita et al., 2000). It may also bias the sex determination of eels (Laffaille et al., 2006; Costa et al., 2008). Despite the large body of literature on diadromous fishes, very few studies have focused on sympatric diadromous fishes and their potential competition in a catchment obstructed by dams (but see Katano et al., 2006). Indeed, an accumulation of the different life stages of diadromous fish downstream to the dams is likely to enhance intra- and interspecific competition for food and habitats and promote generalization for abundant species and specialization for rare ones.

A diadromous niche can be studied through stable isotope analysis, as such analysis provides quantitative measures of both resource and habitat, generally represented in a multivariate space. This is particularly useful in the context of resource partitioning among sympatric species (Newsome et al., 2007); it informs on spatial and temporal variations of resources and consumers (Hobson, 1999). Due to isotope fractionation between prey and consumer, N stable isotope ratios ($\delta^{15}N$) of fish inform on their trophic position, while C stable isotope ratios ($\delta^{13}C$) indicate which type of C fuels their food chains, primary producers such as plant or algae, or decomposers. Both C and N stable isotope ratios are commonly used in combination to depict energy sources and transfers within food webs (e.g., Kostecki et al., 2010; Kostecki et al., 2012; Teichert et al., 2022a; Teichert et al., 2022b). In aquatic systems, $\delta^{13}C$ indirectly informs on salinity variations, with marine ecosystems being ^{13}C enriched compared to freshwater ones (Peterson and Fry, 1987; Hobson, 1999; Herzka, 2005; Reis-Santos et al., 2015). Thus, a diadromous fish entering a river after a significant feeding period in the ocean has the typical ^{13}C enriched signature of the marine environment (Hobson, 1999). Comparatively, freshwater river resident fish can display a large range of ^{13}C-depleted values compared to marine fish, depending on the origin of items they feed on, from the riparian ecosystem (leaf litter, terrestrial plants, or invertebrates) to aquatic primary producers (e.g., algae, plants, and microphytobenthos), invertebrates or fish. When studying the isotopic niche of a consumer, one can sample all the preys and alimentary items and then run an isotopic analysis to decipher which preys and items are more specifically consumed (e.g., Kostecki et al., 2010). This is nevertheless subjected to individual variations in life stage, size, and sexes and also to previously encountered habitats for migrating individuals (Saboret and Ingram, 2019). Therefore, instead of using the exact prey and alimentary items consumed by fishes, one can focus on the basal carbon and nitrogen sources of the isotopic ratio of the consumer (e.g., Lafage et al., 2021). This approach is particularly adapted to diadromous fish species with complex life histories, as they use different trophic strategies and habitats in terms of salinity.

In this study, we analysed the interspecific competition through niche partitioning for trophic and habitat resources between diadromous species in the sea–estuary–freshwater continuum on the Sélune River (Normandy, France). This continuum is obstructed by two large electric dams, which reduce the watercourse accessibility of diadromous fish to 12 km in the downstream part of the river. We hypothesize that an accumulation of different life stages of diadromous fish below a dam is likely to enhance intra- and interspecific competition for food and habitats, increasing niche overlaps and promoting generalization for abundant species and specialization for rare ones. We measured stable C and N isotope values of basal sources (particular organic matter, microphytobenthos and biofilm, and plants) along the continuum and compared the values with those of juveniles to adults of European eels (*Anguilla anguilla*), salmonids (*Salmo salar* and *Salmo trutta*), lampreys (*Lampetra fluviatilis* and *Petromyzon marinus*), European flounders (*Platichthys flesus*), and Mugilidae caught in the same study site. We ran Bayesian simulations (mixing models and ellipse areas) on isotopic data to infer feeding habitat, trophic position, niche width, and overlaps between the species by life stages.

2 Material and methods

2.1 Study site and sampled diadromous species

The Sélune River is 91 km long from its source to the Mont-Saint-Michel Bay (Normandy, France). Two large hydropower dams, La Roche-qui-Boit (height = 16 m) and Vezins (36 m), were constructed in the early 20th century, constraining the diadromous fish community to use the downstream most 12 km of the river (Figure 1). This community is composed of catadromous species (i.e., reproduction at sea), which grow in the estuary and/or the river, such as the European eel (*A. anguilla*), a complex of species belonging to the Mugilidae family (*Chelon ramada*, *Chelon auratus*, and *Chelon labrosus*). The European flounder (*P. flesus*), a facultative catadromous species (some individuals reproduce in brackish or freshwater areas), is found in the downstream part of the river and the estuary. Finally, anadromous species (i.e., reproduction in the river) are also observed below the dams: two species of lamprey (*L. fluviatilis* and *P. marinus*) and two species of salmonids (*S. salar* and *S. trutta*, the latter being facultative anadromous). These seven diadromous species use the Mont-Saint-Michel Bay, the estuary, and the Sélune River as adults, sub-adults, or juveniles throughout the year (Table 1). Elvers of *A. anguilla* arrive from March to May and then grow for several years until metamorphosing in the silver stage (Acou et al., 2005; Teichert et al., 2022a). Departure for migration of silver eels occurs from August to December. Adults of lamprey *P. marinus* and *L. fluviatilis* enter the river in winter and spring to spawn, while the juveniles grow in the river for several years before moving to sea from early fall to early spring. Adults of *S. salar* and *S. trutta* arrive from spring to autumn, enter the river, and reproduce in December and January, and then juveniles stay 1 or 2 years before migrating to the ocean as smolts. Juveniles of *P. flesus* and Mugilidae also grow in the Sélune River after their respective arrival from June to August and April, May, and July (Table 1). Sporadically, shads (*Alosa alosa* and *Alosa fallax*, not included in this study) can also be observed in the Sélune River.

2.2 Sampling and sample preparation

Samples were collected by INRAE (UMR DECOD) and MNHN (Marine Station of Dinard) between 2009 and 2020. Such a large

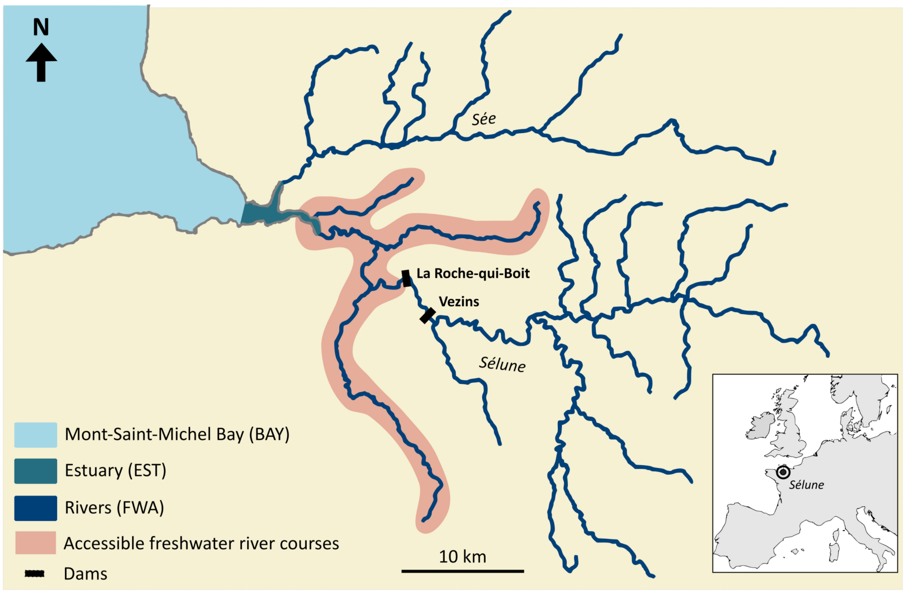

FIGURE 1
Map of the Mont-Saint-Michel Bay (BAY), estuary (EST), and rivers of the Sélune and surrounding ones (FWA). Dams of La Roche-qui-Boit and Vezins are represented as black rectangles. The accessible freshwater river courses are depicted in red.

TABLE 1 Diadromous species temporal presence (in blue) in the Sélune River with months of arrival (A), reproduction (R), and departure from (D).

		J	F	M	A	M	J	J	A	S	O	N	D
Anguilla anguilla	Juvenile*	🟦	🟦	A	A	A	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Sub-adult**	D	🟦	🟦	🟦	🟦	🟦	🟦	D	D	D	D	D
Lampetra fluviatilis	Juvenile	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	D	D	D	🟦
	Adult	A	A	A–R	R	🟦						A	A
Petromyzon marinus	Juvenile	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	D	D	D	🟦
	Adult				A	A–R	R	R					
Salmo salar	Juvenile	🟦	🟦	D	D	D	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Adult	D	D	D–A	D–A	A	A	A	A	A	🟦	🟦	R
Salmo trutta	Juvenile	🟦	D	D	D	D	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Adult	R–D	D	D–A	A	A	A	A	A	🟦	🟦	🟦	R
Platichthys flesus	Juvenile***	🟦	🟦	🟦	🟦	🟦	A	A	A	🟦	🟦	🟦	🟦
	Adult												
Mugilidae	Juvenile	🟦	🟦	🟦	A	A	🟦	A	🟦	🟦	🟦	🟦	🟦
	Adult	🟦	🟦	🟦	A	A	🟦	🟦	🟦	🟦	D	D	D

Column letters represent months. Based on Bruslé and Quignard (2001) for *A. anguilla, L. fluviatilis, P. marinus, S. salar*, and *S. trutta* and Keith et al. (2020) for *P. flesus* and Mugilidae.
*Juvenile group of elvers and yellow eels.
**Sub-adult group of silver eels.
***Unknown departure time.

temporal scale lessens the risk of a bias coming from a single specific year or season and allows for depicting a broad view of the isotopic niche of species and their interactions. All samples originated from the Sélune River watershed and Mont-Saint-Michel Bay, downstream to the lowest dam in the river continuum to the sea (i.e., La Roche-qui-Boit) (Figure 1 and see Appendix A for locations). The use of already collected tissues aimed at avoiding an additional sampling on natural populations, in accordance with the 3 R principle (replacement, reduction, and refinement) in animal studies (Russell and Burch, 1959). For adult *S. salar*, scales collected from 2000 to 2014 were used on fish that stayed one winter at sea (1SW, n = 69, size range 450–700 mm) and two winters at sea (2SW, n = 75, size range 700–850 mm) while returning to the Sélune River to spawn. As they do not feed on the studied catchment, they were not included in the models. Muscle samples of juveniles of *S. trutta* (n = 38, size range 60–80 mm), *P. marinus* (n = 4, size range 130–150 mm), *P. flesus* (n = 115, size range 20–205 mm), Mugilidae (undetermined genus and species, n = 15, size range 20–90 mm), sub-adults of *A. anguilla* (n = 90, size range 510–860 mm), and adults of *L. fluviatilis* (n = 7, size range 250–350 mm) were obtained. Three basal sources were collected from the Mont-Saint-Michel Bay (BAY), the estuary (EST), and the freshwater part of the Sélune River (FWA) downstream of the dam of La Roche-qui-Boit (Table S1, Appendix A) (Figure 1). Photosynthetic organisms (PLA) consisted of aquatic vascular plants in FWA, halophytes in EST, and algae in BAY; they were collected by hand and carefully cleaned out to remove invertebrates. Particulate organic matter (POM) came from 1 l of water filtered on decarbonated (4 h at 550°C) GF-F filters (47 mm diameter, Whatman) at the laboratory. Freshwater samples of POM were also taken upstream to the dams, as they are susceptible to influencing the trophic network downstream (Figure 1; Appendix A). Microphytobenthos and photosynthetic biofilm (MPBB) were sampled in the marine and freshwater environments, respectively (downstream to the lowest dam). The microphytobenthos were extracted from the superficial layer (5 mm) of scraped muddy sediment by exposing them to light for 2 h. The sediment was then covered with a 100-µm nylon filter and sand previously sieved (63 and 250 µm) and decarbonated (5 h, 550°C). After waiting several hours for the microphytobenthos to migrate to the surface through the nylon filter, the superficial layer (2 mm) was scraped and sieved through seawater on a 45-µm filter. The content of the filter was then filtered again under decarbonated GF-F filters (4 h, 550°C). In the river, biofilms were collected on the bottom substratum. Large stones (10 to 20 cm) were picked up, and the biofilm was retrieved by gently brushing until a concentrated solution in a 5-ml vial before filtration on decarbonated GF-F filters (4 h, 550°C) at the laboratory. All samples were kept in a cooler at the field before being frozen (except for the GF-F filters), lyophilized, and ground into a fine powder. Samples were weighed to the nearest 0.01 mg into tin cups in anticipation of stable isotope analyses.

2.3 Stable isotope analyses

C and N isotope analyses were performed at the Stable Isotopes in Nature Laboratory (Fredericton, New Brunswick, Canada) using Carlo Erba NC2500 elemental analyser and a Finnigan Mat Delta XP IRMS. The carbon and nitrogen isotope ratios were expressed in the delta notation $\delta^{13}C$ and $\delta^{15}N$, where $\delta^{X} = [(R_{Sample}/R_{Reference}) - 1] \times 1000$, where X = $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio ^{13}C:^{12}C or ^{15}N:^{14}N in the sample and the reference material. Results are referred to Vienna Peedee Belemnite Carbonate (VPDB) for C and to atmospheric nitrogen for N and expressed in units of ‰ ± standard deviation (sd). Data were corrected using working standards (bass muscle, bovine liver, nicotinamide, and acetanilide) that were previously calibrated against International Atomic Energy Agency (IAEA) standards CH6, CH7, N1, and N2. Repeated analyses of IAEA standards and working standards showed that maximum standard deviations for δ^{13}C and δ^{15}N values were 0.26‰ and 0.37‰, respectively. Standard deviations of samples were analysed in duplicate (n = 10) and averaged 0.11‰ and 0.19‰ for δ^{13}C and δ^{15}N, respectively; single measurements were then carried out on all other samples. The analytical precision (standard deviation for repeated measurements of internal standards) was ±0.2‰ and ±0.3‰ for δ^{13}C or δ^{15}N, respectively.

2.4 Statistical analyses

C:N ratios were checked to identify possible bias in δ^{13}C values due to high lipid content in the tissue (Post et al., 2007). When C:N ≥ 3.5, δ^{13}C values were corrected following Post et al. (2007). Similarly, δ^{13}C values obtained from scale tissues were corrected for high concentrations of glycine and proline according to Satterfield and Finey (2001). Analyses of isotopic data obtained for basal sources and diadromous fish were performed in R 4.2.1 (R Core Team, 2022) using Bayesian mixing models and analytical tool suite proposed by MixSIAR 3.1.12 (Su and Yajima, 2012; Stock and Semmens, 2016; Stock et al., 2018). δ^{13}C and δ^{15}N values were used to estimate the contributions of basal sources (PLA, MPBB, and POM) to diadromous species for habitats (FWA, EST, and BAY) whose contribution was above the 0.30 threshold. An exception was made for *P. marinus* for which the small sample size did not allow to have more than three basal sources for the model to converge. For this species, basal sources were studied only in FWA, as this habitat is more likely used (Quintella et al., 2003). For each diadromous species, models were set up with the following characteristics: three chains with 300,000 iterations and a burn-in of 200,000 with a thin of 100 to allow for adequate model convergence. Trophic enrichment factor values were derived from Kostecki et al. (2012) and Selleslagh et al. (2015). Values for aquatic habitat (FWA, EST, and BAY) and carbon origin (POM, MPBB, and plants for FWA and BAY) models were 2‰ ± 0.1‰ and 5.8‰ ± 0.1‰ for δ^{13}C and δ^{15}N, respectively. All MixSIAR models were run with residual and process errors set as TRUE. Model convergence was checked using Gelman–Rubin and Geweke's diagnostics. Isotopic niche widths (δ^{13}C and δ^{15}N) of each diadromous species and overlaps were analysed using the R package, SIBER 2.1.7 (Jackson et al., 2011; Rossman et al., 2016). Posterior ellipsoids were calculated after 2×10^4 iterations, a burn-in of 1×10^3, over two chains; Bayesian standard ellipse areas (SEA_B) were calculated, and the 95% predicted Bayesian confidence interval (SEA_B CI95) was used to estimate the proportion of overlapping between species. Details of all the R script, raw data, and model results used in this study are available in Appendix B.

3 Results

3.1 Species position along the river–sea isotopic continuum

The trophic position of diadromous species/life stage and basal sources are based on their mean values of δ^{13}C and δ^{15}N, which were added to trophic enrichment factors for diadromous species. Figure 2 shows the overall organization of the food web of the different species making up the diadromous community. In particular, we see their relative position and the relative influence of basal sources according to their origin: freshwater, estuarine, and marine habitats (Figure 2). From the position of each diadromous species within the trophic network (Figure 2) and the results of the mixing models (Figure 3), we can define the relative contributions of basal sources (MPBB, POM, and PLA) according to habitats (FWA, EST, and BAY).

FWA basal source was the major contributor to the isotopic signatures of sub-adult *A. anguilla* and juveniles of *P. marinus* and *S. trutta* (Figures 2, 3A, Table S2). MPBB were the most likely basal source for sub-adult *A. anguilla* and juvenile *S. trutta*, while POM and MPBB were for juvenile *P. marinus* Figure 3B). Conversely, equal average contributions of FWA, EST, and BAY were found for juveniles of *P. flesus* and Mugilidae, suggesting that individuals could exploit trophic resources from different habitats along the land–sea continuum (Figures 2, 3A, Table S2). Juveniles of these species found their carbon origin mainly on MPBB in FWA and BAY, except for *P. flesus* in BAY, where individuals relied equally on all three basal sources (Figure 3B). Adults of *L. fluviatilis* had more typical marine signatures (Figures 2, 3A, Table S2), with marine POM being their most likely basal source (Figure 3B). Adults *S. salar* also had typical marine signatures, with higher δ^{15}N values for 2SW compared to 1SW fish (Figure 2). Mixing models using basal sources from the three habitats were not run for *S. salar* since the species do not feed when migrating back to freshwater.

3.2 Isotopic niches of diadromous fishes

Isotopic niche widths of diadromous species varied between species and life stages. Mean SEA_B [CI_{95}] was maximum for *A. anguilla* (12.314 [9.853–15.039]) and then decreased for *P. flesus* juveniles (7.675 [6.251–9.225]), *S. trutta* juveniles (4.250 [3.063–5.869]), Mugilidae juveniles (1.037 [0.614–1.793]), *P. marinus* juveniles (0.334 [0.104–1.211]), and *L. fluviatilis* (0.203 [0.094–0.480]) (Figure 4, Table S3). Correction for sample size applied to SEA_B did not significantly alter the niche widths of diadromous species, but marginally for *P. marinus* (SEA_B = 0.334, SEAc = 0.086) (Table S3).

The isotopic niche of *A. anguilla*, which is the widest niche observed in this dataset (Figure 4, Table S4), overlapped with several other diadromous species as juveniles, such as *P. flesus*, *S. trutta*, *P. marinus*, and Mugilidae (Figure 5, Table S5). Juveniles of *P. flesus*, the second widest isotopic niche observed in this dataset, overlapped with sub-adults of *A. anguilla* and juveniles of *S.*

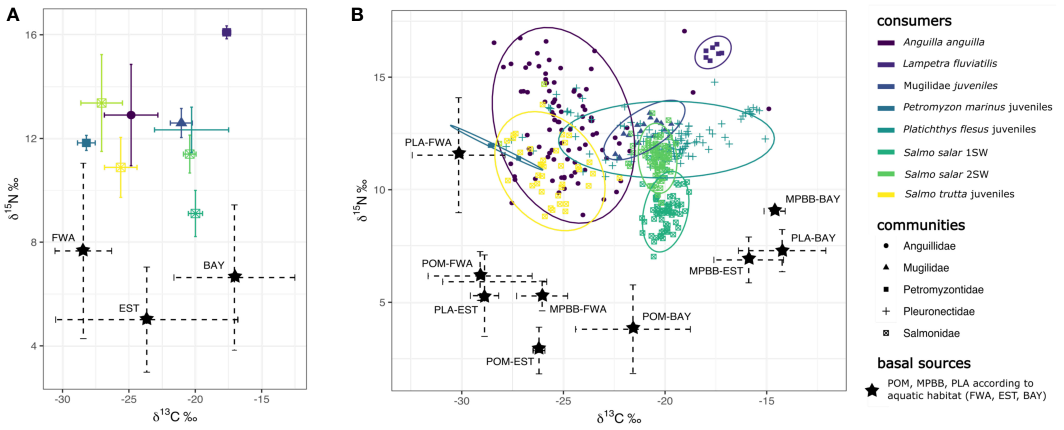

FIGURE 2

(A) Biplot of the means and standard deviations of $\delta^{13}C$ (x-axis) and $\delta^{15}N$ values (y-axis) of basal sources and diadromous studied along the Mont-Saint-Michel Bay to Sélune River continuum. **(B)** Biplot of the means and standard deviations of $\delta^{13}C$ (x-axis) and $\delta^{15}N$ values (y-axis) of basal sources and $\delta^{13}C$ and $\delta^{15}N$ values and their 95% ellipses for each of the diadromous studied. Basal sources are displayed according to aquatic habitat (estuary (EST), freshwater (FWA), and marine (BAY)) and sample type (particular organic matter (POM), microphytobenthos-biofilm (MPBB), and aquatic plants (PLA)). Different colours represent the various diadromous species (family for Mugilidae) studied, which include sub-adults of *Anguilla anguilla*, adults of *Lampetra fluviatilis* and *Salmo salar* 1SW and 2SW, and juveniles of Mugilidae, *Petromyzon marinus*, *Platichthys flesus*, and *Salmo trutta*. The same shapes correspond to diadromous belonging to the same family. *S. salar* 1SW and 2SW spend respectively one and two winters at sea to grow before migrating to the Sélune for reproduction.

trutta and Mugilidae (Figure 5, Table S5). The isotopic niche of *S. trutta* as juveniles overlapped with sub-adults of *A. anguilla* and juveniles of *P. flesus* and *P. marinus*. The isotopic niche of juveniles of Mugilidae overlapped with sub-adults of *A. anguilla* and juveniles of *P. flesus*.

The isotopic niches of *A. anguilla* and juveniles of *P. flesus* overlapped more with other diadromous niches than they were impacted. Indeed, their niche width impact is greater on the left panels compared to the right panels (Figure 5, Table S4). On the contrary, the isotopic niches of juveniles of *S. trutta*, Mugilidae, and *P. marinus* were more impacted by other diadromous niches that they overlapped with (Figure 5, Table S4). The isotopic niche of adult *L. fluviatilis*, characterized by a typical marine signature, did not overlap with other diadromous species niches and was not impacted by them [not represented in Figure 5, as overlap values were below 0.05 (Table S5)].

4 Discussion

The various diadromous species studied here are all simultaneously present in the Sélune River where they are confined to the 12-km downstream reach below the dam and estuary. Although they do not arrive, colonize, and reproduce at the same time, they all co-occur at some point for their development, growth, or migration for reproduction. The Sélune River and estuarine system is thus a peculiar aquatic ecosystem, where several diadromous species reside for some times: one is critically endangered (*A. anguilla*), another is vulnerable (*S. salar*), and others are least concern (*S. trutta*, *P. flesus*, Mugilidae, *P. marinus*, and *L. fluviatilis*), as classified by the International Union for Conservation of Nature (IUCN) red list of threatened species in Europe (IUCN, 2023). This study provides the first isotopic analysis by means of basal carbon sources to infer the trophic ecology and habitat use of several diadromous species living in the same river. Basal carbon sources are not directly assimilated by the diadromous species studied here, but they are transferred along the food chains from primary consumers to fish. Focusing on the basal carbon sources instead of the diet allowed us to infer and compare the niche partitioning of these species, although they feed on different sources of prey.

Results confirm that sub-adults of *A. anguilla* (Cucherousset et al., 2011), juveniles of *P. marinus* (Quintella et al., 2003), and *S. trutta* (Michel and Oberdorff, 1995) exploit mainly the freshwater, or the marine part for adults of *L. fluviatilis* (Kelly and King, 2001), while some others, such as juveniles of *P. flesus* and Mugilidae (Lafage et al., 2021; Teichert et al., 2022b), use all habitats of the land–sea continuum. Several diadromous adults do not feed when they migrate in the Sélune aquatic system. This is the case of *P. marinus* and *L. fluviatilis*, which feed as external parasites of marine fishes and cetaceans, but also of *S. salar* 1SW and 2SW, spending respectively 1 and 2 years at sea to grow before migrating in the Sélune for reproduction. *S. salar* 1SW and 2SW were not included in the Bayesian models because they do not feed near the environment of the Sélune aquatic system (Keith et al., 2020), as opposed to *L. fluviatilis*, whose hosts are thought to live in marine habitats close to the Sélune River (Elliott et al., 2021). Indeed, *S. salar* 1SW feed and grow in Greenland seas, and *S. salar* 2SW in North Ireland and England seas (MacKenzie et al., 2012). In the same way, *A. anguilla* fast on their spawning migration from freshwater to the Sargasso Sea (Wright et al., 2022). However, the $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures remain stable for approximately 1 month in their muscles (Buchheister and Latour, 2010) and therefore reflect the eel diet in the freshwater growth habitat they came from.

Niche partitioning between these diadromous fishes also occurs through the distinct use of basal carbon sources, but this depends on

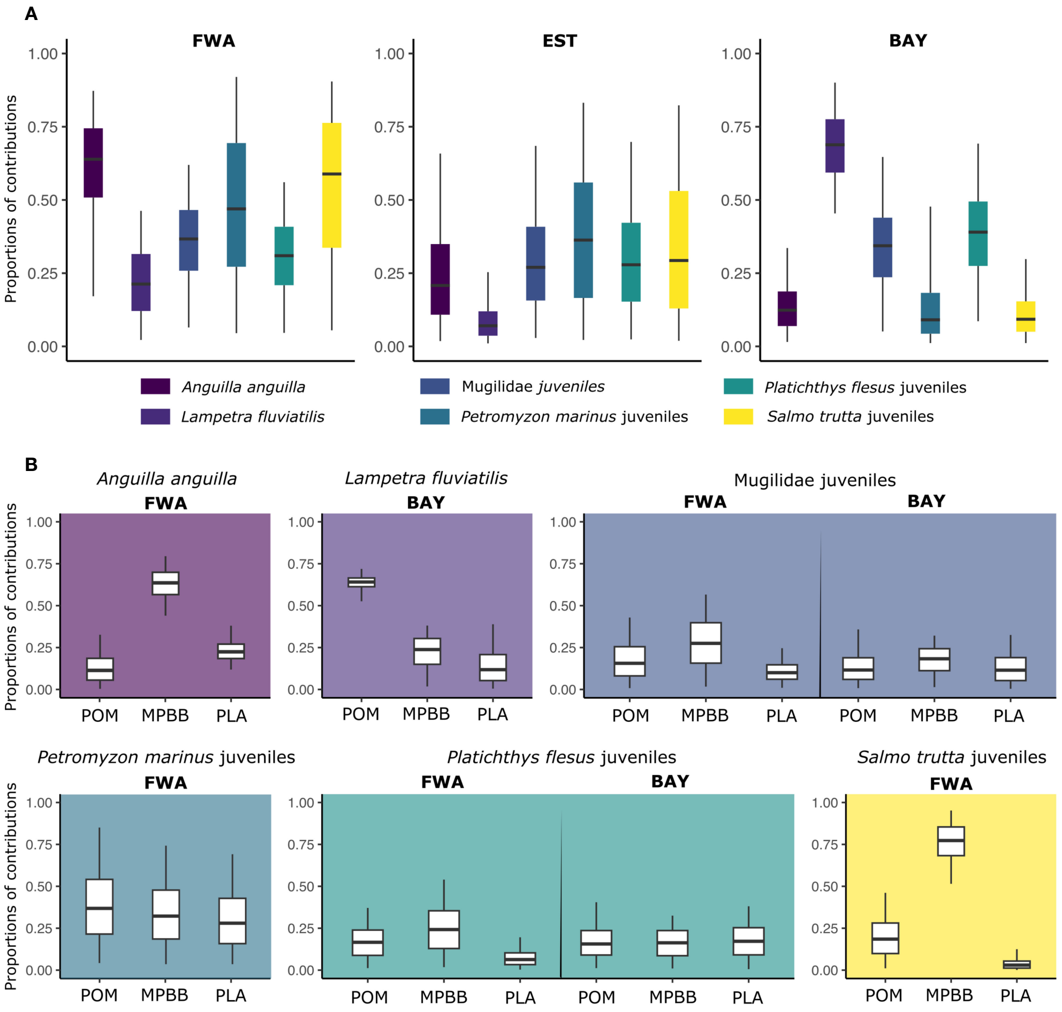

FIGURE 3
Boxplots of median contributions (with 50% and 95% Bayesian confidence intervals) of each basal source to diadromous fish consumers. **(A)** Contribution of each habitat type (freshwater (FWA), estuary (EST), and marine (BAY)). **(B)** Contribution of each sample type (particular organic matter (POM), microphytobenthos and biofilm (MPBB), and aquatic plants (PLA)) within the most dominant habitat type. Between three and six basal sources and a maximum of two different habitats were included in each model to maximize model convergence. A summary of the contribution proportions is presented in Table S2.

the habitat used. Indeed, sub-adults of *A. anguilla* and juveniles of *S. trutta*, *P. flesus*, and Mugilidae all use MPBB as their primary source of carbon in freshwater. In this habitat, juveniles of *P. marinus* equally relied on MPBB and POM as basal sources of carbon, but the small sample size for this species did not allow us to clearly infer their basal carbon source. In the marine habitat, diadromous basal carbon sources are more diverse, ranging from POM for adult *L. fluviatilis*, to POM, MPBB, and PLA for juveniles of *P. flesus* and Mugilidae even though MPBB is the main source of basal carbon for the later. Competition over basal carbon sources is thus more likely in the freshwater part of the land–sea continuum, and from our results, we identified three factors that could exacerbate this competition. Firstly, we found that diadromous species in the Sélune River watershed and Mont-Saint-Michel Bay depend more on the freshwater than on the marine habitats, and secondly, they all rely on the same basal carbon source (i.e., MPBB) in the freshwater habitat. Thirdly, these diadromous species, exploiting the freshwater habitat of the land–sea continuum, are physically coerced by the dams, particularly species that would normally colonize upper parts of rivers (i.e., *A. anguilla*, *L. fluviatilis*, *P. marinus*, *S. salar*, and *S. trutta*). These factors certainly play a role in increasing both intra- and inter-species competition between these diadromous when co-occurring in the same river. By contrast, we found that juveniles of *P. flesus* and Mugilidae exploit both the marine and freshwater parts of the land–sea continuum of the Sélune River watershed and Mont-Saint-Michel Bay, and they developed different strategies to exploit different sources of basal carbon. This could be a strategy to relax the likely competition both within and between these species. Niche partitioning through space is widely described in the literature, and strategies to minimize competition take place not only between but also within species (Sexton et al., 2017).

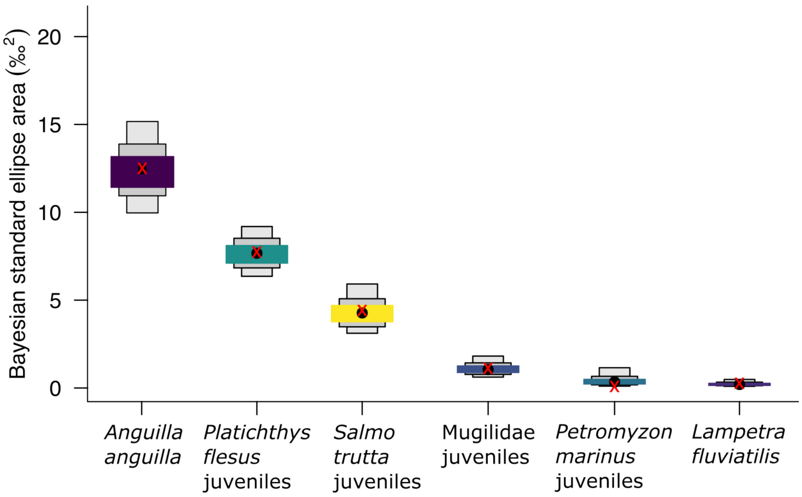

FIGURE 4
Diadromous isotopic niche widths as Bayesian standard ellipse areas (SEA_B) for $\delta^{13}C$ and $\delta^{15}N$ of diadromous species. Box width and colour denote credible intervals (colours: 50%, medium; grey, 75%, narrow; light grey, 95%); black dots, median; red crosses, predicted standard ellipse area of 95% (2.5% to 97.5%) corrected by sample size (SEAc). See also Tables S3 and S4.

Nonetheless, the wider picture of potential competition within and between these diadromous fishes is not easily retrieved from their use of habitats (freshwater, estuarine, and marine) and carbon sources (POM, MPBB, and plants). Niche overlap assessment is thus essential to estimate the competition between diadromous species. Our results showed that niche overlaps occurred between diadromous, despite the use of indirect sources of carbon (we concentrated on basal primary producers as basal sources). This means that any basal source compartment alteration could impact diadromous fish and possibly the competition between each other. Some diadromous species such as *A. anguilla* (sub-adults) and *P. flesus* (juveniles) overlapped other diadromous species' niches, more than they were overlapped by *P. marinus* and Mugilidae, both as juveniles. This is mainly because they have a wider niche than the impacted species. The dominance of *A. anguilla* in this system, in terms of both niche use and width, is congruent with

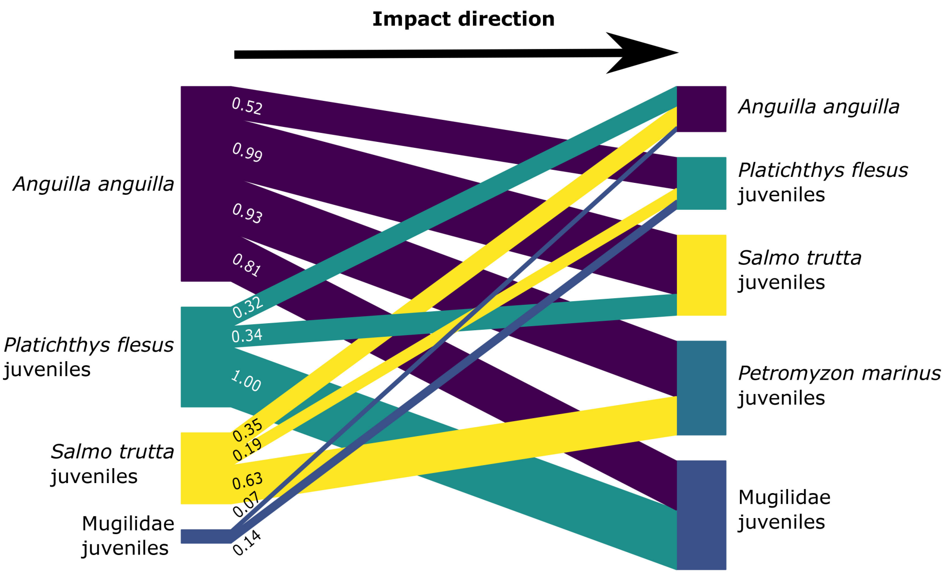

FIGURE 5
Bipartite graph of the overlap impacts of diadromous species/life stage (left group) on the isotopic niche width of others (right group). Niche width is retrieved as Bayesian standard ellipse areas (SEA_B) for $\delta^{13}C$ and $\delta^{15}N$ of diadromous species. The width of the bars between the left and right groups represents the proportion (see numbers) of impact from the left diadromous species/life stage on the right ones, calculated as the overlap between the two species divided by the niche width of the right one. *Petromyzon marinus* is absent from the left group because its impact on the right diadromous species was below 0.05 or null. *Lampetra fluviatilis* is absent from the left diadromous species for the same reason, and in the right group because it is not impacted. See also Table S4.

other studies (Cucherousset et al., 2011; Denis et al., 2022) and explains why this euryecious and opportunistic species was classified, in France until 1984, as a pest in salmonid producing rivers before their decline (CSP, 1998). In *A. anguilla*, some individuals are more specialized in fish and others in invertebrates (Cucherousset et al., 2011). This translates not only in morphological differences but also in distinct habitat niche use in a river, with individuals of the former being located further from the riverbank (Cucherousset et al., 2011). A similar pattern of specialization is observed for *P. flesus* where some individuals exploit different habitats of the land–sea continuum (Teichert et al., 2022b) and different sources of basal carbon, albeit no morphological differences have been described in this species. Globally at the scale of the studied area, *A. anguilla* and *P. flesus* appeared to be more generalist than other diadromous species, as individuals strategically exploit different sources of carbon and/or habitats within the same watershed. The other diadromous fishes; juveniles of *S. trutta*, *P. marinus*, and Mugilidae; and adults of *L. fluviatilis* appeared more specialized in their habitat use and basal source of carbon.

Intraspecific competition is one of the main drivers of inter-individual variation (individual specialization; Bolnick et al., 2003), with theory predicting an increase in phenotypic variation leading to population niche expansion as competition increases (Van Valen, 1965; Bolnick, 2001; Svanbäck and Bolnick, 2005; Sexton et al., 2017). Phenotypic variation in the head morphology of *A. anguilla* has been demonstrated according to their specialization degree in fishes or invertebrates (Cucherousset et al., 2011). This suggests that *A. anguilla* presents some level of intraspecific competition in the Sélune watershed, as demonstrated by their wide niche. This idea is reinforced by the presence of dams obstructing the Sélune watershed over more than a century; the La-Roche-qui-Boit and Vezins dams were built in 1914 and 1927, respectively. The concentration of different diadromous species on an obstructed catchment is expected to lead to co-occurrence of species that do not co-occur in an open watershed and vice versa because of alteration/delay of the species-specific patterns of migration. Patterns of migration depend on the local environmental conditions experienced by individuals, and intraspecific competition will decrease the availability of individual resources. This will in turn increase interspecific competition over the same resources exploited by different species.

In the presence of interspecific competition, specialization and therefore niche width reduction are favoured when species are locally rare, while generalization is favoured when species are locally abundant (relative to other species) (Sargent and Otto, 2006; Sexton et al., 2017). How niches are partitioned, how intraspecific and interspecific competitions impact them, and whether abundant and rare species differ in their niche width are critical questions, as these will determine their ability to cope with changes (global change and/or anthropogenic pressures) (Colles et al., 2009; Sexton et al., 2017). There are concerns and signals of the global decline of specialist species (Clavel et al., 2011), and some generalist species such as *A. anguilla* are already critically endangered. In the Sélune River, dam removal is expected to relax the likely competition within and between diadromous species as densities downstream of the dams will decrease, rendering novel habitats upstream of the dams accessible (Merg et al., 2020). This may increase the niche width of diadromous species relaxing their local densities and potentially altering their generalist/specialist feeding strategy. Thus, restoration actions of the watersheds used by diadromous fish, such as dam removal, improved connectivity, and promotion of habitat diversity, are evidently needed for their conservation.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because tissue samples were retrieved from collections.

Author contributions

AL: conceptualization, data curation, validation, formal analysis, methodology, and writing—original draft, review and editing. AC: conceptualization, methodology, funding acquisition, supervision, and writing—review and editing. J-MR: conceptualization, validation, formal analysis, methodology, and writing—review and editing. NT: methodology, formal analysis, and writing—review and editing. EF: conceptualization, funding acquisition, and writing—review and editing. AA: conceptualization and writing—review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1242452/full#supplementary-material

APPENDIX A

All raw data organised per source and species/life stage of diadromous, and details of the mixing models.

APPENDIX B

R scripts and packages used in the analysis of this article.

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Deconstructing dams and disease: predictions for salmon disease risk following Klamath River dam removals

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The health of fish populations and the river systems they inhabit have broad ecological, cultural, recreational, and economic relevance. This is exemplified by the iconic anadromous salmonid fishes native to the West Coast of North America. Salmon populations have been constrained since the mid nineteenth century by dam construction and water reallocation. In the Klamath River (Oregon and California, USA), a series of dams built in the early-mid 20th century cut the basin in two and blocked anadromous fish access to more than 600 river kilometers. This dramatic loss of habitat, coupled with infectious diseases and resulting epizootics, have impacted the wellbeing of these salmonid populations. In 2023-2024, the Klamath River will undergo the largest river restoration project in US history. Removal of the four lowermost dams will cause profound physical changes to the river, including flow, water temperature, and channel geomorphology. The dam removals will reconnect the lower and upper portions of the basin, and provide fish passage after a century of segregation. Reestablishment of upstream and downstream fish movements will also alter the occupancy and abundance of the salmonid hosts and their pathogens. The increased habitat availability and longer migration routes will increase duration of pathogen exposure and potential impacts on juvenile survival and adult pre-spawn mortality. However, restoration of more natural flow and sediment regimes will decrease overall fish disease risk by disrupting complex parasite life cycles. To better understand these multifarious, competing factors, we review the salmonid species in the Klamath River, and provide an overview of their historical pathogen challenges and associated diseases and use this as a framework to predict the effects of dam removals on disease dynamics. Our review and predictions are a synthesis of expertise from tribal biologists, fish health specialists and fish biologists, many of whom have lived and worked on the Klamath River for decades. We conclude with recommendations for expansion of current pathogen monitoring and research efforts to measure changes in host-pathogen dynamics basin-wide.

KEYWORDS

Klamath River, salmonids, dam removals, disease, redistribution, pathogens, parasites, *Ceratonova shasta*

1 Introduction

We are on the cusp of the largest dam removal project in history - four large dams on the Klamath River, USA, will be removed in 2023-2024, with key goals being ecosystem restoration and the recovery of salmon populations. In addition to meeting indigenous cultural and subsistence needs, salmon restoration will have far-reaching ecological, recreational, and economic benefits.

The Klamath River dams blocked access to more than 600 river kilometers of habitat for anadromous fishes and severed the basin in two. Consequences included the extirpation of anadromous salmon populations upstream of the dams and a shift in the dominant life history in salmonid populations both upstream and downstream of the barriers. The removal of these dams and the coincident closure of a major mitigation hatchery below the dams will change the distribution, species composition and life-history diversity of salmon populations (Quiñones et al., 2015). The opening of new habitat in the tributaries and mainstem river upstream of the dams will restore many historical processes, habitat features and populations of anadromous fishes, which include ecologically and economically important Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*O. kisutch*) and Steelhead (anadromous *O. mykiss*). After dam removals, the basin will become a more varied and dynamic environment that will allow for reexpression of diverse salmonid life-history types, leading to more resilient, viable and self-sustaining populations with varied migration timings and growth patterns, as anadromous species disperse into the Hydroelectric Reach and upstream (Williams et al., 2006).

Physical changes in the environment will alter fish-pathogen interactions and disease risk. Dam removals will result in changes to river sediment transport and geomorphology, flow and temperature regimes and water quality which are expected to benefit ecosystem function and salmon health (e.g., Bellmore et al., 2019). While many of these changes are likely to be positive in the long term, there will also be some challenges. Here, we use these interactions as a framework for our analysis of how salmon disease risk will respond to dam removals on the Klamath River. There are few published studies examining how dam removal impacts fish disease risk. In a much smaller system, Manatawny Creek Dam (PA, USA), a decreased incidence of fish parasites in former impoundments was observed (Hart et al., 2002). Prior to the removal of two large dams on the Elwha River (WA, USA; in 2011 and 2014), a targeted pathogen survey assessed the risk of anadromous fish introducing pathogens to isolated upriver populations, and detected only *Renibacterium salmoninarum* in non-anadromous fishes (Brenkman et al., 2008). The Elwha system has not had any detections of routinely monitored viral pathogens, either endemic or exotic, prior to and since the dams have been removed (M. House, NW Indian Fisheries Commission, pers com.). While these scenarios provide some insights into potential outcomes following dam removals, these systems differ markedly from the Klamath River, both in terms of scale and pathogen concerns.

Klamath River salmon encounter and host a variety of freshwater pathogens, first as juveniles migrating downstream to the ocean and then as adults returning to spawning grounds. The myxozoan parasite *Ceratonova shasta* is a primary factor affecting salmon recovery in the Klamath River (Fujiwara et al., 2011; Ray et al., 2014) because of its impacts on juvenile salmon, by direct mortality or predation associated with disease morbidity. Long-term monitoring and research on this parasite have informed current fisheries management, and resulted in models that can inform predictions on the effects of dam removal on this disease (Ray et al., 2015). Thus, our predictions in this paper will largely focus on *C. shasta*. However, other pathogens present in the Basin also have the potential to cause serious disease. Although large epizootics in salmonids are rarely documented, in summer 2002 thousands of adult salmon died as a result of combined infections of the ciliate parasite *Ichthyophthirius multifiliis* and the bacterial pathogen *Flavobacterium columnare* (Belchik et al., 2004). We use available data on presence and characteristics of these, and other pathogens of concern in the Klamath River, to predict how host-pathogen interactions and associated risks may change following removal of the four hydroelectric dams and reconnection of the upper and lower basins.

Herein, we present an overview of the Klamath River and the changes that are predicted to occur following dam removals, and of the salmonid species of concern and their historical pathogen challenges. We consider the effects of dam removals on infection dynamics and disease occurrence of important fish pathogens in salmonids in the Klamath River, then offer informed predictions of these effects on fish health. We draw on a combination of Western Science and Traditional Ecological Knowledge to inform these predictions. Our process involved hybrid workgroup meetings and discussions in the context of available data, and relied on expert opinions to develop conceptual models for perceived risks under the context of dam removals. This assessment provides a foundation to guide monitoring programs and management plans, and to understand the associated benefits and risks to salmonid populations in the Klamath River basin following dam removals.

2 Klamath River and hydroelectric project before dam removals

The Klamath River flows more than 400 km through southern Oregon and northern California, on the west coast of the United States (Figure 1). As of 2023, greater than 80% of the upper basin, previously freshwater marshland, has been converted to land that supports farming, ranching, and the city of Klamath Falls. Upper Klamath Lake (UKL), the source of the Klamath River, is fed by the Williamson and Sprague rivers, which originate in the high desert of southern Oregon. Downstream from Klamath Lake the river flows through a series of six dams that provide water storage for irrigation and hydroelectric power, before entering the canyon that flows through the Klamath Mountains to the Pacific Ocean. In the lower basin the river is fed by major tributaries that include the Shasta, Scott, Salmon and Trinity rivers. Given the complex and contentious nature of surface water allocation in the Basin, Federal Regulators issued directions to attempt to balance water budgets for irrigation while conserving fish. These Biological Opinions specified flow release requirements (for dilution, surface and deep flushing flows) to reduce disease incidence for Coho Salmon downstream of Iron Gate Dam (NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service), 2013; NMFS (National Marine Fisheries Service), 2019).

The Klamath River basin is home to multiple groups of indigenous peoples, including the Yurok, Karuk and Hoopa Valley tribes in the canyons of the lower basin, and the Klamath, Modoc and Yahooskin tribes in the upper basin. For thousands of years, people have harvested returning adult salmon and other aquatic resources that are central to their identity and existence. Western colonial expansion in the 19th and 20th centuries brought increased harvests of fish and timber, and hydrological alterations first for hydraulic mining for gold, then for agriculture and power generation. The Klamath Project, beginning in 1906, transformed the basin by diverting stream flows and converted marsh to agricultural use in the upper Klamath Basin.

Beginning in 1917, a series of dams was constructed between river kilometers (rkm) 305 and 409. These comprise the four lowermost mainstem dams that are being removed, Iron Gate, Copco I and II and JC Boyle, and two upstream dams, Keno and Link River, which will remain in place. The Link River Dam, at the mouth of Klamath Lake, stores most of the water used for irrigation of the Klamath Project and historically provided hydropower. Keno Dam impounds water to form Lake Ewauna, which supplies a limited amount of water for irrigation of adjacent land. In addition to these Project diversions, ongoing water withdrawals occur in all the major tributaries to the Klamath River.

In response to the impacts of the mainstem dams on anadromous salmon, in particular loss of access upstream of Copco I and II dams, a hatchery and rearing facility was established on Fall Creek (Figure 1). This facility ran from 1919-1948 as a hatchery, then up to early 2000s as rearing ponds. Completion of the furthest downstream and largest dam, Iron Gate, in 1961-1964, blocked all upstream movement of salmonids,

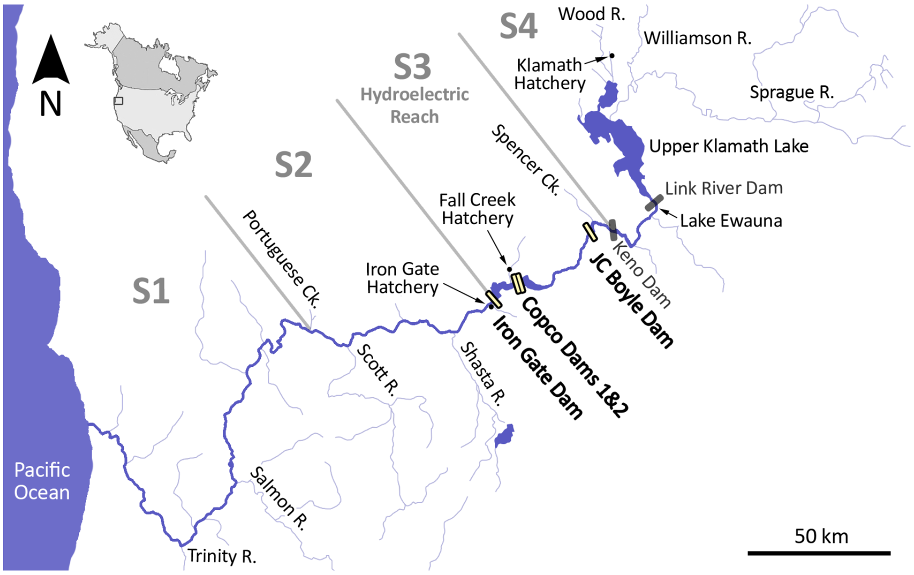

FIGURE 1
Map of the Klamath River Basin, showing major tributaries, features and sections mentioned in the text. Dams are shown as boxes; those with bold labels and outlines represent the four dams that are being removed. Fish ladders at Keno Dam and Link River Dam will allow upstream fish migration past those remaining barriers. Iron Gate Hatchery will be decommissioned with the removal of Iron Gate Dam; Fall-run Chinook Salmon and Coho Salmon production will be continued at Fall Creek Hatchery for up to eight years following dam removal. Klamath Fish Hatchery will be used for active reintroduction of Spring-run Chinook Salmon in the Upper Klamath Basin.

including access to Fall Creek. Hence, Iron Gate Hatchery (1961-2023) was established to mitigate impacts of dam construction on Chinook Salmon and Coho Salmon. The hatchery, situated immediately below the dam at the congregation point for returning adults, was used to spawn these fishes, and then rear and release juveniles (yearlings and smolts) each spring and fall. Additionally, Trinity River Hatchery was constructed lower in the basin on the Trinity River to compensate for salmonid spawning habitat lost following the completion of Lewiston Dam in 1963.

3 Physical changes to the Klamath River with dam removal

The 50-year federal license for four of the Klamath River dams expired in 2006. The owner of these dams, PacifiCorp, entered into a Settlement Agreement that in 2016 resulted in transfer of ownership of the dams and related facilities to an independent nonprofit entity, the Klamath River Renewal Corporation. As a result of this agreement, the Corporation developed the schedule for dam removals in the 2018 Definite Plan Report, based on the assumptions and schedule outlined in the USBR analysis (U.S. Bureau of Reclamation [USBR], 2011; CSWRCB (California State Water Resources Control Board), 2018). Removal of the lowermost four Klamath River dams began in 2023 with deconstruction of Copco 2. Drawdown of the three reservoirs was scheduled for January-March 2024, which the Renewal Corporation identified as the period of least impact to aquatic species in the Klamath River downstream of Iron Gate Dam. By the end of 2024, all four dams will be removed, concurrent with instigation of restoration work, which will continue well beyond 2024.

Salmon disease risk is driven by a multitude of abiotic and biotic factors. The following sections detail the short- and long-term physical changes that dam removal will have on these factors. Abiotic effects that will alter salmon disease dynamics include changes to flow and temperature regimes, sediment transport, water quality, and re-establishment of connectivity. These changes will produce short- and long-term biotic responses.

3.1 Short-term changes

Short-term impacts of reservoir and dam removals will commence with reservoir draining ("drawdown") starting January 2024 and continuing through approximately December 2024. The impacts we consider for salmon disease risk include immediate effects on river discharge, hereafter termed "flow," temperature, release of trapped sediments, and water quality. We cover connectivity under long-term changes as fish movements in the short term will be disrupted.

3.1.1 Flow dynamics and thermal regime

Short-term alterations to flow and temperature regimes will result from the releases of water stored in the reservoirs during drawdown (planned for approximately January-March 2024), and following removal of physical structures (CSWRCB (California State Water Resources Control Board), 2018). During this period, water release patterns will be stable and low, with planned maximum rates corresponding to 3 - 15% of a peak flow magnitude that recurs every two years (or less than half of typical winter flows). Water temperatures are expected to be marginally warmer during drawdown due to the release of water from the reservoirs, if drawdown occurs on schedule (January-March 2024).

3.1.2 Sediment transport

Dam removals will result in short-term increases in suspended sediments and turbidity from the release of sediments trapped within the reservoirs. The estimated 12 million cubic meters of sediment accumulated in the reservoirs is comprised of inorganic particles including clay/silt (~85%), with sand (~12%), gravel and larger material (~3%) making up the remainder (Stillwater Sciences, 2010; U.S. Bureau of Reclamation [USBR] and California Department of Fish and Game [CDFG] (2012), CSWRCB (California State Water Resources Control Board), 2018). Mobilization and flushing of the majority of trapped sediments is expected to occur rapidly in the 4 to 8 months following reservoir drawdowns because of the dominance of fine particles. During the first year, sediment releases will bury mainstem salmonid spawning areas (e.g., Greig et al., 2005; Levasseur et al., 2006) and habitat for invertebrate hosts of parasites with complex life cycles (e.g., Doeg and Koehn, 1994). These effects will primarily occur in the 15 rkm downstream of Iron Gate Dam (Stillwater Sciences, 2008).

3.1.3 Water quality

The downstream transport of trapped sediment will also affect water quality over the short term. Released reservoir sediments will depress dissolved oxygen levels due to high concentration of organics (primarily derived from dead algae) in the reservoir sediments. The pulses of sediment that will co-occur with storm events until organic sediments are metabolized or flushed, will likely continue to drive periodic short-term dissolved oxygen sags (Stillwater Sciences, 2010).

3.2 Long-term changes

The long-term impacts of reservoir and dam removals include restored fish access (connectivity) to historical habitat upstream of Iron Gate Dam, and hydrograph, temperature, sediment transport and nutrient cycling dynamics that more closely resemble historical conditions.

3.2.1 Connectivity

Removal of the four lower Klamath River dams will reconnect the lower and upper basins, which have been divided for over a century. This provides the context for anadromous fish species' long-term recovery and persistence (Ebersole et al., 1997; Williams and Reeves, 2003), and allows anadromous salmonids to use habitat that has been inaccessible for >100 years. These tributary and mainstem areas above the dams represent approximately 500 rkm, 125 rkm, and 700 rkm of historical habitat for Chinook Salmon, Coho Salmon, and Steelhead, respectively (Hamilton et al., 2005; Hamilton et al., 2011; Ramos and Ward, 2023). These habitats include Fall Creek, Shovel Creek, Spencer Creek, Big Springs, and their cool-water refugia (Hamilton et al., 2011).

3.2.2 Flow dynamics

In the Klamath River, dams altered the flow regime and decreased the magnitude, frequency, and duration of flooding events, and reduced flow variability. Dam removals will result in a flow regime more characteristic of historical pre-dam conditions, with greater intra- and inter-annual variability (Hardy et al., 2006). The greatest long-term changes in hydrology will occur in the reach comprising the four dams and associated reservoirs to be removed, and immediately downstream. The restoration of a more natural flow regime within sections currently subject to alteration (e.g., bypassing, hydropeaking and otherwise managed) will drive shifts in fish host distribution and abundance, and those of their pathogens.

Iron Gate Dam, completed in 1962 to re-regulate hydropeaking from the upriver Copco facilities, altered the timing, magnitude, and duration of downstream flows (peak and baseflow). Although Iron Gate Dam operations created a more natural hydrograph than one that hydropeaks daily, the resultant flow regime deviated from historical conditions. The outcome was higher discharge in fall, but significantly decreased discharge in spring and summer. The operations altered the timing of peak runoff and shifted the onset of baseflow at least two months earlier (in some years, baseflow began in March). These changes had important consequences for salmon disease. Dam removals will largely restore seasonality to the flow regime through tributary inflows and spring flow accretions (e.g., Big Springs, ~7 m^3/s in the JC Boyle Bypass Reach).

3.2.3 Thermal regime

Temperature stratification occurs in large, deep reservoirs when the upper layer (epilimnion) warms and decreases in density, while cooler water remains on the bottom (hypolimnion). The release of water from the hypolimnion, which is common practice, decreases downstream temperature, particularly at lower flows (e.g., Petts, 1986). Two of the three reservoirs that will be restored to riverine habitats are large enough to have an effect on downstream water temperatures (Iron Gate and Copco). These reservoirs alter the timing of seasonal warming and cooling of river water temperatures (CSWRCB (California State Water Resources Control Board), 2018). For example, the largest of the reservoirs (Iron Gate), draws water from the hypolimnion, which delays warming in late winter and early spring. Thermal buffering from the reservoir also delays river water temperature cooling in fall, downstream.

Reservoir and dam removal are predicted to result in a 1 - 2.5°C increase in water temperatures during spring months and a 2 - 10°C decrease in water temperatures during the fall months (PacifiCorp, 2004; Dunsmoor and Huntington, 2006; North Coast Regional Board (North Coast Regional Water Quality Control Board), 2010; PacifiCorp, 2018). Elimination of the thermal lag caused by reservoirs will result in river temperatures consistent with those that historically co-occurred with salmon migration and spawning. The warmer spring temperatures will drive earlier fry emergence (Sykes et al., 2009), with potential consequences for disease risk. Fall-run Chinook Salmon spawning will gradually shift earlier and co-occur with cooler fall water temperatures, potentially reducing risks of pre-spawn mortality (Benda et al., 2015). In addition, the shift in discharge from thermally altered reservoirs to groundwater inputs (e.g., springs in the JC Boyle Bypass Reach are anticipated to account for 30 - 40% of the total summer discharge) will provide temperature relief for non-anadromous salmonids year-round, and in spring will benefit adult Spring-run Chinook Salmon during their migration. In addition to restoring a more natural thermal regime, dam removals will result in overall increases and diel variability in dissolved oxygen, and lower microbial oxygen demand due to decreased organic load.

3.2.4 Nutrient cycling and water quality

The upper Klamath River was naturally highly eutrophic, but damming and reservoir operations increased nutrient and organic loading and altered the temporal dynamics of nutrient cycling downstream (Asarian et al., 2009). Elevated nutrient levels stimulate the growth of periphyton (benthic algae), which serves as habitat for annelid hosts of salmon parasites. Similarly, species composition and densities of suspended algae and diatoms, which provide a food source for invertebrate hosts (e.g., annelid hosts of myxozoan parasites and snail hosts of trematodes), were elevated as a result of reservoirs.

The restoration of reservoir reaches to riverine habitat will decrease water residence time from several weeks to less than a day, resulting in reduction of primary productivity (including nuisance algae that produce toxic microcystin), and reduced settling of suspended particles. Reservoir and dam removals will also result in overall increases in dissolved oxygen due to aeration provided by a more dynamic river channel and shallower, more agraded bed and lower microbial oxygen demand, due to decreased organic load. The temporal dynamics of nutrient cycling will be more comparable to historical conditions.

3.2.5 Restored sediment transport and debris loading

Dam and reservoir removals should restore sediment dynamics to historical conditions. The greatest changes to sediment and debris transport will occur within and downstream of the Hydroelectric Reach (Figure 1). The Hydroelectric Reach lies within volcanic terrain, in a region characterized by being more bedrock-controlled and having lower rainfall and less sediment than below Iron Gate Dam (PacifiCorp, 2004; National Research Council, 2008). Stream gradients in this reach are higher than below the dams, but riverbed scour may be less frequent because of groundwater and springs in this river section relative to downstream river sections (PacifiCorp, 2004; PacifiCorp, 2018). Pool and riffle habitats, which are suitable for Fall-run Chinook Salmon, are abundant in the riverine sections of the Hydroelectric Reach (PacifiCorp, 2005; PacifiCorp, 2018). Following dam removals, the relative proportions of pool-riffle habitats are expected to remain similar, however the expansion of habitat to include areas previously flooded by reservoirs, will provide increased habitat not only for salmon but also for invertebrate hosts (e.g., *Manayunkia occidentalis*). In contrast, downstream of the location of Iron Gate Dam, the restored sediment input and transport following dam removals will create new gravel bars, a more heterogeneous and dynamic streambed, more suitable spawning habitat and reduced invertebrate hosts habitat.

3.3 Fish production and stocking changes

For over 50 years, Iron Gate Hatchery has reared and released up to 6 million salmonids annually (primarily Fall-run Chinook Salmon during late May-early June) to mitigate for Iron Gate Dam. Operations of this hatchery require Iron Gate Reservoir for adequate water supply. With removal of the dam, Iron Gate Hatchery will no longer be able to operate. To support fish production during the removal and transition to the cessation of hatchery operations, Fall Creek Hatchery will be updated to provide supplementation of Chinook Salmon and Coho Salmon for no more than eight years following dam removal. Preliminary numbers of Chinook Salmon smolts released from this facility will be lower than previous output from Iron Gate Hatchery, and release will be volitional, with one release occurring prior to March 31, and a second beginning May 1. Also, fewer yearling Coho Salmon and Chinook Salmon will be released mid-March to May and mid-October to mid-November, respectively (Klamath River Renewal Corporation and PacifiCorp, 2021).

The two remaining dams, Keno and Link River, have fish ladders to permit upstream migration, thus fish biologists expect volitional return of Coho Salmon upstream as far as Spencer Creek (inclusive), and Fall-run Chinook Salmon, Steelhead and Pacific Lamprey (*Entosphenus tridentatus*) upstream and into UKL and its headwater tributaries. Oregon plans to implement an active reintroduction program for Spring-run Chinook Salmon upstream of Link River Dam (Hereford et al., 2021), with the goal of re-establishing viable, self-sustaining populations that do not require hatchery supplementation. No changes are anticipated for Trinity River Hatchery production.

4 Scope and definitions used in this assessment

4.1 Salmonid species

Once the third most abundant salmon producing river in the US (excluding Alaska), Chinook Salmon (Spring- and Fall-run ecotypes) and Steelhead/Redband Trout (anadromous/non-anadromous *O. mykiss*) occurred throughout the Basin, including the tributaries of UKL[1]. Coho Salmon likely migrated as far upstream as Spencer Creek (rkm 366; and into Spencer Creek itself) (Hodge et al., 2016). Populations of Coastal Cutthroat Trout (*O. clarkii clarkii*) existed downstream of the location of Iron Gate Dam (Hamilton et al., 2005). Chum Salmon (*O. keta*) and Pink Salmon (*O. gorbuscha*) were observed in the lower portions of the Basin, but persistent populations were unlikely. Spring-run Chinook Salmon, believed to have once been the dominant Chinook Salmon life history in the Basin, have decreased in number by about 98% (Higgins et al., 1992). Coho Salmon are now ESA-listed as Threatened, and populations are at historically low levels (Olson, 1996; Federal Register, 1997). Fall-run Chinook Salmon runs decreased to an extent that prompted closure of the ocean commercial and sport fishing in 2008, 2009 and 2023 (CDFW- California Department of Fish and Wildlife- News, 2023). Herein, we focus on Chinook Salmon, Coho Salmon, and Steelhead/Redband Trout (Table 1; Figure 2); we do not discuss the other species because of their historically low numbers or limited distributions.

4.2 Pathogen species

We considered pathogens that were present historically (in the previous 25+ years) in the Klamath River and for which there has been documented evidence of salmonid disease. Disease in wild salmon populations is difficult to detect, as sick and moribund juvenile fish are removed rapidly by predators. Thus, what we know about disease impacts is often a result of large epizootics in adult fish, which may be less frequent but more visible. The occurrence of an adult salmon epizootic in the Klamath River in 2002 led to enactment of a long-term monitoring program (Bartholomew et al., 2022), which provided some of the most comprehensive data on fish pathogens in a large ecosystem (Lehman et al., 2020). This monitoring identified *C. shasta* as the dominant pathogen of juvenile Klamath River salmon and a primary factor limiting recovery of salmon populations in the Klamath system (Fujiwara et al., 2011). Thus this pathogen provides the primary scaffolding for structuring our predictions for salmon disease risk in a post dam ecosystem.

The other pathogens that we consider here represent a range of bacterial, protozoan and metazoan species, with life cycles that are direct (fish-to-fish, or fish-to-fish via an off-host development phase) or indirect (requiring other host/s) (Figure 3). They exhibit different host specificity, but all are endemic to and distributed throughout the Klamath River Basin (Supplemental Table 1). Pathogens present in salmonid populations elsewhere, for example *Myxobolus cerebralis* (causative agent of whirling

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[1] For the purposes of this paper, we combine *O. mykiss* (anadromous and non-anadromous) and Redband Trout (*O. m. newberrii*) in the Upper Klamath Basin, since introduced non-native non-anadromous *O. mykiss* are infected by a different genotype of *C. shasta* than native *O. mykiss* and Redband Trout. Historically, Redband Trout were distributed east of the Cascade Range, typically considered Upper Klamath Lake and its tributaries. The dispersal and changes in the distribution (sympatric and allopatric) of anadromous and non-anadromous *O. mykiss* and Redband Trout, and impacts of *C. shasta* on these populations following dam removals, will be of great interest (Messmer and Smith, 2007; Currens et al., 2009).

TABLE 1 Salmonid species/strains and risk factors for developing disease predictions.

Species	Life History	Juvenile migration and rearing habitat	Adult migration and spawning habitat
Chinook Salmon *Oncorhynchus tshawytscha*	Anadromous Fall-run	Fry emerge in winter then migrate in early spring. Small proportion migrate the following fall or early winter; rarely migrate as yearlings.	Return to fresh water in fall, then spawn in the mainstem and major tributaries in early winter.
Chinook Salmon *Oncorhynchus tshawytscha*	Anadromous Spring-run	Fry emerge in winter and remain in tributaries until migrating to the ocean in the fall, or the following spring. Use of non-natal habitat for rearing is not well understood following construction of dams.	Return to fresh water in spring, where they spend the summer in thermal refugia. Then spawn in tributaries in late summer and early fall.
Coho Salmon *Oncorhynchus kisutch*	Anadromous	Fry emerge in spring; out-migrate the following spring to fall with most occurring in fall. Juveniles are not restricted to their natal stream for summer, fall, or over-winter rearing.	Return to fresh water in late fall and spawn in the late fall predominantly in tributaries with some mainstem spawning.
Steelhead *Oncorhynchus mykiss*	Anadromous	Freshwater residence 1–3 years then out-migrate in spring. Also can exhibit a non-anadromous life history (i.e., Rainbow Trout).	Return to fresh water in spring and fall, and spawn in late fall and winter in the tributaries. Iteroparous (do not necessarily die after spawning and can spawn more than once).
Redband Trout *Oncorhynchus mykiss newberrii*	Non-anadromous (resident)	Move between tributary streams and the mainstem river (in the lower basin) or lake (in the upper basin); adfluvial life history.	Upper Basin: Reside in the lake and migrate to tributaries to spawn in winter and spring; Lower Basin: reside and spawn in the tributaries.

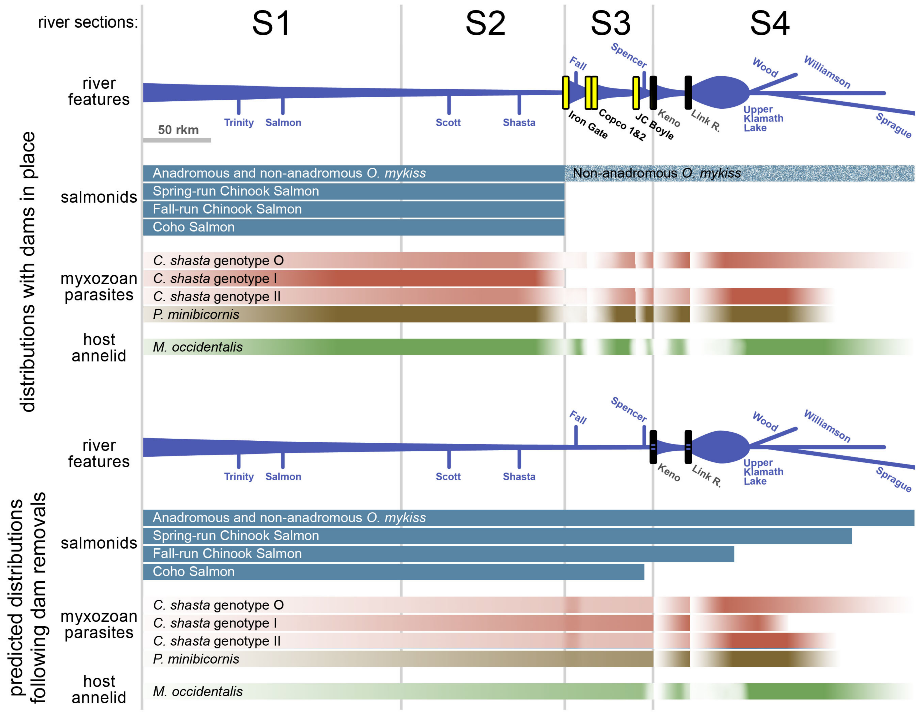

FIGURE 2
Schematic diagrams showing distributions and relative abundances of Klamath River salmonid fishes and the myxozoan pathogens *Ceratonova shasta* and *Parvicapsula minibicornis*, and their host annelid, *Manayunkia occidentalis*, during juvenile out-migration (spring). Major features of the river (dams, tributaries, lakes) are indicated. The top diagram shows fish distributions with dams in place, and the bottom diagram shows predicted distributions following removal of the lowermost four dams. Predicted fish ranges are based on historical data and represent habitat that will be accessible after dam removals; predicted pathogen and annelid distributions are based on changes to the river basin (refer to main text).

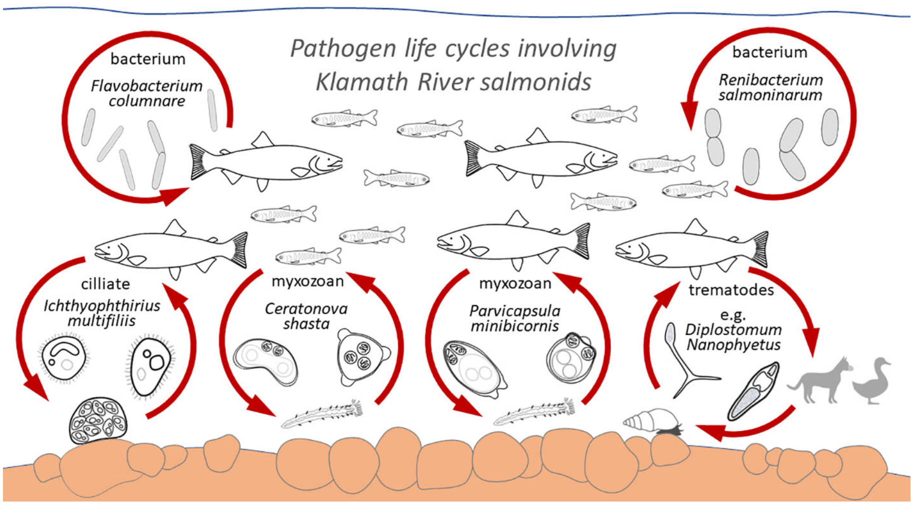

FIGURE 3
Life cycle relationships for the pathogens of concern to Klamath River salmonid fishes, showing life stages and alternate hosts. The hosts and pathogens are not shown to scale. Refer to main text for references.

disease), and a range of viruses, are not discussed here because they have not been detected in Klamath Basin populations of naturally produced and hatchery salmon in the previous 25+ years by the state and federal agencies that conduct fish health monitoring.

4.2.1 Multi-host parasites (indirect life cycles): Myxozoan and trematode parasites

4.2.1.1 *Ceratonova shasta*

This myxozoan parasite (formerly *Ceratomyxa shasta*) only infects salmonid fishes in the Pacific Northwest of the US and Canada. In rivers where the parasite is endemic, like the Klamath River, native fish have developed a degree of resistance to severe disease. Nevertheless, *C. shasta* can be a major contributor to mortality in juvenile salmonids, depending on the environmental conditions. For example, an epizootic occurred in juvenile Chinook Salmon in the warm, dry spring of 2021. Weekly monitoring during out-migration that year documented a peak *C. shasta* infection prevalence of 98% and more than half of the fish sampled were determined to have a fatal infection (Voss et al., 2022). *C. shasta* is not considered a contributor to adult pre-spawn mortality in the Klamath River, as most adult salmon enter the river in the fall when parasite abundance is lower, and their freshwater residency time prior to spawning is short. However, the parasite has been implicated in pre-spawn mortality in salmon that have longer freshwater residencies (Chapman, 1986) and suffer from loss of immune functions (Dolan et al., 2016). Long-term monitoring (out-migrant sampling, sentinel fish exposures, annelid sampling and water sampling) has been critical to understanding the factors that result in disease and population level impacts in juvenile salmon (reviewed by Bartholomew et al., 2022); however, there are fewer data on infection prevalence and disease severity in adults.

The life cycle of *C. shasta* is indirect, involving an aquatic annelid host, *Manayunkia occidentalis*, and two waterborne spore stages (Figure 3; Bartholomew et al., 1997; Atkinson et al., 2020). The actinospore released from the annelid infects the fish through the gill. The parasite then travels through the bloodstream to reach the intestine, where it can cause severe inflammation and tissue necrosis. Here it matures into a myxospore, which is released into the water column. Adult salmon acquire *C. shasta* infections when re-entering fresh water in the lower river [there is no evidence for infection in ocean fish (Slezak, 2009)] and transport the parasite upstream as they migrate. Actinospores that infect adult salmon in the lower river come from annelids infected by myxospores released from out-migrating juveniles, whereas actinospores that infect juvenile salmonids further upstream come from annelids infected by myxospores from the previous season's adult fish. In fatally-infected juvenile Chinook Salmon and Coho Salmon, myxospore release can occur during out-migration, 3 - 4 weeks after infection (Ray et al., 2012; Benson, 2014). In adults, myxospores are released after fish die post-spawn (Slezak, 2009; Kent et al., 2014; Foott et al., 2016b). In Steelhead/Redband juveniles and adults, myxospores may be released from apparently healthy infected fish (Bartholomew et al., 2022). The filter-feeding annelid host then ingests these myxospores to complete the cycle.

Effects of *C. shasta* differ among salmonid species and strains because *C. shasta* genotypes have differences in host specificity and virulence (Figure 2; Atkinson and Bartholomew, 2010a; Atkinson and Bartholomew, 2010b; Bartholomew et al., 2022). Infection in Chinook Salmon and Coho Salmon by genotypes I and II, respectively, can result in high mortality when conditions favor the parasite. In contrast, infections in Steelhead/Redband Trout with genotype 0 rarely result in overt disease and these fish may carry and disperse myxospores throughout their life. The severity of infection is a function of parasite dose and water temperature, which together affect disease progression in the fish, with 70,000 actinospores and 15°C considered a threshold for severe disease (mortality) in juvenile Chinook Salmon (Ray et al., 2012; Ray and Bartholomew, 2013); the threshold for mortality of Coho Salmon is lower (Hallett et al., 2012). Because *C. shasta* is not transmitted between fish, fish density is not directly a risk factor for infection.

However, high densities of post-spawn adult salmon releasing myxospores in proximity to annelid hosts drive disease risk indirectly.

Before dam removals, *C. shasta* was well documented from the Williamson River in the upper basin, throughout the Klamath River mainstem to the estuary; it was not established in tributaries (Hendrickson et al., 1989; Hallett and Bartholomew, 2006; Stocking et al., 2006). Genotypes 0, I and II were found downstream from the dams to the estuary (Atkinson and Bartholomew, 2010a; Atkinson and Bartholomew, 2010b). An "infectious zone" of high waterborne actinospore abundance of genotypes I and II occurred episodically between the confluences of the Shasta and Salmon rivers, when water temperature rise in the spring, during juvenile salmon out-migration (Hallett et al., 2012; Voss et al., 2023). The myxospore input that drove this infectious zone likely came from the high densities of adult salmon that spawned directly downstream from Iron Gate Dam and the adjacent hatchery: a single adult salmon carcass can contribute millions of myxospores (Foott et al., 2016b). Upstream of the dams, genotype I was absent because migration of its Chinook Salmon host was blocked. Despite the absence also of Coho Salmon upstream of Iron Gate Dam (UKL, Williamson River), genotype II was present at high densities in water samples and annelids (Figure 2), suggesting that non-native trout or landlocked salmon serve as an alternate host. Genotype 0 persisted in the upper basin in non-anadromous *O. mykiss* (Redband Trout).

The obligate annelid host limits parasite distribution because transmission only occurs where there is spatial and temporal overlap between salmonids and infected annelids. Distribution and density of infected *M. occidentalis* are predictors of salmon disease risk and consequently, changes to either variable will have knock on effects. The annelids are patchily distributed throughout the mainstem Klamath River and in the Williamson River (Figure 2; Stocking and Bartholomew, 2007; Alexander et al., 2014; Alexander et al., 2016). While these annelids tolerate a broad range of environmental conditions (e.g., water temperature and dissolved oxygen extremes), their distribution is primarily driven by disturbance (flow events) and substrate. High *M. occidentalis* densities are generally restricted to stable substrates (boulder/bedrock) that co-occur with moderate depths and low velocities, but annelids are highly plastic in their habitat use and can use a range of substrates when disturbance is low (Stocking and Bartholomew, 2007; Jordan, 2012; Alexander et al., 2014; Alexander et al., 2016). In the reservoirs, *M. occidentalis* is restricted to the inflows and edges (Stocking and Bartholomew, 2007). It has not been observed in tributaries, which is likely related to the more dynamic flow regimes in those environments.

4.2.1.2 *Parvicapsula minibicornis*

Another myxozoan parasite, shares the same life cycle as *C. shasta* (Bartholomew et al., 2006), with the same annelid and salmonid hosts. Although its distribution mirrors that of *C. shasta*, it is generally detected earlier in the year and at higher densities (Bartholomew et al., 2007; Voss et al., 2023). *P. minibicornis* has intra-specific genetic differences that may map to specific salmon host species, but this is not as well established as for *C. shasta* (Atkinson et al., 2011). The parasite infects the gills and kidney glomeruli (Bradford et al., 2010) and spores are shed from the fish in urine, a dispersal mechanism that doesn't require the death of the fish host. This difference in transmission strategy for migrating adult salmon (continuous shedding from live fish), likely results in greater dispersal of *P. minibicornis* myxospores than *C. shasta*.

While *P. minibicornis* is not considered a primary contributor to mortality in the Klamath River, out-migrating juvenile salmon have a high prevalence of infection with clinical disease signs (kidney swelling, multifocal glomerulonephritis and interstitial hyperplasia); however, fish collected in the estuary showed signs of recovery (Bartholomew et al., 2007; Voss et al., 2023). Juvenile fish are often co-infected with both *C. shasta* and *P. minibicornis* (Stone et al., 2008), and the parasite likely has sublethal effects in juvenile salmon as a stressor, particularly in co-infections, and its effects on saltwater survival are unknown.

In Klamath River adult salmon, high infection prevalence, with development to mature myxospores, has been observed in Chinook Salmon, Coho Salmon, and Steelhead, and disease (glomerulonephritis) was reported in Chinook Salmon (Bartholomew et al., 2007), but not identified as a cause of pre-spawn mortality. In other rivers, *P. minibicornis* impedes performance (Wagner et al., 2005) and contributes to morbidity and mortality of adult salmon (St-Hilaire et al., 2002; Jones et al., 2003; Bradford et al., 2010), particularly when there is a long freshwater residency.

4.2.1.3 Trematodes (flukes)

Several trematode species have been reported from salmonids in the Klamath Basin, including the eye fluke *Diplostomum pseudospathaceum*, the blood fluke *Sanguinicola klamanthensis*, *Nanophyetus salmincola* which infects muscle and kidney, and a gill fluke, possibly *Apophallus* sp. (Walker and Foott, 1993; USFWS unpublished survey data). These parasites have complex life cycles involving freshwater snails and often a second vertebrate host (e.g., bird, canid). Trematode snail hosts have a broad habitat preference, and have been reported from clean, running water and solid substrates, muddy-sand bottoms of small and medium lakes and from slow flowing streams (Clarke, 1981; Min et al., 2022). We lack comprehensive information on the distribution and abundance of snail hosts in the Klamath River.

There have been no reported health effects of trematode infections on salmon in the Klamath River. Generally, trematode-associated morbidity is linked to parasite density and fish size (thus younger fish are more likely to be affected), therefore, there is potential to have a localized effect if shedding snail populations are large and salmonid fry rear in the same edge habitat. In other rivers, adverse health effects and lower early marine survival were correlated with high *N. salmincola* loads in juvenile Steelhead (Chen et al., 2018) and Coho Salmon, with a lesser effect on Chinook Salmon (Jacobson et al., 2008). Reduced fitness (Ferguson et al., 2011; Ferguson et al., 2012) and increased sensitivity to other infections and predation (Jacobson et al., 2003;

Roon et al., 2015; Puget Sound Steelhead Marine Survival Workgroup, 2018) have also been reported. For *Diplostomum* (eye fluke), prevalence and severity of infection is high in multiple fish species in UKL (Burdick et al., 2017).

As few data exist on the impacts of diseases caused by trematode infections and on the distribution of snail hosts in the Klamath River basin, we have little basis for specific predictions of disease risk following dam removals. Given that this group contains known pathogens of concern, these should be included in monitoring efforts following dam removals.

4.2.2 Single host parasites (direct life cycle with off-host development)

4.2.2.1 *Ichthyophthirius multifiliis*

"Ich", a ciliated protozoan parasite that causes white spot disease, is named for the distinct trophont (feeding) stages that encyst in the skin and gills of its fish host. When present in high numbers, the parasites can disrupt osmoregulation and respiration, and the feeding wounds make the fish vulnerable to secondary bacterial and fungal infections. The life cycle of *I. multifiliis* is direct (no intermediate host, but has off-host development) and temperature dependent: the complete life cycle takes 3 - 4 d at 21 - 24°C, 10 - 14 d at 15°C and > 5 wks at 10°C (Warren, 1991). Because the parasite has a direct life cycle, it transmits rapidly when fish congregate at high densities, and disease impacts have been reported in spawning Sockeye Salmon in constrained spawning channels (Traxler et al., 1998), and in aquaculture production where disease is more easily observed. The parasite has low host specificity and can be transmitted between salmonid and non-salmonid fishes, and is present throughout the Klamath River. This parasite contributed to the 2002 epizootic in adult Chinook Salmon, which occurred during a low flow event that crowded the returning salmon in the lower Klamath River (Belchik et al., 2004). Following that mortality event, an adult salmon monitoring program was established (Belchik, 2015). High density of resident fish (e.g., speckled dace (*Rhinichthys osculus*)) harboring *I. multifiliis*, even at low prevalence or intensity, may provide a reservoir for the parasite in the lower river (Foott et al., 2016a). Additional outbreaks of *I. multifiliis* in returning adult salmon occurred in 2014 and 2016, but lethal events are thought to have been prevented by increasing river flow through the managed release of reservoir water (Bodensteiner et al., 2000; Belchik, 2015).

4.2.3 Single host pathogens (direct life cycle with no off-host development)

4.2.3.1 *Flavobacterium columnare*

Is a bacterium that infects the gills and skin of its host fish and causes columnaris disease. Disease signs include necrotic gills and skin, and frayed fins; fish also become lethargic, making them vulnerable to predation. This bacterium has a broad host range, and other fish present in the system can serve as reservoirs. It is present commonly in lakes and rivers and is transmitted rapidly at high fish densities and at warmer temperatures. *F. columnare* is a species complex composed of four distinct groups; however, the Klamath Basin has the "typic" *F. columnare* (LaFrentz et al., 2022).

This bacterium, along with *I. multifiliis*, contributed to the 2002 epizootic in adult salmon in the lower Klamath River. Disease epizootics in the Klamath River basin as a result of columnaris have been reported in other fish species; the earliest report of an epizootic in suckers and Tui Chub (*Siphateles bicolor*) in UKL in 1898 (Gilbert, 1898) was likely a result of *F. columnare*. Epizootics have been reported periodically since then (Perkins et al., 2000), including an outbreak in UKL in August 1971 where ~14 million fish died (Rohovec and Fryer, 1979). Fish affected by these epizootics include adult Shortnose Suckers (*Chasmistes brevirostris*), Lost River Suckers (*Deltistes luxatus*), Tui Chub, Blue Chub (*Gila coerulea*), Large Scale Suckers (*Catostomus macrocheilus*), Marbled Sculpin (*Cottus Klamathensis*) and rarely Rainbow Trout. In some reports, the dying fish were co-infected by various parasites such as *Lernaea*, leeches, *Ichthyobodo*, *Trichodina* and trematodes. Severe environmental conditions in UKL play a significant role in the predisposition and development of *F. columnare* infections. Hypoxia, caused by the collapse of blue green algae *Aphanizomenon flos-aquae* blooms, was identified as the primary mechanism that triggered the 1995 - 1997 fish kills (Perkins et al., 2000). Susceptibility of the fish to hypoxia was probably enhanced by chronic exposure to high water pH and ammonia levels, and low dissolved oxygen during the summer months; these water quality stressors increased susceptibility of fish to pathogens such as *F. columnare*. In August 2022, *F. columnare* caused the death of Chinook Salmon in the lower Klamath Basin, in a mortality event associated with higher water temperatures, the congregation of fish in cooler-water refugia, and co-infection with *I. multifiliis*.

F. columnare infections in juvenile Steelhead, Chinook Salmon, and Coho Salmon begin to occur when water temperatures reach 15°C and become progressively more severe as temperatures increase to 20 - 24°C (Holt et al., 1975). Most of the severe fish epizootics in UKL have occurred in August (summer) when water temperatures were 20 - 25°C; however, there are reports of high temperatures and fish loss or clinical disease as early as May (spring): e.g., mortality of Fathead Minnows (*Pimephales promelas*) and chubs in the Link River and head of Lake Ewauna in May 1987; detection of *F. columnare* gill lesions in apparently healthy adult suckers at the mouth of the Williamson River in May 1997 (Thorsteinson et al., 2011). Thus, infections of *F. columnare* can occur in the UKL watershed beginning in May and extending to September if water temperatures are elevated.

4.2.3.2 *Renibacterium salmoninarum*

Is the causative agent of bacterial kidney disease, a chronic granulomatous inflammatory infection of the kidney in salmonids (Delghandi et al., 2020). Although disease progresses most rapidly at higher temperatures (15 - 20°C), mortality is often highest at cooler temperatures (7 - 12°C) due to the chronic nature of the infection (Sanders et al., 1978). The bacterium can be transmitted both vertically (from adult to progeny through the egg) and horizontally (between fish), and its chronic nature makes detection of infected fish difficult as they may not display disease signs. Non-salmonid species are not infected by the bacterium and thus do not present a risk as reservoirs of infection.

The bacterium has been detected historically in Chinook Salmon, Coho Salmon, and Steelhead in the lower Klamath River (Walker and Foott, 1993), and from Rainbow Trout, Brown Trout (*Salmo trutta*), Brook Trout (*Salvelinus fontinalis*) and Kokanee Salmon (*Oncorhynchus nerka*) in the upper Klamath River basin (Oregon Department of Fish and Wildlife - ODFW - data). Chinook Salmon are particularly susceptible to severe disease (Elliott, 2017), and studies prior to dam removals show that exposure of naive Spring-run Chinook Salmon in Upper Klamath Lake for one week results in *R. salmoninarum* infection (ODFW-Oregon State University preliminary data).

4.2.4 Other pathogens

Other infectious agents have been detected in the Klamath River, but are not specifically considered in this assessment for one or more of the following reasons: they are rarely detected (e.g., *IHNV*), they have low pathogenicity (e.g., *Trichodina* sp., *Ichthyobodo* sp., *Chilodonella* sp., *Gyrodactylus* sp.), or we lack information on how basin changes could alter the pathogen's effects (e.g., *Lernaea salmonea*, which has been detected episodically at high densities on Redband Trout in the UKL).

4.2.5 Other stressors

Physical and biological stressors can cause mortality on their own, or alter the host's response to pathogens. Dam removals will alter the magnitude and timing of many physical stressors, with somewhat unknown consequences for fish communities (Brenkman et al., 2008). Acute mortality can be caused by physical stressors including: abrasions from passage through artificial structures (e.g., the remaining Keno Dam spillway and gates), turbidity associated with reservoir drawdowns, gas supersaturation (Weitkamp and Katz, 1980), predation, high water temperature, low dissolved oxygen, and high pH. Chronic stressors can cause sublethal effects that may increase susceptibility to pathogens and/or exacerbate infections that might otherwise be tolerated.

Additional stressors are associated with the effects of climate change. Southern Oregon and northern California have become warmer and drier, and experienced a multi-year drought with increased frequency of wildfires. In summer 2022, the McKinney Fire adjacent to the Klamath River created a burn area that together with unseasonably-heavy rains caused a flash flood and debris flow in the river. The resultant combination of low oxygen levels and high turbidity caused a local fish die-off and subsequent higher disease-related mortality that season, due to the additional stressors of persistent high turbidity and high river water temperatures (26°C).

Biological stressors include nutritional factors (e.g., thiamine), algal blooms and co-infections by other pathogens. Co-infection is common (e.g. *C. shasta* and *P. minibicornis*; *I. multifiliis* and *F. columnare*), yet effects on hosts are complicated and unpredictable. For example, prior infection with *N. salmincola* increased mortality when Chinook Salmon were exposed to certain bacterial pathogens, including *Vibrio anguillarum* (Jacobson et al., 2003) and *F. columnare*, but not in co-infection with *Aeromonas salmonicida* (Roon et al., 2015). In contrast, some pathogens can actually increase fish performance (McElroy et al., 2015; Lauringson et al., 2023), demonstrating that infection does not always result in a disease state.

4.3 River sections used in this assessment

Based on fish and pathogen distributions, river conditions, and barriers to fish movement, prior to dam removals, we stratified the river into four sections: numbered from the estuary to the headwaters (Figure 1). Other studies have used different schemes (e.g., geomorphology) for delineating river reaches, but for the purposes of this assessment we defined the sections to best characterize anticipated changes in disease risk in response to dam removals.

- S1: Estuary to Portuguese Creek – includes the Trinity River and Salmon River tributaries.
- S2: Portuguese Creek to Iron Gate Dam – encompasses the highly infectious zone for *C. shasta* prior to dam removals; includes the Scott River and Shasta River tributaries.
- S3: Iron Gate Dam to Keno Dam – Hydroelectric Reach; will change dramatically in geomorphology, flow and temperature as reservoirs revert to riverine habitat. And in both physical and biological diversity as salmon and other species re-establish.
- S4: Keno Dam upstream – includes the Klamath Project water retention dams, Keno and Link River (which will remain), Upper Klamath Lake and its tributaries. Changes will be driven primarily by shifts in fish distribution and diversity as salmon populations re-establish in the upper tributaries.

5 Predicted effects of fish disease following dam removals

Factors that contribute to alterations in disease risk following dam removals include the abiotic elements discussed in the previous section, and biotic components that include: pathogen virulence and abundance, pathogen replication rate, ability of a pathogen to persist in the environment, how a pathogen is transmitted between hosts, and the presence and overlap of hosts and pathogens in time and space. Progression and severity of pathogen-caused diseases will vary with salmonid species, origin, and time spent in the mainstem Klamath River. We recognize that the Klamath Basin ecosystem is complex, with a multitude of factors that influence host-pathogen disease dynamics. These factors may interact both synergistically and antagonistically. Thus, we have characterized risks qualitatively and offer a prediction of the net change.

This section considers how the pathogens of primary concern (Supplemental Table 1), grouped by their underlying life cycle characters (direct or indirect; Figure 3), will respond to the changes brought about by dam removals. We then make predictions on how fish disease risk from each pathogen will change in each of the four river sections (Figure 1; Table 2). Although our prediction capacity for pathogens other than myxozoans is limited, we felt it important to retain them because future restoration and management could benefit from these limited insights and identification of information gaps.

5.1 General responses of pathogens to dam removals

5.1.1 Multi-host parasites

5.1.1.1 Myxozoans

Factors affecting disease risk from myxozoan infections include presence of stable habitats that support annelid hosts, overlap of fish and annelid hosts in time and space, and water temperatures that

TABLE 2 Predicted changes to physical features, fish movements and associated host-pathogen interactions and disease for each of the four river sections, after dam removals on the Klamath River. The changes are long term unless specified as short term.

Section	Section description and overview of anticipated changes	Itemized changes to physical features and salmonid movements that will affect disease risks	Predicted changes to host-pathogen interactions and disease
S1	**Estuary to Portuguese Creek; tributaries include Trinity River and Salmon River.** Dam removals will result in minimal changes to physical features in S1, after the initial sediment pulse. Minimal direct effect on water temperature as S1 is dominated by tributaries.	Sediment: short term increase results in increased turbidity and burial of river features.	Adult and juvenile salmonids: bacterial or fungal infections may result from sediment-related gill abrasions. Annelid populations smothered/displaced.
		Flow and water temperature: lower summer base flow and consequently warmer water; groundwater-fed cold-water refugia will remain.	Juveniles: higher summer disease risk for Coho Salmon, which reside in the system for a year before they out-migrate. Adults: Fall-run fish that enter the river from August onwards may crowd in refugia, with consequent increased transmission of direct life cycle pathogens (*I. multifiliis* & bacteria). Pathogens will develop faster at higher water temperatures (this risk is present prior to dam removals, so no overall change in the already high risk of *I. multifiliis* and bacterial infections). Annelids: reduced habitat will lower their summer population (and lower overall spore production).
		Water temperature: cooler sooner in fall.	Adults and juveniles: reduced water temperatures reduce disease risks from most pathogens.
		Removal of Iron Gate Hatchery (in S3): causes a shift to earlier, more natural juvenile salmon out-migration through S1.	Juveniles: Decreased overlap of infected fish with high annelid populations will reduce transmission and therefore actinospore production; in turn lowering infection risk to returning adults. Reduction in hatchery fish will immediately reduce their potential myxospore deposition in S1.
		Connectivity: S1 will have out-migrant juveniles from all reaches, with a long migration time for fish from S4.	Annelids: Because out-migrant timing will be temporally dispersed, myxospore input from out-migrants infected in S2-S4 may not overlap with high density annelid populations.
S2	**Portuguese Creek to Iron Gate Dam; tributaries include Scott River and Shasta River.** Dam removals will cause large changes in flow and temperature in S2, with the Klamath mainstem flow becoming warmer/hotter in spring/summer and cooler/colder in fall/winter.	Sediment: short term increase results in burial of river features and increased turbidity.	Annelids: smothered/displaced. Adults and juveniles: sediment-related gill abrasions may promote bacterial infections. Juveniles: delayed migration as a result of short-term increases in turbidity, with potential increased overlap with *C. shasta* and *P. minibicornis.*
		Sediment: long term higher inputs and retention as reservoirs no longer serve as sinks.	Annelids: populations subject to more natural dynamics with persistence in areas protected from scour, removal from areas of mobilized sediment.
		Water temperature: warmer in spring.	Adults: increased risks of infection and or disease severity by *F. columnare* and *I. multifiliis* for salmon that in-migrate (e.g., Spring-run Chinook Salmon). Juveniles: earlier fry emergence may reduce overlap between hosts and pathogens (myxozoans, bacteria), thus lowering disease. Warmer water may shift parasite release earlier with potential for exacerbating disease risk if overlap occurs.
		Water temperature: warmer in summer.	Adults: Fall-run fish that enter the river from August onwards may crowd in cold-water refugia, with consequent increased transmission of direct life cycle pathogens (*F. columnare* and *I. multifiliis*). Spring-run Chinook Salmon would have reduced disease risk if they could utilize cold-water refugia - lower numbers of this stock should mean lower

(Continued)

TABLE 2 Continued

Section	Section description and overview of anticipated changes	Itemized changes to physical features and salmonid movements that will affect disease risks	Predicted changes to host-pathogen interactions and disease
			risk of crowding-associated diseases; later-running fish would be endangered by higher summer water temperatures and associated parasite levels.
		Water temperature: cooler in fall.	Adults: reduced pre-spawn mortality of Fall-run Chinook Salmon.
		Water flow: lower summer base flow.	Annelids: reduced habitat availability.
		Removal of Iron Gate Dam will eliminate flow moderation and result in a more dynamic flow regime.	Annelids: removal of low-velocity, low-disturbance habitat will prevent establishment of high-density populations.
		Increased frequency of threshold critical flow events.	Annelids: patchier distribution.
		Removal of Iron Gate Hatchery: a shift to earlier and more temporally dispersed juvenile salmon migration through S2.	Juveniles: decreased overlap between infected juveniles and peak annelid population densities will reduce infection (as for S1). Reduced transmission efficiency (hence prevalence of infection) of directly transmitted pathogens (*F. columnare* and *I. multifiliis*) to juveniles.
		Removal of hotspot of myxospore input from adults spawning downstream of Iron Gate Dam.	Annelids: reduced infection prevalence and lower subsequent actinospore production.
S3	**Iron Gate Dam to Keno Dam - Hydroelectric Reach** S3 will see the greatest change in both physical and biological diversity as salmon and other species re-establish. For S3, we have the greatest uncertainty regarding future temperatures and flows, and where and when fish will be migrating. Thus our predictions may need to be updated with changes in operational plans, especially those related to flow management.	Reservoirs drained: stream restored to run/riffle/pool structure.	Annelids: reduced habitat with consequently lower myxozoan disease risk.
		Sediment: short term increase results in burial of river features and increased turbidity.	Adults and juveniles: in resident populations, bacterial or fungal infections may follow sediment-related gill abrasions; anadromous populations not yet established.
		Sediment: long term higher input of sediment from tributaries with loss of reservoirs as sinks.	Annelids: more natural dynamics with persistence in areas protected from scour, removal from areas of mobilized sediment.
		Water temperatures: cold water springs will dominate input at base flow.	Adults and juveniles: reduced parasite development in cooler water conditions will reduce disease risk (myxozoans, trematodes, *I. multifiliis*, bacteria).
		Water temperatures: restoration of more natural thermal regime due to cessation of hydropeaking; more variable thermal regime in former bypass reaches due to reconnection with main river channel.	Adults and juveniles: may avoid migrating during periods when temperatures are high, and would utilize myxozoan-free tributaries and larger springs as thermal refuges. Adults: reduced water temperatures are predicted to lessen disease risk from bacteria in fall returns.
		Connectivity: reinstatement of volitional anadromous fish movements.	Adults: pathogen transmission success lower due to more distributed spawning (and thus more distributed myxospore inputs rather than the hotspots that existed prior to dam removals; reduced concentrations of bacteria).
		Connectivity: establishment of parasites in novel upstream areas.	Adults and juveniles: increased length of exposure during migration may increase disease risks.
		Connectivity: reinstatement of anadromous fish movements	Adults: possible pre-spawn mortality from *P. minibicornis* and *C. shasta* as observed in other long-migration rivers. - Spring-run Chinook Salmon that enter the river in late spring and migrate

(Continued)

TABLE 2 Continued

Section	Section description and overview of anticipated changes	Itemized changes to physical features and salmonid movements that will affect disease risks	Predicted changes to host-pathogen interactions and disease
		and increased species diversity; longer migration times.	to S4, will have longer, warmer migration times, thus increased exposure to pathogens and thereby increased disease risk. - Risk of pre-spawn mortality for Fall-run Chinook Salmon and Steelhead will be lower, as they will be entering the Klamath River during a time when parasite levels and water temperatures are lower.
		Fall Creek Hatchery: reinstated with an 8-year production plan, will volitionally release fishes, resulting in a shift to earlier, more natural juvenile salmon migration.	Annelids: expect low/none in Fall Creek, so any myxospore concentration at hatchery should not increase disease risk. However, unknown if infectious area will develop in the mainstem Klamath River as a result of myxospore input from adults spawning in Fall Creek. Juveniles: wider temporal variation in movements should reduce overlap between hosts and parasites, thus lowering disease risk.
S4	**Keno Dam upstream – includes the Klamath Project water retention dams, Keno and Link River (which will remain), Upper Klamath Lake and its tributaries.** Minimal-to-no changes to physical features. Controlled water releases to augment downstream managed flow events. Disease risk changes in S4 will be a consequence of re-establishment of anadromous salmonids and their interactions with resident species, and establishment of formerly down-river pathogens/genotypes.	Connectivity: large change with reinstatement of anadromous fish movements and increased species diversity.	Juveniles: migration timing critical to avoid poor summer water quality in UKL and Keno reservoir. Adults and juveniles: exposure of anadromous fish to direct life cycle pathogens (*F. columnare, R. salmoninarum, I. multifiliis*) during residency in UKL coincident with periods of poor water quality.
		Episodic congregation at fish ladders of the two remaining dams.	Adults: higher transmission of direct life cycle pathogens (*I. multifiliis*, bacteria).
		Connectivity: longer migration times.	Adults: possible pre-spawn mortality with *P. minibicornis* and *C. shasta* as seen in other long-migration rivers. Spring-run Chinook Salmon that enter the river in late spring and migrate to S4 will have longer, warmer migration times, thus increased exposure to myxozoans and thereby increased disease risk. Risk of pre-spawn mortality for Fall-run Chinook Salmon and Steelhead will be lower, as they will be entering the Klamath River during a time when parasite levels and water temperatures are lower.
		Connectivity: establishment of parasites into novel upstream areas.	Adults and juveniles: increased length of exposure during migration may increase disease risks.

favor disease. The altered timing of fish movement after dam removals should decrease overlap between out-migrating, infected juvenile salmon and peak annelid population densities, thereby lowering annelid infection prevalence and consequently reducing infection risk for juvenile salmon. But for both *C. shasta* and *P. minibicornis*, we expect that the extended migration times (cumulative exposure; Ratliff, 1981) will be associated with the greatest changes in disease risk for juvenile and adult salmon, particularly during periods when water temperatures are warm. Because of the long development of these parasites, actively out-migrating juvenile salmon infected in one section release mature spores in downstream sections of the river. The high prevalence of both myxozoan infections in adult fish suggests that the infection threshold (number of actinospores required to elicit an infection) is likely low in adults (Foott et al., 2016b).

5.1.1.2 Trematodes

Factors likely to affect severity of infections caused by trematodes are the density of snail hosts and overlap of fish, bird and snail hosts in space and time. Changes in snail host habitat and population density will affect abundance of trematode parasites and thus effects on salmonids. Similar to other pathogens, high infection rates are associated with warm water temperatures (Schaaf et al., 2017). However, because few data exist on the distribution of snail hosts in the Klamath River Basin prior to dam removals, and there are significant gaps in our knowledge of snail host habitat tolerance, we have little basis for specific predictions of future disease risk. Therefore, we include considerations for the upper two river sections only. In S3, infection from trematodes may be reduced from current levels if the increased flow variability and habitat changes decrease densities of the snail host, and reduce infection intensities in fish (Field and Irwin, 1994). In S4, the high prevalence and severity of infection with *D. pseudospathecum* in multiple fish species in UKL could be indicative of the risk to juvenile Spring-run Chinook Salmon in late spring, which will reside longer (and therefore be exposed longer) than Fall-run Chinook Salmon or Steelhead. For trematodes that require a bird in their life cycle, improved habitat in the upper basin could increase both bird and subsequently trematode abundance.

5.1.2 Single-host pathogens

5.1.2.1 *I. multifiliis*

Factors that we predict are important for future outbreaks are habitats where adult or juvenile fish congregate, high water temperatures and low flows that facilitate rapid transmission and proliferation. This parasite has a broad host range, with other fish species serving as reservoirs for infection (Foott et al., 2016a), thus any post-dam-removal increase in overlap of salmonids with other fishes may increase disease risk when conditions are permissive.

5.1.2.2 Bacteria

Factors affecting disease risk associated with *F. columnare* in salmonids will be similar to those for *I. multifiliis* (see above) given that these pathogens are transmitted directly from fish to fish, have a broad host range and are present throughout the basin. Outbreaks of *F. columnare* infections are associated with areas of high salmonid densities, high water temperature and low flows. In contrast, *R. salmoninarum* has a narrow host range and is not widely documented in the Klamath River (primarily in S4), but its chronic nature and its ability to transmit both between fish and vertically to their progeny make it difficult to control.

5.2 River section 1 (S1) - Estuary to Portuguese Creek

The effects of dam removals on temperature and flow will be relatively minor in S1 compared to S2 and S3, given the dominance of tributary inputs in this section, and will be most significant in summer months (at baseflow). Lower summer baseflows will mean water temperatures are more sensitive to ambient air temperature, and so will be higher. Increased temperatures in S1 would increase disease risk associated with all pathogens, with fish mortality more likely to result from pathogens with a shorter, more direct life cycle (such as *F. columnare* or *I. multifiliis*).

5.2.1 Multi-host parasites

5.2.1.1 Myxozoans

S1 is located downstream from the main infectious zone for both *C. shasta* and *P. minibicornis*, but both juvenile and adult salmonids become infected here. Juvenile fishes migrating downriver continue to be exposed as they migrate through S1, and juveniles from S1 tributaries (Trinity and Salmon rivers) become infected upon entering the mainstem Klamath River (Voss et al., 2022). Returning adults become infected by both myxozoans after entering the river (there is no evidence that either of these parasites are present in adult fish prior to their return to freshwater; Slezak, 2009). Adults then move both parasites upriver as they return to their spawning grounds.

5.2.1.1.1 Impacts on annelid hosts

Prior to dam removals, annelid hosts had peak distribution and density in summer and early fall, with prevalence of *C. shasta* highest in late summer to early fall (JDA unpublished data). Thus, annelids in S1 appear to be important for transmitting *C. shasta* (and maybe *P. minibicornis*) to returning adult salmon which in turn transport the parasite upriver, with out-migrating juvenile salmon infected upriver in S2 providing the source of myxospores to infect these annelids the following season (Robinson et al., 2020).

After dam removals, short-term effects on annelids will likely be minimal because the timing of reservoir drawdowns overlap with the period of low population density (population expansion occurs after baseflow in S1). The long-term restoration of a more natural and variable flow regime will likely restrict annelid distribution and reduce densities in S1 because: i) the lower baseflows during summer and fall will reduce habitat availability and co-occur with peak annelid population density in this section; ii) the increased variability will reduce habitat suitability and further restrict annelids to flow refugia; and iii), the restored sediment supply may further prevent the establishment of high-density annelid populations in this section.

5.2.1.1.2 Predictions for juvenile salmon

For juvenile salmon originating in S1, disease risk will continue to be low as they have a short migration time to the ocean and parasite densities in the water are lower than in S2. The disease risk for juvenile salmon migrating from upriver sections following dam removals will primarily depend on factors discussed in those sections. Long-term, disease risk should be decreased for fish migrating through S1, as a result of reduced overlap between infected juvenile salmon releasing myxospores and annelid populations there.

5.2.1.1.3 Predictions for adult salmon

The reduction in annelid habitat in S1, combined with changes to salmon migration timing, may translate into reduced infection risk for returning adult salmon in early fall. Unlike for juvenile salmon, the infectious dose threshold for adults is unknown (but likely low), and thus we expect continued high infection prevalence in adult salmon, particularly Spring-run Chinook Salmon entering the river in late spring and early summer when waterborne parasite densities are usually highest. Consequently, returning adults will continue to contribute myxospores to S2, and provide myxospore inputs to S3-S4. If in-migration co-occurs with warmer temperatures and lower baseflow, infection risk may increase in S1 following dam removals. Pre-spawn mortality associated with either myxozoan has not been observed in S1 and we do not expect this to change because adults will likely move upstream before the parasites have had sufficient time for development and cause disease.

5.2.2 Single-host pathogens

5.2.2.1 *I. multifiliis*

Prior to dam removals, outbreaks in returning adult Fall-Run Chinook Salmon have occurred in S1. Following dam removals, cooler river temperatures during their fall in-migration will promote both upstream migration beyond this section (and limit congregation and associated bottlenecking) and reduce the concentration of waterborne infectious stages. However, the increase in numbers of Spring-run Chinook Salmon will mean more adult fish entering S1 in spring/summer when water temperatures are high and conditions cause congregation in cool-water refugia that promotes fish-to-fish transmission. Disease risk will likely remain high in S1 but will be affected by each years' specific environmental conditions and management decisions (e.g., water allocation in the Upper Klamath Basin and major tributaries) that may affect flow.

5.2.2.2 Bacteria

Long term, lower summer flows and higher temperatures in S1 will increase *F. columnare* proliferation and transmission, and thus disease risk, for salmon that in-migrate or are already present (e.g., returning Spring-run Chinook Salmon or yearling Coho Salmon) when mainstem water temperatures are above 18°C. These conditions will drive increased use of cool-water refugia, and consequently, the likelihood of salmonid congregation. The higher density of fish in refugia will increase *F. columnare* transmission among fish, but the lower temperature will decrease proliferation, and thus the overall disease risk is difficult to predict.

5.3 River section 2 (S2) - Portuguese Creek to Iron Gate Dam

Prior to dam removals, river flows in S2 were influenced directly by Iron Gate Dam and the Shasta River, with limited sediment coming through the reservoirs. This resulted in low-velocity, low-disturbance habitats in the river downstream. With dams in place, water temperatures in S2 were buffered and temporally lagged. Removal of Iron Gate Reservoir will result in a dynamic flow regime, episodic high flows/floods, increased sediment, and earlier spring warming and earlier fall cooling, plus larger diel fluctuations year-round.

5.3.1 Multi-host parasites

5.3.1.1 Myxozoans

The low-velocity, low-disturbance habitat below Iron Gate Dam supported high densities of the myxozoan annelid host, and an episodic high spore “infectious zone” (Stocking and Bartholomew, 2007; Alexander et al., 2015; Alexander et al., 2016). S2 will be profoundly affected by the removal of the four dams and restoration of a more natural flow regime that will alter myxozoan disease outcomes.

5.3.1.1.1 Impacts on annelid hosts

S2 annelids transmit myxozoan parasites to out-migrating juvenile salmon, which move the parasites downriver where they infect annelids in S1. In low disturbance water years prior to dam removals, S2 annelids were frequently at peak distribution and density year-round, with infection prevalence highest in late winter/early spring. Annelid host distribution and density will change - both immediately after dam removals, and over the long term.

Over the short term in S2, sediment mobilization and deposition will reduce annelid host distribution and densities from a combination of sedimentation/burial and scour, particularly downstream from the location of the former Iron Gate Dam. Habitat complexity may provide refugia from effects of sediment mobilization in some areas, thus annelid populations that persist in these protected areas will expand rapidly, potentially tempering the extent of short-term impacts.

Over the long term, the restoration of more natural and variable flow and sediment regimes will decrease annelid habitat suitability (stability) and prevent establishment of high-density populations (Jordan, 2012; Alexander et al., 2014; Alexander et al., 2016). The predicted increases in frequency of events that disturb substrate and attached periphyton (threshold critical flow events, Curtis et al., 2021) should drive patchier annelid distribution and lower densities overall as a result of mechanical scour and flushing (Alexander et al., 2016). In particular, high density annelid populations within the pre-dam-removal-infectious-zone (within S2), should be reduced greatly after dam removal.

5.3.1.1.2 Predictions for juvenile salmon

In the short term, the mobilization of fine sediments following the first major precipitation event is expected to depress annelid distribution and density resulting in fewer waterborne actinospores. In the long term, the far more dynamic flow regime will decrease stability of microhabitats and prevent establishment of high-density annelid populations (Jordan, 2012; Alexander et al., 2014; Alexander et al., 2016). Consequently, the overlap between annelids and myxospores, and in turn, myxozoan infection and disease risk for migrating juvenile salmon, should be reduced.

Warmer spring temperatures will also alter host-pathogen overlap. Earlier fry emergence (Sykes et al., 2009) and their faster growth will encourage earlier migration downstream (Bartholow et al., 2004; FERC (Federal Energy Regulatory Commission), 2007; Hamilton et al., 2011). Similarly, changes in hatchery operation to volitional releases of juveniles will allow fish to migrate earlier than before dam removals, when they were deliberately released after naturally produced fish had migrated downstream. Although we expect that *C. shasta* and *P. minibicornis* actinospore release will occur approximately 2 to 3 weeks earlier in S2 (Chiaramonte, 2013), we expect that many juveniles will migrate before the peak of waterborne spore abundance, similar to migration times of naturally produced fish prior to dam removal. Furthermore, with the expanded release window, fewer fish will be migrating simultaneously and thus overlap of juveniles and peak spore densities, and consequent disease risk, should be reduced. For juvenile salmon migrating in the fall, actinospore levels are expected to be lower as a result of the cooler water temperatures. The lack of temporal overlap between juvenile salmon migration and *C. shasta* is attributed to why the parasite is not a major cause of juvenile salmon mortality in the Fraser River, British Columbia, Canada (Margolis et al., 1992). Similarly, in the Klamath River it is likely that a greater diversity of salmon life histories will eventually have the opportunity to be expressed, with some of those types more likely to avoid parasite exposure by migrating earlier or overwintering in tributaries and migrating in the fall.

5.3.1.1.3 Predictions for adult salmon

Pre-spawn mortality of Fall-run Chinook Salmon and Steelhead from myxozoan infections was not reported in S2 prior to dam removals. We expect this mortality risk will not increase for these fishes, as spawning in the mainstem Klamath River would occur under cooler water temperatures (CSWRCB (California State Water Resources Control Board), 2018), slowing the proliferation and development of myxozoan parasites. Spring-run Chinook Salmon adults migrating through S2 during summer months may be at risk for pre-spawn mortality because they will encounter pathogens and warmer water temperatures. However, this risk may be mitigated if fish are able to access cold-water refugia and tributaries during migration to the upper basin, or through life history variability (e.g., earlier freshwater migration). Without knowing when peak migration will occur and if it will overlap with actinospore release, more certain predictions cannot yet be made.

5.3.2 Single-host pathogens

5.3.2.1 *I. multifiliis*

In juvenile fish, infection prevalence of *I. multifiliis* may be reduced in S2 if there is more dispersal as a result of volitional hatchery releases and warmer water temperatures, which will encourage fish to migrate earlier. In adult salmon, the intensity of *I. multifiliis* infections lessens typically as they migrate upstream and through S2 (Belchik, 2015) and we do not anticipate this to alter after dam removals.

5.3.2.2 Bacteria

The short-term pulse of reservoir sediments and increased turbidity and suspended sediment may increase risks of infection by *F. columnare* if river water temperatures are above 15°C in S2 due to gill abrasion. However, over the long term, the infection risk for *F. columnare* for juvenile salmon is likely to remain similar to the risk prior to dam removals, or decrease, as volitionally released fish will be more dispersed in space and time. For adult Spring-run Chinook Salmon, warmer water temperatures in S2 during their spring migration present some risk. However, for adult salmon returning in fall, reduced water temperatures are predicted to lessen disease risk.

5.4 River section 3 (S3) - Hydroelectric Reach - Iron Gate Dam to Keno Dam

The greatest long-term physical and biological changes to the river will occur in S3 due to the restoration of connectivity and habitats, and changes in flow and temperature regimes. Dam removals will result in access to historically used salmon habitat, and fishes are expected to rapidly (e.g., within 3 to 4 fish generations) reoccupy habitat upstream of Iron Gate Dam (Huntington, 2004; Huntington, 2006; Department of the Interior [DOI], 2007; Cunanan, 2009; Department of the Interior and U. S. Department of Commerce, and National Marine Fisheries Service [NOAA Fisheries], 2013). Restoring connectivity to the upper basin will result in a broader future distribution of Chinook Salmon and alter the abundance and distribution of pathogens that currently occur in S2 (Bartholomew and Foott, 2010; NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service), 2013; NMFS (National Marine Fisheries Service), 2019).

Fish disease risk in S3 after dam removals is difficult to predict because there will be losses and gains of the habitats that support both the re-establishing salmonids and parasite invertebrate hosts (i.e., annelids, snails). The cessation of hydropeaking operations will affect the former hydropeaking reach below JC Boyle Dam; approximately 27 rkm (25%) of S3. Prior to dam removals these operations resulted in daily flow (3-fold increase/decrease) and temperature fluctuations (up to 10°C). Their cessation will result in a flow regime more similar to that of more natural riverine habitats and temper the diel temperature swings (CSWRCB (California State Water Resources Control Board), 2018), improving habitat suitability for salmonids and invertebrate hosts. Restoration of the reservoirs to riverine sections will affect ~60 rkm (60%) of the mainstem S3 (former reservoir reaches), and will both eliminate inflow environments that supported high annelid densities (Stocking and Bartholomew, 2007) and expose new areas that were previously unsuitable habitats. Consequently, although there will certainly be a marked change in invertebrate host distributions following dam removals, there may be no net change in abundances. Elimination of reservoirs will also result in more variable water temperatures throughout S3. Groundwater spring inputs (~11°C), many of which were previously submerged under reservoirs, will create intermittent cold-water refugia that are expected to provide benefits to migrating salmonids (through reduced parasite dose and proliferation, and stress).

5.4.1 Multi-host parasites

5.4.1.1 *Myxozoans*

Chinook Salmon and Coho Salmon re-establishing above the former location of Iron Gate Dam will introduce *C. shasta* genotypes I and II. Predictions on these changes are discussed below. However, for Steelhead, we expect no adverse change in disease risk as infection by genotype 0 rarely causes overt disease.

5.4.1.1.1 Impacts on annelid hosts

The impacts of dam and reservoir removal will be significant for S3 annelids. The greatest short-term changes will occur in reservoir inflows. Reservoir drawdown will desiccate high density populations, the majority of which were distributed throughout reservoir inflow reaches. The cessation of daily hydropeaking operations will increase riverine stability and in turn, habitat suitability. However, over the long term, annelid host re-establishment is not expected to occur to the same extent as under conditions prior to dam removals in S3 because the restoration of reservoirs to riverine habitat will provide less optimal habitat for the annelids and they will not be able to i) redistribute to previously inundated areas (now dry), and ii) re-establish at the same densities due to restored flow regime. Annelids in S3 did not have a role in transmitting *C. shasta* to anadromous salmon prior to dam removals. Following dam removals, we expect infection dynamics to be similar to those of post-dam S2.

5.4.1.1.2 Predictions for juvenile salmon

Prior to dam removals, moderate densities of *P. minibicornis* and *C. shasta* genotypes 0 and II were detected in S3 (Hallett and Bartholomew, 2006; Bartholomew et al., 2007; Atkinson and

Bartholomew, 2010b). After dam removals, *C. shasta* genotype I will be reintroduced to S3 and S4 by returning adult Chinook Salmon infected in S1 and S2, and the lower river biotype of genotype II introduced to S3 by returning Coho Salmon. These introductions will create new infection sources for juvenile Chinook and Coho Salmon. Densities of genotype 0 are likely to remain similar to pre-dam removal levels, and thus risks to Steelhead/Redband are likely to remain low.

Once *C. shasta* genotype I establishes in S3 and S4, juvenile Chinook Salmon migrating from these sections will have a prolonged exposure (as a result of the extended migration route). Post-dam removals, redistribution of adult salmon to Fall Creek and other tributaries is expected to reduce myxospore input from these fish into the mainstem and eliminate the conditions that drive the infectious zone downstream from Iron Gate Dam (discussed under Adults). Thus we do not expect juvenile Chinook Salmon to encounter high densities of *C. shasta* genotype I. We predict this will also be true for Coho Salmon and genotype II in S3. This altered exposure regime (reduced densities, prolonged exposure) should enable the fish's natural resistance to resolve the infection prior to completing their downstream migration, and in turn reduce myxozoan-related mortality in out-migrating juvenile salmonids. Further, while fluctuating temperatures under post-dam conditions will not directly affect myxozoan disease processes in juvenile salmon (Chiaramonte et al., 2016), fish may avoid migrating during periods when temperatures are high, and instead use low infection risk tributaries and the larger springs as temperature refuges. The spring-fed, cold-water refugia in S3 will reduce temperature stress and thus disease risk for both juveniles and adults (Ray et al., 2012).

5.4.1.1.3 Predictions for adult salmon

Adult salmon infected with either myxozoan will benefit from the earlier decrease in temperature in the fall, which will reduce the rate of myxozoan replication, and thus reduce the risk of infection progressing to disease that could otherwise result in pre-spawn mortality. However, the net change in risk is unknown, particularly for Spring-run Chinook Salmon that enter the river in late spring and will experience prolonged exposure to myxozoans coincident with high water temperature. This may increase disease risk and pre-spawn mortality, although some of this risk may be mitigated by residence in cold-water refugia.

The relocation of hatchery operations from downstream of Iron Gate dam to Fall Creek introduces some risk for creating a novel infectious area in S3, below this potential new concentration of spawning adults. However, as Fall Creek Hatchery is located ~2 km upstream from the confluence with the Klamath River, this should reduce dispersal of myxospores into the river mainstem. Adult salmon will also not face a barrier to further migration and so fish not collected by the hatchery for broodstock will be able to migrate further, to spawn either in the Klamath River mainstem or upriver tributaries. However, the emergence of a novel myxozoan "infectious zone" downstream of Fall Creek should be considered in future monitoring programs.

5.4.2 Single-host pathogens

5.4.2.1 *I. multifiliis*

Because of the coldwater inputs in S3, the risk of infections will be low, especially for out-migrating juvenile fish early in the year. Risks will be greater for adult salmon if there are areas they are congregating and the temperatures and flow are permissive for *I. multifiliis* proliferation and transmission.

5.4.2.2 Bacteria

In S3, similar to S2, the short-term release of reservoir sediments may increase risks of infection by *F. columnare* due to gill abrasion if river water temperatures are above 15°C. The infection risk for *F. columnare* for juvenile salmon will increase as populations re-establish and fish densities increase; however, we expect volitionally released hatchery fish will be dispersed in space and time compared to historical controlled hatchery releases. For adult Spring-run Chinook Salmon, warmer water temperatures in S3 during their spring migration present some risk. For adult salmon returning in fall, cold water spring inputs will lessen disease risk.

5.5 Upstream from Keno Dam to headwater tributaries

Upstream of Keno Dam there will be no alterations to river structure or flow as a result of dam removals, so disease risks in the S4 reservoir and lakes will be a consequence of re-establishment of anadromous salmonids and their interactions with resident species. Adult Spring- and Fall-run Chinook Salmon and Steelhead are expected to migrate through Klamath Lake and into the Williamson River and Sprague River.

5.5.1 Multi-host parasites

5.5.1.1 Myxozoans

Prior to dam removals, *P. minibicornis* and *C. shasta* genotypes O and II were well established in the lower 18 rkm of the Williamson River (Hendrickson et al., 1989; Bartholomew et al., 2007; Hurst and Bartholomew, 2012). Neither *C. shasta* genotype was detected in its main tributaries, the Sprague River and Spring Creek (Hurst and Bartholomew, 2012). The Williamson River supports high densities of annelid hosts in this lower 18 rkm reach between the confluence of the Sprague River, and Williamson River inflow to upper Klamath Lake (Hurst et al., 2012).

5.5.1.1.1 Impacts on annelid hosts

While we do not expect changes in annelid host distribution and density in S4 post dam removals, we do expect changes in infection dynamics. Over the short term, changes in infection prevalence will not be particularly evident because it will take some time for *C. shasta* (genotype I and Coho Salmon biotype of genotype II) to become established. Over the long term, we expect to observe changes in annelid infection patterns that reflect the spatial and temporal changes associated with the re-establishment of anadromous salmonids.

5.5.1.1.2 Predictions for juvenile salmon

The re-establishment of adult Chinook Salmon spawning in the mainstem Williamson River downstream of the Sprague River confluence will likely result in establishment of genotype I, potentially at densities similar to the current densities of upper river genotype II. Fish that rear here will be exposed to *P. minibicornis* and to their associated genotypes of *C. shasta*, and will continue to be exposed throughout their migration. As discussed in S3, we do not know what this extended exposure regime will mean for disease risk in these populations. These disease pressures are likely to be strong selective factors for both migrating adults and juveniles from the UKL. Infection outcomes for juvenile fish migrating from S4 will likely be more dependent on water conditions than for fish originating from downstream sections because of the length of migration.

5.5.1.1.3 Predictions for adult salmon

Spring-run Chinook Salmon that migrate into the Klamath River in spring and migrate upriver to this section are at risk for pre-spawn mortality from prolonged exposure to *C. shasta* and *P. minibicornis* (Chapman, 1986; Bradford et al., 2010), the combined effects of pathogens, other temperature-dependent processes (e.g., low dissolved oxygen) and natural senescence (Hinch et al., 2012). Risk of pre-spawn mortality for Fall-run Chinook Salmon and Steelhead will be lower, as they will be entering the Klamath River during a time when parasite levels and water temperatures are lower.

5.5.2 Single-host pathogens

5.5.2.1 *I. multifiliis*

In S4, *I. multifiliis* will likely be a risk factor for both juvenile and adult salmon that congregate as they migrate through Keno and Link River dams' fish ladders, and in UKL and Lake Euwana during periods of poor water quality and high temperatures. Potential areas for bottlenecks like fish ladders (i.e. Keno Dam) will require monitoring for *I. multifiliis* and *F. columnare* in both adult and juvenile salmon (upstream and downstream migration).

5.5.2.2 Bacteria

F. columnare is an environmental bacterium that is maintained in non-salmonid fish populations in S4. Risks to both juvenile and adult salmon include crowding during migration through Keno and Link River dams' fish ladders, and periods of poor water quality and high temperatures in UKL and Lake Euwana. Elevated water temperatures will be an important factor in future *F. columnare* outbreaks, particularly in UKL where there are reservoir hosts for this bacterium and prolonged fish transit time.

R. salmoninarum is present in S4 in resident, native non-anadromous trout and Kokanee (remnants of stocked non-native populations). Rainbow trout (*O. mykiss*) are relatively resistant to the effects of disease, however, Spring-run Chinook Salmon are highly susceptible, and this introduces a risk that they have not encountered in the lower river. Because this bacterium is vertically transmitted, infected adults can pass the bacterium to eggs, and the resulting juveniles may be more vulnerable during periods of stress, such as smoltification. Factors that we consider important for future impacts from *R. salmoninarum* include the likelihood for interaction between susceptible salmonid populations (especially Chinook Salmon) and carriers of the infection.

6 Fish disease management - present and future options

With dams in place, the Klamath River was hydrologically regulated, and mitigation hatcheries were the primary source of endemic salmon. Following the 2002 epizootic, resulting from infections of *F. columnare* and *I. multifiliis*, two primary management strategies were implemented to avoid similar outbreaks: prescribed flow events (flushing and dilution flows) and modified release timing of hatchery fishes. A comprehensive fish health monitoring program was implemented in the lower basin, with a focus on these pathogens and others of concern (*C. shasta, P. minibicornis*). All of these efforts are planned to continue following dam removals, with limitations and modifications.

6.1 Flow manipulation

Discharge in the Klamath River mainstem and also the Trinity River has been increased to mitigate disease associated with *C. shasta*, *I. multifiliis* and *F. columnare*. For *C. shasta*, three different flow regimes were implemented to reduce enteronecrosis (Hillemeier et al., 2017) and each had a different application, dependent upon their timing (season), magnitude and duration. Two were aimed directly at reducing host annelid populations by moving different sediment types: a "deep flushing flow" of high discharge and short duration in spring every other year, and a "surface flushing flow" of moderate discharge and longer duration each winter. In response to an impending disease outbreak (informed by direct measurement of parasite spore densities in water samples and testing of trapped out-migrating juveniles from the river), an enhanced flow was implemented to reduce exposure dose for out-migrating salmon by diluting parasite spores and reducing exposure time (the increase in discharge, up to a threshold, encourages juveniles to out-migrate) [2013 and 2019 BiOps: NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service), 2013; NMFS (National Marine Fisheries Service), 2019]. For *I. multifiliis*, prescribed discharge from the Trinity River (Lewiston Dam) in response to high intensity of infection in returning adults (number of parasites per gill arch) has been utilized to mitigate disease.

After dam removals, options for directly manipulating river flow will be more limited, and the challenge to mimic the natural flow regime while retaining water for agriculture in the upper basin will remain. In general, water availability during dry water years will limit the ability to conduct surface flushing flows. To reach magnitudes similar to those achievable pre-dam removals, any flow action would have to be tied with natural water inputs such as rain on snow events, or timed to coincide with predicted high rainfall. However, bed mobility thresholds will be lower following removals (sediments become armored downstream of dams, requiring more flow to mobilize them), so lower magnitude flushing flows should have relatively more benefit after dam removals.

6.2 Shifting of hatchery release timing

The second management strategy considered after the 2002 epizootic was timing of release of juvenile hatchery salmon to reduce their risk of disease and improve survival to the ocean. This approach was only used once, in 2021, in response to a lack of water available to increase river discharge below the dams (and comply with the BiOp; NMFS (National Marine Fisheries Service), 2019) when *C. shasta* densities and river temperatures surpassed disease thresholds (unrecoverable disease or mortality). Millions of juvenile Fall-run Chinook Salmon, usually released from Iron Gate Hatchery into S2 in spring, were held into fall until conditions improved. Monitoring (Voss et al., 2022) and modeling (Robinson et al., 2020) support the efficacy of using this approach in dry water years. Following the shift of operations from Iron Gate Hatchery to Fall Creek Hatchery, this approach may warrant consideration under certain water year and disease risk contexts.

6.3 Climate change

Dam removal will not be the sole driver of change in the Klamath Basin; following dam removals, the basin will continue to evolve in an altered climate realm. Shifting patterns for two central abiotic factors, temperature (predicted to increase) and precipitation (timing and form predicted to alter), will have ramifications for host-pathogen dynamics. Aspects of climate change relevant to the Klamath Basin and salmonid disease are well considered for *C. shasta* (see case study by Ray et al., 2015) and many of those influences will also apply to other pathogens in the Basin; reiterating or delving further into these potential impacts are beyond the scope of this review.

The impacts of dam removals and climate change have been modeled for prevalence of infection in adult salmon in the Klamath Basin (Schakau et al., 2019); however, neither prevalence of disease in this life stage or any aspect of infection in the juvenile life stage were considered. This limited focus is misplaced as infection prevalence in either host does not always correlate with disease (see Voss et al., multiple years) and is an unsuitable predictor of population level impact. It would therefore be more relevant and informative to model the impact of major changes on prevalence of disease, particularly in the juvenile life stage.

6.4 Research and monitoring

Predicting future pathogen abundance and distribution is complex, therefore it is critical that a comprehensive research and monitoring program is in place to capture changes during and after river restoration, and to address information gaps in our knowledge of pathogen transmission and host-pathogen interactions. Before dam removals, pathogen monitoring was multifaceted, and largely focused on S1 and S2, where disease outbreaks in salmon have been observed. Monitoring targets included: *C. shasta* - molecular quantification of waterborne stages in water samples, molecular tests and microscopy for prevalence of infection and severity of infection in outmigrants and sentinel fishes, and prevalence of infection in, and density of, annelids; *P. minibicornis* - prevalence of infection in outmigrants, with several years of quantification of waterborne stages in water samples; *I. multifiliis* - direct, lethal sampling of returning adults; *F. columnare* - presence of disease signs in juveniles and returning adults. Surveillance of fish in the upper basin has been opportunistic.

In the years immediately before dam removals, existing long-term monitoring efforts were expanded into S3 and S4 to characterize pathogen occurrence prior to reconnection of the upper and lower basin. Additional studies (ODFW; 2022-2024) included experimental releases of tagged (acoustic, radio, and PIT tags) Spring-run Chinook Salmon smolts, which were used to inform reintroduction protocols, and develop and coordinate monitoring programs. Sentinel cage exposures with subsets of these fish were also used to inform their susceptibility and associated disease risk to pathogens present in the Upper Klamath Basin prior to dam removals (ODFW and Oregon State University; 2022-2023). After dam removals in the Klamath Basin, continuation of these monitoring programs to track the distribution and abundance of fish pathogens in water, fishes and invertebrate hosts will be critical to inform the health status of fish during basin restoration efforts.

6.5 Research and monitoring recommendations

- Conduct sentinel fish exposures and collect annelid and water samples to monitor potential emergence of a new *C. shasta*-infectious zone in the mainstem, below the confluence with Fall Creek and in the former reservoir habitats.
- Conduct sentinel fish exposures and collect annelid and water samples to monitor changes in distribution of myxozoan parasites.
- Sample returning adult salmon, particularly Spring-run Chinook Salmon, to understand prevalence and progression of myxozoan infection and spore development (infection status upon river entry, proportion contributing myxospores, range in production per fish, when sporulation occurs).
- Conduct survey of pre-spawn salmonid mortalities for all target pathogens.
- Conduct survey of adult and juvenile salmon for both *I. multifiliis* and *F. columnare*, during upstream and downstream migration at potential areas for bottlenecks such as fish ladders at the remaining dams.

- Monitor *R. salmoninarum* risk to Spring-run Chinook Salmon in S4.
- Conduct survey for snail hosts of trematodes in the Basin, and monitor for prevalence of trematode disease.
- Conduct surveys to determine which hosts perpetuate *C. shasta* genotype II in S4.
- Conduct experiments to determine how *C. shasta* genotype II interacts with Coho Salmon.
- Conduct experiments to determine the susceptibility of Spring-run Chinook Salmon to *C. shasta* genotype I.
- Conduct experiments to better understand the effects of co-infections in juvenile salmonids.
- Conduct experiments to better understand effects of *P. minibicornis* infections on juveniles (see Voss et al., 2018).
- Conduct experiments to understand the effects of thiamine deficiency on disease severity associated with infectious agents in juvenile salmonids.
- Conduct experiments that assess the effects of low, but prolonged exposure doses for myxozoans (to better understand the impact of longer migration routes and infection periods).
- Conduct fish disease risk assessments prior to implementing habitat restoration.
- Include fish pathogen distributions as an important factor in risk assessment frameworks (Brenkman et al., 2008).

7 Conclusion

The removal of four dams on the Klamath River will dramatically alter the biotic and abiotic components of the Basin. Dam removals alone will restore a number of physical and ecological processes towards historical, pre-dam conditions. This will result in a more dynamic environment for salmon, trout and their pathogens, reducing the impacts of many of these current stressors (Williams et al., 2018; Bellmore et al., 2019). However, dam removal is only one component of the river restoration story. To meet the project's overarching goal – the recovery of salmon populations for tribal cultural and subsistence needs – it is imperative that the pathogens that affect these fishes be understood in the context of a re-connected river, which is additionally undergoing significant climatological shifts. Our role as architects of this renewal includes being active in monitoring changes and if necessary intervening to promote fish health, for the benefit of all Basin inhabitants. The predictions we make in this study should assist in achieving these goals.

Author contributions

SH conceived the synthesis theme. SH, JB, JA and SA conceptualized and designed the study and undertook primary writing and editing. JA led sections related to annelid hosts and on physical attributes, JB led sections on pathogens, SH contributed the management section. JB, SA, SH, JF, AV, SB, RH contributed to pathogens, parasites and disease. TS, BM, JA, AG, MB contributed historic and present tribal knowledge. THW, TGW, NS, MH, MB contributed to fish biology and predicted physical changes. SA created the figures. All authors contributed critically to the drafts and approved submission.

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Conflict of interest

Publisher's note

Supplementary material

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Diadromous fish run assessment: a double-observer model using acoustic cameras to correct imperfect detection and improve population abundance estimates

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Introduction: Diadromous fish populations have strongly declined over decades, and many species are protected through national and international regulations. They account for less than 1% of fish biodiversity worldwide, but they are among the most perceptible linkages between freshwater and marine ecosystems. During their migration back and forth, diadromous fish species are subjected to many anthropogenic threats, among which river damming can severely limit access to vital freshwater habitats and jeopardize population sustainability. Here, we developed a method based on a double-observer modeling approach for estimating the abundance of diadromous fish during their migration in rivers.

Methods: The method relies on two independent and synchronous records of fish counts that were analyzed jointly thanks to a hierarchical Bayesian model to estimate detection efficiencies and daily fish passage. We used simulated data to test model robustness and identify conditions under which the developed approach can be used. The approach was then applied to empirical data to estimate the annual silver eel run in the Touques River, France.

Results: The analysis of simulated datasets and the study case gives evidence that the model can provide robust,accurate, and precise estimates of detection probabilities and total fish abundance in a set of conditions dependent on the information provided in the data (annual distribution of fish passage, annual number of observation, pairing period, etc.).

Discussion: Then, the method can be applied to various species and counting systems, including nomad acoustic camera devices. We discuss its relevance for programs on river continuity restoration, notably to quantify population restoration associated with dam removals.

KEYWORDS

abundance estimates, Imperfect detection, migratory fish, acoustic camera, hierarchical Bayesian model, double observer, population monitoring

1 Introduction

Estimating abundance is a major issue for the management and conservation of animal species. Abundance informs about demographic trends and responses to various pressures at local and global scales (McGill, 2010; McShea et al., 2016). In the case of exploited populations, a robust assessment of abundance is a prerequisite to designing suitable harvest regulations (Chrysafi and Kuparinen, 2016). For several hundreds of animal species, exploited or not, the European Union directives request regular reports on their status. These reports should include estimates of population size and temporal trends in abundance being key criteria to set up a proper management strategy for their conservation (IUCN, 2022).

Over decades, diadromous fish populations have strongly declined, and many species are currently protected by national and international regulations (Renaud, 1997; Feunteun, 2002; Aprahamian et al., 2003; Limburg and Waldman, 2009). These species typically share their lifetime between freshwater and marine ecosystems; thus, they are exposed to human-induced pressures in both ecosystems (Limburg and Waldman, 2009; Robinson et al., 2009; Runge et al., 2014). For example, while migrating back and forth as juveniles and adults, river damming can drastically impede access to spawning, nursery, or foraging vital habitats. For instance, the number of rivers inhabited by Atlantic salmon (*Salmo salar*) has regressed since the 19th century in France alongside dam constructions on the largest rivers (Thibault, 1987). By restoring connectivity along the watershed–ocean continuum, dam removal is a necessary, if not sufficient, option to recover diadromous fish populations and the many ecosystem services associated with them (Ouellet et al., 2022).

To monitor these populations, fish traps or video or resistivity counters have been in operation for decades on a limited number of rivers to observe annual runs (i.e., cumulative numbers of fish entering or leaving the watershed each year) in Atlantic salmon, shads (*Alosa* sp.), European eel (*Anguilla anguilla*), or lampreys (*Lampetra* sp. and *Petromyzon* sp.) (Reddin et al., 1992; Hard and Kynard, 1997; Forbes et al., 1999; Legrand et al., 2019). Such counting facilities, however, require significant financial investment and civil engineering work to be set up, which may not be desirable or appropriate for continuity restoration programs. When dam decommissioning and removal are consented to on a river with no pre-existing data, an alternative method to catch variations in annual diadromous fish runs must be anticipated.

Estimating annual runs of diadromous fish ascending or descending a river is no easy task. Most of the time, only a fraction of the migrating fish is counted either because a portion of the river channel is not monitored or because environmental factors hamper fish observation. For instance, water turbidity can significantly reduce observation while using video camera systems (Mallet and Pelletier, 2014; Figueroa-Pico et al., 2020). Ignoring imperfect detection leads to substantial biases in population estimates (Royle and Dorazio, 2006; Kéry and Schmidt, 2008) and precludes proper comparisons between years and rivers. Therefore, assessing detection probability at fish-counting facilities is necessary before using available data to assess diadromous fish runs.

Several options exist to account for the imperfect detection of individuals while estimating animal population abundance, among which the most popular methods are capture–mark–recapture (Borchers et al., 2002; Williams et al., 2002; Desprez et al., 2013), repeat counts (Royle, 2004; Kéry et al., 2005; Dail and Madsen, 2011), removal (Farnsworth et al., 2002; Wyatt, 2002; Rivot et al., 2008; Chandler et al., 2011; Reidy et al., 2011), distance sampling (Buckland et al., 1993; Marques et al., 2010), and multiple observers (Nichols et al., 2000; Kissling et al., 2006; Durban et al., 2015). The method most commonly used to estimate the abundance of fish in rivers is removal, and capture–mark–recapture is commonly used to estimate the efficiency of fish-counting facilities worldwide (e.g., Roper and Scarnecchia 2000; Rivot and Prévost, 2002; Servanty and Prévost, 2016). It requires several handling steps for preparing the fish, which is labor-intensive and may present a risk to animal welfare (Dunkley and Shearer, 1982). Moreover, the migratory behavior of fish may be altered by handling, and a bias in efficiency estimates can be suspected. For these reasons, a less intrusive way to correct for imperfect detection at fish-counting facilities would be welcomed.

In the present paper, we chose to adopt a double-observer approach to correct imperfect detection at fish-counting facilities in order to upgrade existing counting data into abundance estimates. The double-observer approach has been used for many animal species, more specifically on mammals and birds (Cook and Jacobson, 1979; Aastrup and Mosbech, 1993; Forsyth and Hickling, 1997; Nichols et al., 2000; Kissling et al., 2006; Suryawanshi et al., 2012), but to our knowledge, this method has not yet been used on migratory fish. During a pairing period, two independent observers (primary and secondary observers) simultaneously count individuals from a given population and can infer individual numbers outside the pairing period when only the primary observer is operating. We applied this principle to a setting made of two independent fish-counting devices to estimate the annual number of migratory fish passing by the devices. We developed a hierarchical Bayesian model that jointly analyzes the daily records by each observation device to estimate detection rates and assess population abundance. First, we used simulated datasets that mimic the migration of diadromous fish i) to test the robustness of our model and ii) to provide recommendations about minimum data standards needed to run the model (duration of the pairing period, number of observations, and phenology of migration). Thereafter, iii) we applied our approach to a real-life case study where we combined a nomad acoustic camera equipment (secondary observer) with a stationary video counter (primary observer) to highlight the potential of our double-observer model. Compared to video cameras, acoustic camera technology has the great advantage of being insensitive to water turbidity fluctuations (Martignac et al., 2015). Once set up, the two devices synchronously produce independent counts of European eel (*A. anguilla*) adults moving downstream the Touques River (France). These data are fed into our model to infer detection probabilities and the total annual abundance of eels emigrating the river toward their spawning areas in the Atlantic Ocean. The advantages and limits of such a method based on nomad acoustic camera devices are discussed, notably for quantifying population restoration associated with river continuity restoration and dam removal projects.

2 Materials and methods

2.1 Data matching in a hierarchical Bayesian model

Fish-counting facilities can have various designs depending on the monitoring equipment used and river channel configuration. Moreover, they can target different diadromous fish species during their migration upstream or downstream at different frequencies (hourly, daily, weekly, or more). The model to develop should be easily adapted to these various cases. In addition, the double-observer framework requires the deployment of a secondary, autonomous device that must be synchronized with the primary fish-counting facility for a certain period of time. The model partly relies on this pairing period between the two independent observers and uses data matching to estimate the detection rates of each observer. In order to perform data matching, the two monitoring devices need to be placed in close proximity to each other i) to allow tracking of individual fish passage on both devices and ii) to ensure that no mortality occurs between the two observations. The model was developed in a hierarchical Bayesian framework, as described (Figure 1).

2.1.1 The total abundance

The number of fish seen by the primary monitoring device, $C1S_t$, during a given time step t is modeled as probabilistic issues of binomial experiments. Two underlying hypotheses must be fulfilled: 1) all fish behave independently, and 2) all fish are detected using the same detection probability within a given time step. Under these hypotheses, the number of individuals seen by the primary monitoring device each time step t, $C1S_t$, is modeled using a binomial distribution with the fish abundance at t Nfr_t and the detection probability of the primary observer $p1$:

$$C1S_t \sim Binomial(Nfr_t, p1)$$

The number of fish seen by the secondary observation device $C1S2S_t$ is modeled using a binomial distribution conditionally on the number of individuals seen on the primary monitoring device $C1U2S_t$, conditionally on the number of individuals unseen on the primary monitoring device $C1U_t$, and dependent on the detection probability of the secondary observer $p2$:

$$C1U_t = Nfr_t - C1S_t$$

$$C1S2S_t \sim Binomial(C1S_t, p2)$$

$$C1U2S_t \sim Binomial(C1U_t, p2)$$

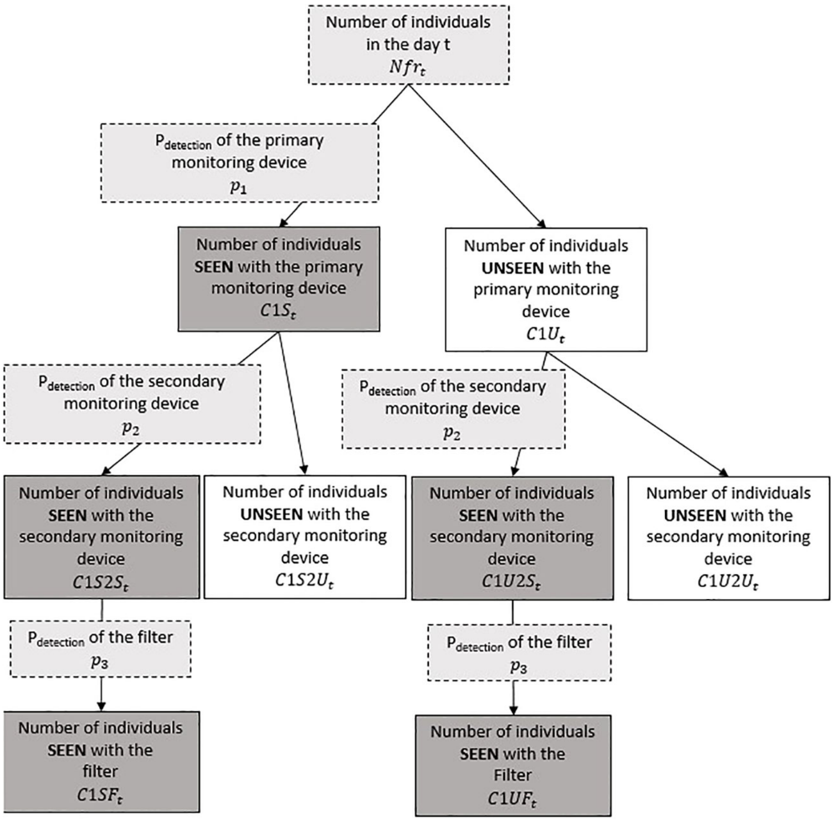

FIGURE 1
Diagram representing the model structure. Dark gray indicates the data provided to the model, pale gray indicates the parameters and variables of interest that will be estimated, and white indicates the other estimated variables.

The phenology of fish migration depends on species, the geographical position of the environment monitored, and environmental conditions or the time step chosen. As a result, we define the highly variable abundance of fish for each time step, Nfr_t, as follows:

$$Nfr_t = round(Yfr_t)$$

where Yfr_t is considered to be partially exchangeable and is modeled using a gamma distribution conditionally on the shape $r.y_t$ and the inverse scale $mu.y_t$.

$$Yfr_t = \ Gamma(r \,.\, y_t, mu \,.\, y_t)$$

$$r \,.\, y_t = \frac{1}{CV \,.\, y_m^2}$$

$$mu \,.\, y_t = \frac{1}{E \,.\, y_m \times CV \,.\, y_m^2}$$

The two parameters $r \,.\, y_t$ and $mu \,.\, y_t$ are dependent on the expected mean $E \,.\, y_m$ and on the coefficient of variation $CV \,.\, y_m$ where $m \ \in$ 1:12 represents a random effect of the month of observation to allow intra-seasonal variability in fish abundance estimates. $E \,.\, y_m$ is normally distributed with unknown expected mean, $\mu \,.\, E_m$ and standard deviation depending on the month, $\sigma \,.\, E_m$ such as:

$$E \,.\, y_m \sim Normal(\mu \,.\, E_m, \sigma \,.\, E_m)$$

The total abundance of fish that migrated by the observation devices over the whole study period is defined as follows:

$$NT = \sum_t Nfr_t$$

2.1.2 Detection probabilities

The detection probability of the primary and secondary observers depends on the study site and the technology of the observation device. It may also vary over time as a function of environmental conditions (e.g., turbidity). However, there is a potential confounding effect of environmental conditions on fish detection and fish abundance. For instance, flood conditions may result in i) low detection probability of the video counter because of increased turbidity and ii) high fish abundance because high flow triggers migration in, e.g., salmon or eels (Stevens and Miller, 1983; Vøllestad et al., 1986; Bultel et al., 2014; Lebot et al., 2022; Lagarde et al., 2023). Thus, to avoid confusion within the model, we do not account for the environmental covariates, but such an effect could be implemented if needed. The detection probability of the primary and secondary observers where set independently and constant over the study period. A logit scale was used for the detection probabilities. $logit(p1)$ and $logit(p2)$ follow uninformative Normal distributions.

$$logit(p1) \sim Normal(0, 0.1)$$

$$logit(p2) \sim Normal(0, 0.1)$$

2.1.3 Adding a data pre-processing module to the model

Some observation devices produce continuous recordings of the river, like optic or acoustic cameras. An entire reading of the datasets is highly time-consuming; most studies integrate a pre-processing filter that aims to focus only on observations of fish species of interest. This filter should be set based on known morphological or behavioral characteristics of the target species. The probability of a filter in detecting a fish within the available records may depend on a large number of parameters, such as the diversity and number of fish passages, the clarity of images, the pre-processing algorithm, and the criteria selected to discriminate the species of interest. We thus develop a specific module to describe this specific step of data pre-processing in the model without any *a priori* knowledge of the pre-processing filter used and estimate its associated specific detection probability $p3$ (Figure 1). When applying this filter to the second observer (Figure 1), the number of fish seen by the primary observer and detected by the filter, given it was recorded by the secondary observer, $C1SF_t$, is modeled using a binomial distribution conditionally on the number of fish seen by the primary and secondary observers ($C1S2S_t$). The detection probability of the filter $p3$ follows an uninformative Normal distribution. The number of fish unseen by the primary fish counter but seen by the filter after the secondary observer is modeled using a binomial distribution conditionally on the number of fish unseen by the primary observer and seen by the secondary observer ($C1U2S_t$) and the detection probability of the filter $p3$.

$$logit(p3) \sim Normal(0, 0.1)$$

$$C1SF_t \sim Binomial(C1S2S_t, p3)$$

$$C1UF_t \sim Binomial(C1U2S_t, p3)$$

To obtain the number of fish seen by the primary observer and secondary observers $C1S2S_t$ and the number of fish unseen by the primary observer and secondary observers $C1U2S_t$, the operator conducts on a regular basis an exhaustive examination of records from the secondary observer, e.g., without using the pre-processing filter.

2.1.4 Prior specification for free parameters

Prior distributions were assigned to all free parameters (i.e., parameters that are not conditioned by any other quantity of the model). For all, uninformative prior distributions were used in order to let the Bayesian posterior inferences reflect the information brought by the data (Table 1).

2.1.5 Computation

We fitted the model within the Bayesian framework using three chains of 300,000 iterations with a burn-in of 270,000 iterations, each with different initial values. We monitored the R ê parameter to assess model convergence (Brooks and Gelman, 1998). We used the R software version 4.2.1 (R Development Core Team, 2022) to simulate the data, and we performed the analyses using the JAGS software from R through the package jagsUI (Kellner, 2021).

TABLE 1 Prior distributions of the free parameters.

Parameters	Distribution
$\mu.E_m$	*Normal* (1,10)
$\sigma.E_m$	*Uniform* (1,10)
$CV.y_m$	*Uniform* (1,3)
α_{p1}	*Normal* (1,10)
β_{p1}	*Normal* (1,10)
σ_{p1}	*Normal* (1,5)

2.2 Simulation study

2.2.1 Assessing the limits of the model using simulated datasets

We aimed to test the model to assess its performance at estimating fish run abundance under different conditions of observation. We ran the model using a dedicated set of simulated datasets, simulating daily observation of fish over a period of 1 year, to investigate the effect of 1) the detection probability of each of the two observers; 2) the distribution of observation over time; 3) the total number of observations; 4) the duration of the pairing period, when the two observers are active; and 5) the timing of the pairing period, with regard to the migration phenology.

To ensure biologically reasonable simulations, we built our simulated datasets based on the range of conditions encountered at main French and European fish-counting facilities (Eatherley et al., 2005; Almeida and Rochard, 2015; ICES, 2021; Briand et al., 2022; ICES, 2022), such as the following.

2.2.1.1 Detection probabilities

The detection probability of the fish observation devices is well documented (Fewings, 1992; Reddin et al., 1992; Eatherley et al., 2005) and generally varies between 70% and 100%. The detection probability depends on local site configuration and the species, as one setting would not fit all purposes equally. However, the proportion of migrating fish that do not pass in front of the observation device because of possible bypass is generally unknown. This proportion of escapees is virtually null at large impassable hydropower dams (e.g., in river Perhonjoki for lampreys; Ojutkangas et al., 1995) or extremely high when most of the river flow is diverted into many reaches or when downstream migration can take place through weir spillover. Given these elements, we simulated datasets for detection probabilities of the primary observation device equal to 0.05, 0.2, and 0.7 (three modalities). Assuming that a secondary observation device would be installed in a way to maximize observation of the species of interest, we simulated datasets for detection probabilities of the secondary observation device equal to 0.2 and 0.7 (two modalities) and detection probabilities for the filter equal to 0.2 and 0.7 (two modalities). The list and ID of combinations of detection probabilities are presented in Table 2.

2.2.1.2 Annual distribution of fish passage

Six diadromous species are mainly targeted at fish counters in Europe: Atlantic salmon (*S. salar*), sea trout (*Salmo trutta*), European eel (*A. anguilla*), shads (*Alosa alosa* and *Alosa fallax* spp.), and sea lamprey (*Petromyzon marinus*). In all these species, the migration phenology is characterized by one or two seasonal peaks of migration when most observations take place (Rochard, 2001; Jonsson & Jonsson, 2002; Orell et al., 2007; Almeida and Rochard, 2015; Sandlund et al., 2017). Thus, we simulated datasets for three modalities derived from the main difference in the migration phenology in those fishes: i) a migration pattern with one peak of fish passage in November, ii) a migration pattern with two peaks of fish passage in July and in November, and iii) a migration pattern with a quasi-homogeneous distribution of fish passage throughout the year with no clear peak, as observed in holobiotic species, as a reference.

2.2.1.3 Annual number of observations by the primary observer

Over the period 2011–2015, most video-counting sites in France recorded between 0 and 200 observations per species of interest annually (Pers. Com. C. Briand). Thus, we selected values of 200, 150, 100, or 50 fish observations for a year ($C1S = \sum C1S_t$) to simulate our datasets (four modalities).

2.2.1.4 Duration of the pairing period

As we aimed to adapt the double-observer approach to situations where the second observer is only operating part of the study time, we tested the effect of the pairing duration on model performance. We simulated periods of three and five consecutive months of paired observations by the two observers (two modalities).

2.2.1.5 Timing of the pairing period

This point is designed to define the best pairing period to set up the temporary secondary observer with respect to the migration

TABLE 2 Combinations of detection probabilities used to create simulated datasets and their identification numbers.

Combination ID	*p1*	*p2*	*p3*
1	0.2	0.2	0.2
2	0.2	0.2	0.7
3	0.2	0.7	0.2
4	0.2	0.7	0.7
5	0.7	0.2	0.2
6	0.7	0.2	0.7
7	0.7	0.7	0.2
8	0.7	0.7	0.7
9	0.05	0.2	0.2
10	0.05	0.2	0.7
11	0.05	0.7	0.2
12	0.05	0.7	0.7

phenology and the annual distribution of observations by the primary observer. For this, we simulated independent datasets with a pairing period starting in each month of the year (12 modalities).

2.2.2 Simulation of the datasets

Unique datasets were created for different combinations of the above-mentioned modalities. To create a simulated $C1S_t$, a random number was generated from a normal distribution with a mean and a standard deviation depending on the month of observation, the seasonal distribution of fish passage, and $C1S$. The daily abundance of fish passing by the primary observer Nfr_t was simulated by making a random draw in a negative binomial distribution, for which simulated $C1S_t$ and detection probabilities $p1$ are the parameters. Likewise, during the pairing period, daily observations $C1S2S_t$ and $C1U2S_t$ were simulated by generating a random number from a binomial distribution using simulated detection probabilities $p2$ and simulated $C1S_t$ or simulated $C1U_t = Nfr_t - C1S_t$, respectively. Similar procedures were used to simulate $C1SF_t$ and $C1UF_t$ using simulated $p3$ and simulated $C1S2S_t$ or $C1U2S_t$ as parameters.

We designed a set of simulated datasets, grouped into three experiments, to investigate the performance of the model to the progressive degradation of the information available, such as the following.

2.2.2.1 Experiment 1: the pairing period

We built our simulations starting with modalities of reference depicting the most informative range of conditions that could be expected from most French fish-counting facilities in terms of detection probability (p1 = p2 = p3 = 0.7) and annual number of observations by the primary observer ($C1S$ = 200). We then investigated the effect of the duration and timing of the pairing period on the model output by simulating datasets for pairing periods of 5 and 3 months, for all 12 starting months. We compared the results between the three types of annual distribution of fish passage (n = 72 datasets).

2.2.2.2 Experiment 2: number of observations

Relying on high detection probabilities (p1 = p2 = p3 = 0.7) and low detection probabilities (p1 = p2 = p3 = 0.2), high duration of the pairing period (5 months), and a favorable starting month (as defined in Experiment 1), we simulated a reduction in the annual number of fish observed by the primary observer ($C1S$ = 150, $C1S$ = 100, $C1S$ = 50 respectively). We compared the results between the three types of annual distribution of fish passage and two contrasted sets of detection probabilities (combination IDs 1 and 8, see Table 2) (n = 24 datasets).

2.2.2.3 Experiment 3: detection probabilities

Relying on the high duration of the pairing period (5 months), a favorable starting month (as defined in Experiment 1), and a high annual number of observations by the primary observer ($C1S$ = 200), we simulated a reduction in detection probabilities. We considered all 12 combinations of detection at the primary observer (p1 = 0.05, p1 = 0.2, and p1 = 0.7), detection at the secondary observer (p2 = 0.2 and p2 = 0.7), and detection of the filter (p3 = 0.2 and p3 = 0.7), as defined in Table 2. We compared the results between the three types of annual distribution of fish passage (n = 36 datasets).

In total, we simulated 132 different datasets and ran our model with each dataset to estimate fish run abundance and the detection probabilities. We then assessed the robustness of the model for every dataset by analyzing two types of results: 1) the statistical convergence of the model, which is achieved when the value of $\hat{R}$ is less than 1.1 (Brooks and Gelman, 1998), and 2) the accuracy of estimates, which is assessed by comparison with the simulated values of the key parameters of the model (detection probabilities p1, p2, and p3 and annual fish run abundance NT). The estimates were considered accurate if their 95% credible interval included the value of the simulated parameters. We selected a pairing period only if the simulated parameters were included within the 95% credible interval of the estimated parameters for all combinations of detection probabilities.

2.3 Case study

The Breuil-en-Auge dam on the Touques River (Normandy, France; coordinates 49.22833188, 0.21336115) was chosen as a study case to estimate the abundance of European eel migrating downstream to the sea. The dam is equipped with a fishway and a fish ladder where a video counter (SYSIPAP computer system, considered as the primary observer) has been operating since 2000. Over the last decade, an average of 230 eels migrating downstream are observed annually, with migration peaking in fall and early winter (Fédération du Calvados pour la pêche et la protection du milieu aquatique, 2015; Fédération du Calvados pour la pêche et la protection du milieu aquatique, 2016; Fédération du Calvados pour la pêche et la protection du milieu aquatique, 2017; Fédération du Calvados pour la pêche et la protection du milieu aquatique, 2018). However, it is suspected that only a small portion of the run is observed and counted because the fishway is likely not efficient in attracting this species on its downstream migration. As shown in Figure 2, eels coming from upstream have several possible routes to migrate downstream: through the fish pass where the video counter is located, through the floodgate gates, or through the diversion reach. An acoustic camera (Adaptive Resolution Imaging Sonar (ARIS), Sound Metrics Corp., Bellevue, WA, USA, considered as the secondary observer) was installed temporarily upstream of all the different pathways (5 m upstream of the fishway entrance toward the video counter) (Figure 2) and recorded continuously the fish moving in its detection beam (1,800-kHz frequency, 5 images per second). The acoustic camera beam was angled to record the greatest proportion of the eels moving downstream the main channel during the period from August 7, 2017, to December 19, 2017. A total of 104 days of simultaneous records (pairing) were retrieved; some records were discarded because of technical issues with the acoustic camera on some days (n = 31). It is known if the operator in charge of analyzing the video records may influence the counts (identification of individuals, identification of species, etc.)

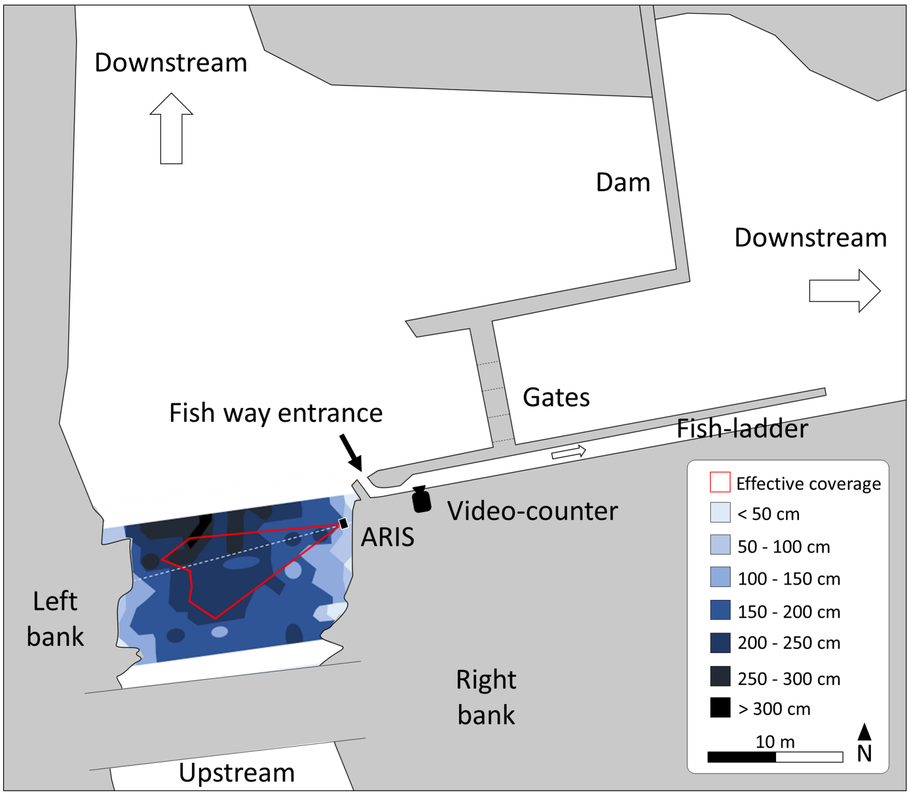

FIGURE 2
Presentation of the study site, with the localization of the primary and secondary observers.

(Holmes et al., 2006; Martignac et al., 2015). To avoid variability in operator efficiency, only one experienced operator per device analyzed all the videos. The observation devices were regularly cleaned and returned to their exact position to ensure optimal and stable conditions of visualization.

Because eels mostly migrate at night (Haraldstad et al., 1985), we defined a time step t as a 24-h day starting at 12 a.m. We applied the model to daily observations recorded on both devices. Following the description of the model structure (Figure 1), $C1S_t$ is defined as the daily number of downstream migrating eels seen by the primary observer, which is the video-counting facility. $C1SF_t$ and $C1UF_t$ are daily numbers of eels seen by the filter of the secondary observer (acoustic camera) that were respectively seen and unseen by the primary observer. In this specific case study, the filter consisted of a subset of records from 10 p.m. to 6 a.m., as most eels are known to migrate at nighttime (Haraldstad et al., 1985). To estimate the detection probability of the filter and the detection probability of the acoustic camera, twice a month during the pairing period, the observer counted eels without the filter (seven times during the experiment). This consisted of checking the full daily recordings from 12 a.m. to 12 a.m., $C1S2S$ and $C1U2S$. Given that a detection probability was defined as the proportion of the fish seen by a specific observer or filter, we considered that missed fish (fish migrating by the observer but not seen) and bypassed fish (fish migrating outside the observer range) were taken into account. We also assumed that the operator was fully efficient in processing the records, which means that he observed all the fish passing by the monitoring device and identified correctly the species of each observed fish. In the absence of individual identification of migrating eel, we assumed that two records of an eel by the primary and secondary observers related to a single individual, if observed within less than 5 minutes, and within the same range of body length (± 8 cm, mean size of eels measured with the two devices = 54 cm ± 11 cm. This decision rule allowed us to provide values of $C1S_t$, $C1S2S_t$, $C1U2S_t$, $C1SF_t$, and $C1UF_t$ as input to the model.

3 Results

3.1 Simulation study

From the two criteria used to assess the robustness of the models, one criterion was met for every model run on simulated data as part of Experiments 1, 2, and 3. The $\hat{R}$ values were always lower than 1.1 for all parameters, suggesting a good convergence (Brooks and Gelman, 1998). Similarly, the Monte Carlo errors (MC errors) for all parameters were less than 5% of the corresponding posterior standard deviations, supporting a good accuracy of the posterior estimates for all parameters. Below, we describe the performance of the models in terms of based on the accuracy criteria, within each experiment.

3.1.1 Experiment 1: the pairing period

The 95% CI on the total fish abundance *NT* encompasses the simulated *NT* in most models; however, only a small number of these models also produced estimates of detection probabilities with good precision (Figure 3). Thus, the structure of the model seems highly sensitive to the selection of the start of the pairing period. This pattern is especially marked for simulated two-peak and holobiotic phenology of fish migration, which appear more difficult to capture by the model than the one-peak phenology of migration. Increasing the duration of the pairing period from 3 months to 5 months generally improves the precision of the model, but it may not always be sufficient to overcome the constraint in the selection of the timing of the pairing period. Among the favorable starting months, we selected September for the one-peak distribution of fish passage and March for the two-peak distribution and holobiotic distribution of fish passage as the starting months of the pairing period to simulate datasets for Experiments 2 and 3.

3.1.2 Experiment 2: number of observations

In general, the precision of the models is little affected by the annual number of fish (Figure 4). Under the range of values

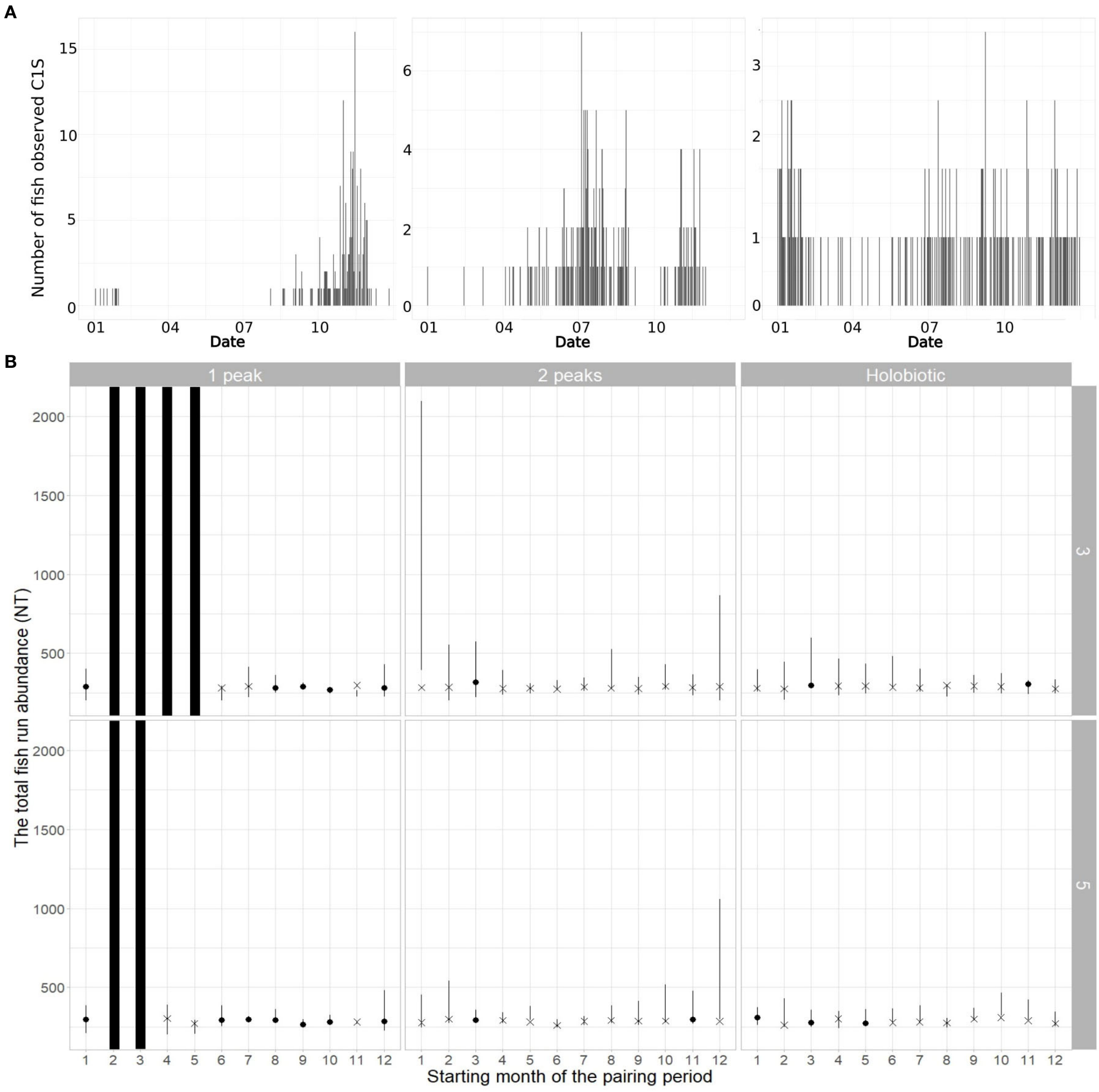

FIGURE 3
(A) Simulated number of fish observed seen at the primary fish counter (C1S) by annual distribution of fish passages. **(B)** Assessing the precision of the models in Experiment 1 by comparing the 95% credibility interval on the total fish run abundance (NT, error bars) with the simulated NT. Additional information is provided to specify whether the 95% credibility interval of the estimated detection probabilities (p1, p2, and p3) and NT all encompass the value of the corresponding simulated parameters (dot) or not (cross). Models within Experiment 1 are ordered as a function of the starting month of the pairing period (x-axis), the annual distributions of fish passages (in columns), and the duration of pairing period (in rows). Black bars indicate that no estimates were produced for some starting months, as there was no observation during the entire pairing period.

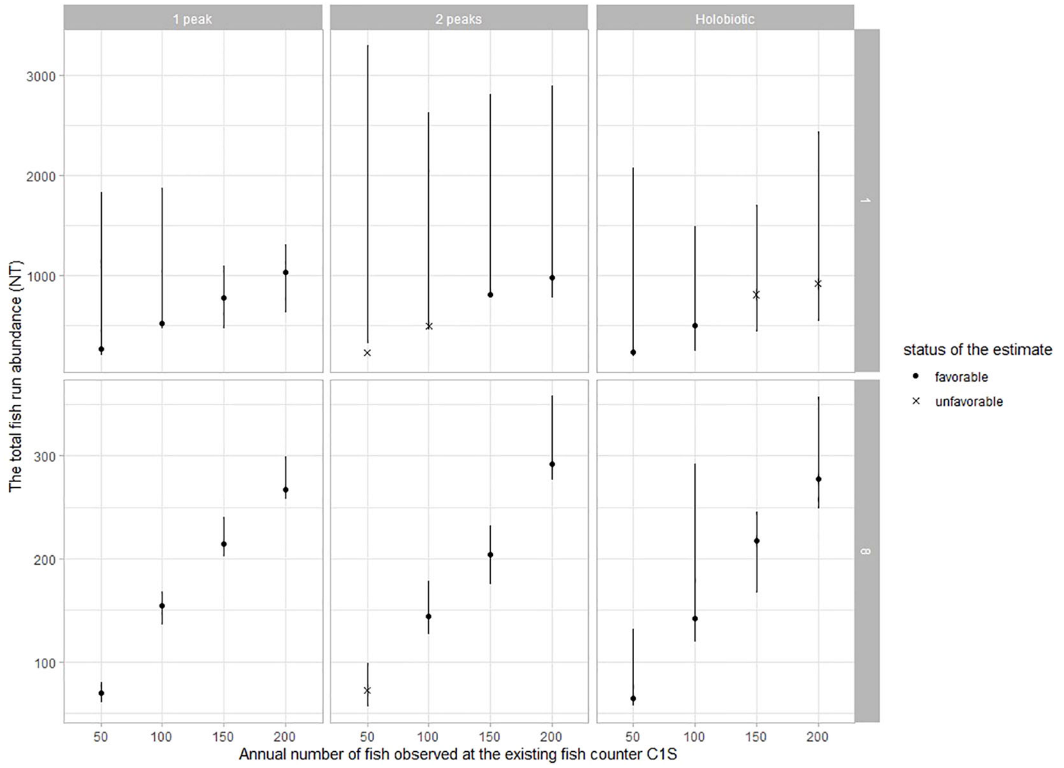

FIGURE 4
Assessing the precision of the models in Experiment 2 by comparing the 95% credibility interval on the total fish run abundance (NT, error bars) with the simulated NT. Additional information is provided to specify whether the 95% credibility interval of the estimated detection probabilities (p1, p2, and p3) and NT all encompass the value of the corresponding simulated parameters (dot) or not (cross). Models within Experiment 2 are ordered as a function of the annual number of observations by the primary observer (x-axis), the annual distributions of fish passages (in columns), and combinations of detection probabilities (in rows, IDs 1 and 8, see Table 2).

simulated in this experiment, the precision of the model is always favorable when $C1S_t \geq 150$. In contrast, the precision of the model and the variability in NT estimates improve substantially when the detection probabilities are high. The seasonal distribution of fish passage is again an element affecting the precision of model estimates for any given set of simulated parameters. Results suggest that the model is always more robust at capturing the signal in the data from one-peak migration phenology than in data from two-peak and holobiotic phenologies.

3.1.3 Experiment 3: detection probabilities

By definition, for a given value of $C1S_t$, the total fish run abundance depends on the detection probability of the primary observer $p1$ (Figure 5). The accuracy of the model is strongly affected by $p1$ and to a lesser extent by $p2$ and $p3$. The seasonal distribution of fish passage is again an element affecting the accuracy of model estimates. When simulating one-peak and two-peak migration phenologies, the model accurately estimate parameters NT and detection probabilities for all the combinations of detection probabilities, thus making it possible to use the model even when the detection probability of the primary observer is very low ($p3 = 0.05$). Unfortunately, the data simulated under a scenario of the holobiotic migration phenology appear much more difficult to handle by the model, leading to unfavorable accuracy of the parameter estimates in six out of 10 models.

3.2 Case study

At the Breuil-en-Auge fish-counting facility (i.e., the primary observer), 584 migrating eels were seen on the video over the whole 2017 year, which is more than the average (Figure 6A). During the pairing period of 104 days, from August to December 2017, 486 eels were seen on the video counter, and 2,339 eels were seen by the filter of the acoustic camera (secondary observer) (Figure 6B). A 7-day full visualization of the acoustic records was performed without the filter (08/15, 08/30, 09/13, 09/14, 10/19, 10/20, and 11/24), during which 94 eels were seen.

The model estimated that the detection probability of downstream migrating eels by the Breuil-en-Auge primary observer (fish-counting facility) was $p1 = 0.085$ (95% credible interval: 0.075–0.095). The secondary observer (acoustic camera) and filter detection probabilities were estimated at $p2 = 0.642$ (95% credible interval: 0.593–0.690) and $p3 = 0.896$, respectively (95% credible interval: 0.876–0.915). The distribution of observations was characteristic of a one-peak migration phenology, leading to an

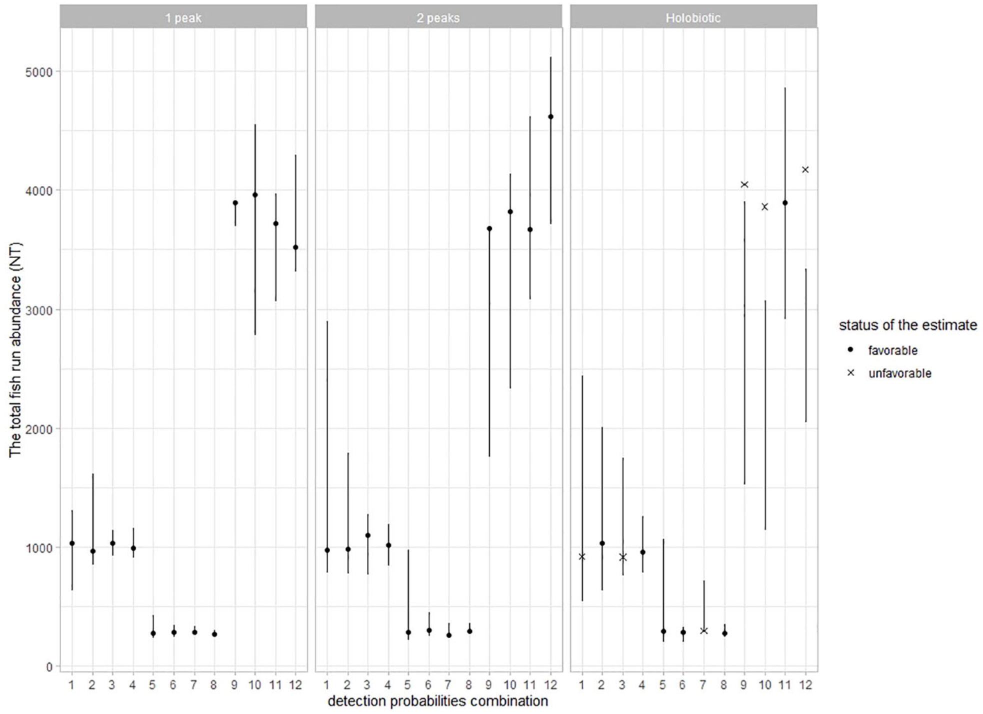

FIGURE 5
Assessing the precision of the models in Experiment 3 by comparing the 95% credibility interval on the total fish run abundance (NT, error bars) with the simulated NT. Additional information is provided to specify whether the 95% credibility interval of the estimated detection probabilities (p1, p2, and p3) and NT all encompass the value of the corresponding simulated parameters (dot) or not (cross). Models within Experiment 3 are ordered as a function of the combinations of detection probabilities (x-axis, see Table 2) and the annual distributions of fish passages (in columns).

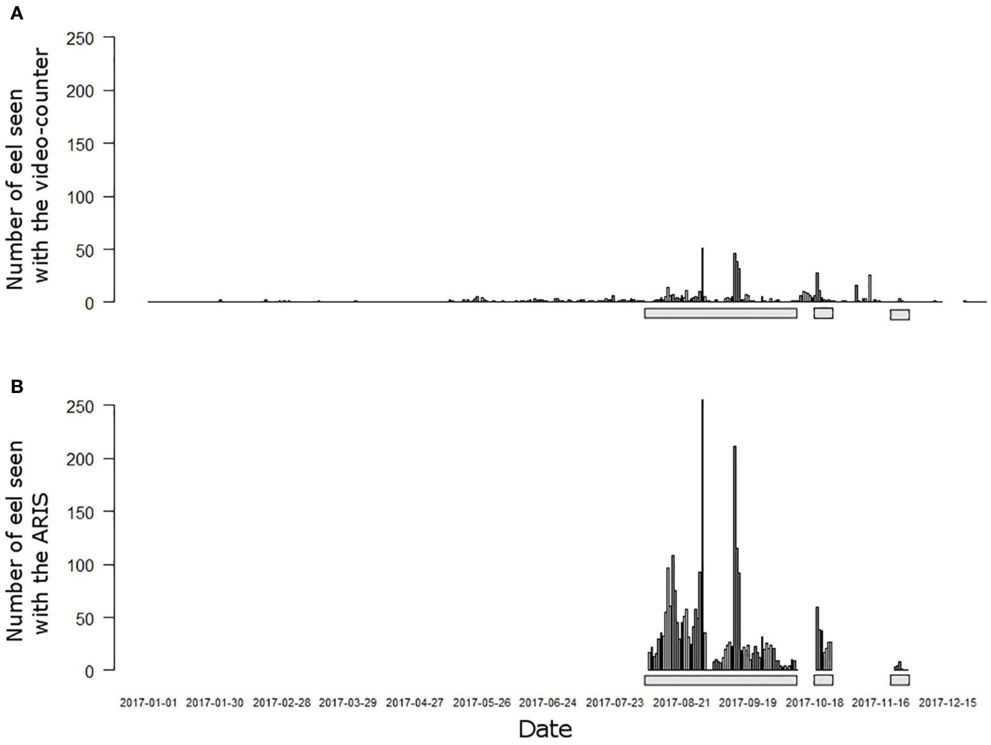

FIGURE 6
Daily number of observations of European eel at the Breuil-en-Auge fish-counting facility in 2017. Observations **(A)** by the first observer, the video counter, and **(B)** by the filter of the second observer, the Adaptive Resolution Imaging Sonar (ARIS) acoustic camera. Gray bars indicate the extent of the pairing period when the two observers were operating simultaneously (n = 104 days).

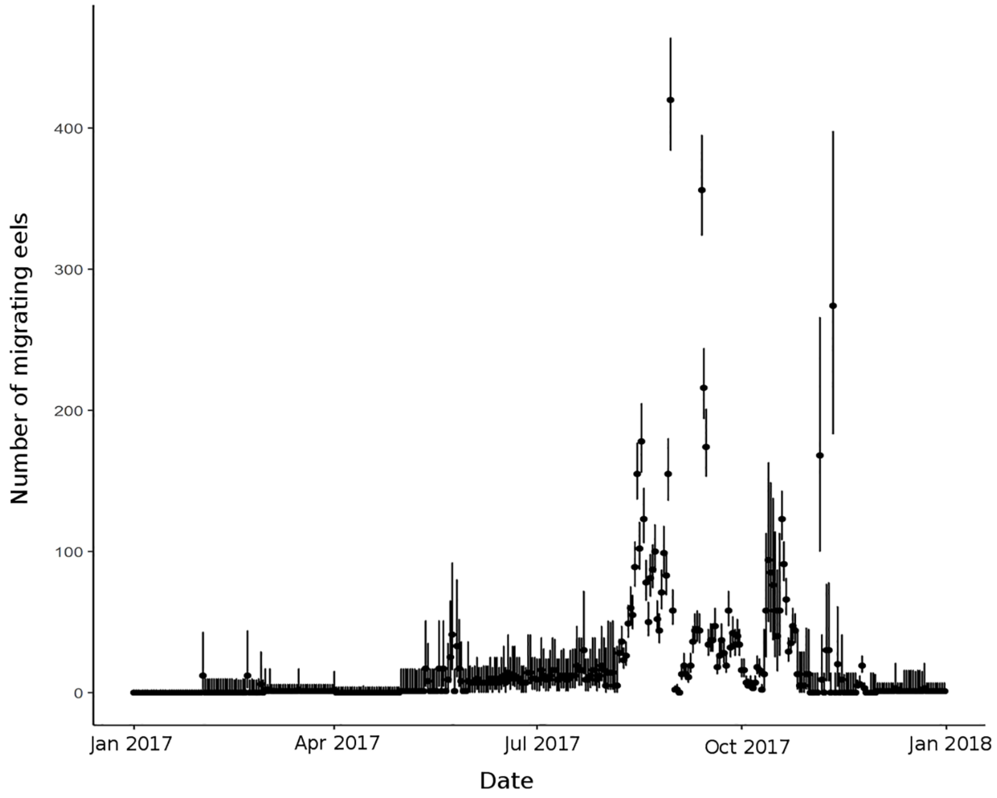

FIGURE 7
Daily number of migrating eels Nd_t, estimated by the model in the Touques River. Black points represent the estimated median and black lines the 95% credible interval.

estimated annual fish run abundance $NT = 6{,}892$ eels (95% credible interval: 6,319–7,559) in 2017 in the Touques River (Figure 7).

4 Discussion

Estimating population abundance is a prerequisite to assess the success of any management action, like the installation of fish ladders or dam removal. Nevertheless, traditional observation systems often provide imperfect counts of individuals and thus fail to accurately quantify changes in abundance in a before–after comparison. In this study, we adopted the double-observer approach to the estimation of the abundance of migrating fish and demonstrated the benefit of temporarily coupling multiple observation systems. Building on three simulation experiments, we provided a detailed investigation of the robustness of our model and discussed the required conditions of its application. In our case study, the use of a nomad equipment as our secondary observer gives support for the generalization of the double-observer approach, with implementation at sites where there is no pre-existing counting device as a perspective.

The analysis of simulated datasets in Experiments 1, 2, and 3 gives evidence that the model can provide robust, accurate, and precise estimates of detection probabilities and total fish abundance in a set of conditions dependent on the information provided in the data. Our results also highlight model limits in estimating key parameters. Throughout the three experiments, we showed that the performance of the model is affected by the seasonal distribution of observations. The model performs well with most datasets simulating a one-peak migration phenology and to a lesser extent datasets simulating a two-peak migration phenology. However, the structure of the model does not seem appropriate to account for observations evenly distributed over the year, as simulated for holobiotic species.

In Experiment 1, we highlighted that the timing of the pairing period is extremely critical. The model achieved its best performance when fed with paired observations encompassing both months of low and high numbers of observations. Setting the pairing period only on the peak months of the migration phenology proved difficult for the model to estimate null daily abundance on days with no observations, which tends to overestimate annual fish run abundance (*NT*). Similarly, a pairing period running only on months with low or null migration activity tends to underestimate detection probabilities, thus producing inaccurately high numbers of daily migrating fish during the peak of the migration.

In Experiment 2, we tested the effect of a degradation in the information provided by the data on model performance through a reduction in the annual number of observations (and an indirect increase in the number of days with zero observation) as well as a reduction in the detection probabilities. Using datasets simulated for appropriate pairing periods, results indicate that it is possible to estimate *NT* and detection parameters with favorable precision (simulated values within the 95% credibility interval) even when the information provided by the data decreases. Experiment 2 shows that simulated data with more than 150 fish observed by the primary observer allow reliable estimates of the key parameters. Nevertheless, the uncertainty on parameter estimates (as measured by the 95% credibility interval) increases as the quantity of information in the data decreases.

In Experiment 3, we further investigated how different combinations of detection probabilities $p1$, $p2$, and $p3$ affect the performance of the model. Interestingly, we highlighted that under the simulated conditions, the model can provide reliable estimates for detection probabilities by the first observer as low as 5%. Nevertheless, the uncertainty on parameter estimates (as measured by the 95% credibility interval) increases as the detection probability by the first observer decreases. This low sensitivity of the model to low detection by the primary observer offers a promising avenue to transfer our approach to a wide range of study cases, including temporary settings under potentially suboptimal observation conditions to monitor the abundance of migratory species in the context of dam removal. Our results show that even in this situation, the approach would provide reliable estimates of key parameters as long as the efficiency of the secondary observer is greater than 20% (detection probability below 0.2).

The study on the Touques River has allowed the implementation for the first time of a double-observer approach for the monitoring of a diadromous fish population. It was carried out under the above-defined suitable conditions of application of the model: one-peak migration phenology, a pairing period spanning more than 5 months with more than 200 annual observations by the primary observer, thus illustrating the feasibility of the double-observer approach. As expected for this site, the detection probability of the Breuil-en-Auge fish-counting facility was very low for downstream migrating eels: 0.085 (95% credible interval: 0.075–0.095) in 2017. This estimate is consistent with the configuration of the fishway that was designed for upstream migrating salmonids and proved to be poorly attractive to downstream migrating eels. The filter after the secondary observer, set up to night time, had a detection probability of 0.896, which is consistent with the predominant nocturnal migration of downstream migrating eel. The detection probability of the secondary observer was 0.642. At the time of setting up the secondary observer, we conducted a mapping experiment to evaluate the wetted surface covered by the ARIS. This allowed us to identify that only 20% of the wetted section was covered by the secondary observer (Figure 2). However, the apparent discrepancy between those two numbers can be explained by the active swimming of eels at the bottom of the riverbed under low flow conditions, thus concentrating the migration within the beam of the ARIS. Images recorded by this secondary observer provided further empirical evidence of migratory eels actively swimming at the bottom of the riverbed.

One of the advantages of our methodology is the use of two recording devices. Continuous recording over a long period of time allows us to estimate the total flow of fish throughout the migrating season, rather than just a snapshot of abundance on a given day. This is of great importance for migratory species, especially in the context of a drastic change in their environment such as when a dam is removed (change in water flow, habitats, etc., that can impact their migratory behavior and capacity). However, continuous recording generates a large amount of data, thus requiring substantial resources (staff time) to dedicate to data analysis (Martignac et al., 2015). By implementing a specific module for post-filter data in our model, we can make the most of recent developments in image processing, aiming at limited viewing time. Current advances in deep learning (Fernandez Garcia et al., 2023) are a promising avenue to limit data processing time and make this approach accessible to a larger number of users.

This analysis validated the use of the double-observer method to estimate the fish run abundance of diadromous fish during the year studied and also to estimate historical and future fish run abundance if we consider that the efficiency of the counting system has remained constant over time. However, the assumption of constant detection efficiency is debatable. Detection efficiency potentially depends on the intrinsic characteristics of the counting system and its interaction with the environmental conditions in which it is operated. Excessive turbidity, for example, can have a negative effect on the efficiency of video counting systems by altering the visibility of the counting system (Baumgartner et al., 2012; Soom et al., 2022). In contrast, acoustic cameras are notoriously insensitive to turbidity (Martignac et al., 2015). Accounting for the effect of relevant environmental covariates in modeling time-dependent detection probability ($p1_t$) would be interesting. If the signal in the data is strong, this improvement may help to decrease the uncertainty around daily abundance estimates Nfr_t and then on the total annual abundance NT. However, as our simulation study has highlighted, further analyses would be needed to identify the benefits and limitations of this approach following such an increase in the complexity of the model. Coupling two counting systems with contrasted characteristics in terms of the detection process may also contribute to overcoming environmental variability.

The application of the double-observer approach under real conditions on the Touques River provides an inspiring illustration of potential gains in quantitative knowledge at monitoring sites. Building on existing facilities, the temporary addition of a secondary observer gives access to valuable estimates of fish run abundance and detection probabilities of fish-counting facilities, which are of key relevance for management. Moreover, our double-observer model offers the potential for wider application settings, e.g., by implementing fully non-permanent monitoring made of two nomad devices. For instance, such a setting could rely on two acoustic cameras on a river where there is no fish-counting facility. In the case of dam removal projects, our model will help estimate diadromous fish population run before and after river continuity restoration. When diadromous fish populations exist on a river catchment, their population increase is taken as a serious argument for dismantling (Duda et al., 2008). Diadromous fish are species of high conservation values and are usually iconic species too, for example, salmon and eel, which have generated a great deal of media attention. In such a case, the gain arising from the continuity restoration program must be clearly addressed.

5 Recommendations

From the combination of simulation experiments and on-field case studies, we identified the minimal requirements for the model to accurately estimate the key parameters of interest and provide technical recommendations to improve data acquisition.

- By definition, the application of the model is only relevant when observation of the target species is imperfect (i.e., escape outside the fish-counting facility is impossible).
- The model can only be applied to observations with marked migration peaks and is not appropriate for the holobiotic type of fish passage. As a consequence, the observation site should be thoroughly selected to monitor active migration while avoiding resting areas or excessive back-and-forth movements that may be generated by the proximity of an obstacle, e.g., dam.
- The target species should be identified without error using both the devices used as the primary and secondary observers.
- A low detection probability by the primary observer (e.g., monitoring device already in place) as long as the total number of annual observations is no less than 150 so that the data are rich enough in information to feed the model.
- For the use of this approach in the field, it is recommended to use simulation datasets corresponding to the case study (phenology) before installing the counting system(s) in order to select the most suitable pairing period and to validate that this methodology can be used.
- The second observer should enable the selected species/stage to be monitored. For example, for the acoustic camera, it is difficult to consider true detection/recognition of individuals smaller than 20 cm unless a very narrow window (<5 m) is recorded (Tušer et al., 2014; Martignac et al., 2015).
- The temporary secondary observer should be installed for a period of five consecutive months so that it covers a large part of the fish migration phenology. It should provide a representative sampling of the fish migration over the duration of the pairing period. If the second observer requires regular handling for maintenance, a system must be put in place to ensure that the device is always in the same position to avoid bias in the data.
- The secondary observation device would ideally be installed in a way that ensures partial overlap with the primary observer, e.g., by pointing at the entrance of the fishway. This setting would allow relieving assumptions for the coupling of individual observations between the primary and secondary observers (e.g., time laps and size matching).

Data availability statement

The raw data for the analysis of the Touques River on european eels are available via this link: https://doi.org/10.57745/6IF2BU. The other raw data for the simulation study will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because we don't manipulate animals, just observe them via video.

Author contributions

CB, FM, J-MR, MN, and LB contributed to conception and design of the study. CB and FM created the protocol for collecting the data. CB developed the model and performed the statistical analysis. CB wrote the first draft of the manuscript. J-MR and MN wrote sections of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Modeling timing and size of juvenile Chinook salmon out-migrants at three Elwha River rotary screw traps: a window into early life history post dam removal

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Chinook salmon (*Oncorhynchus tshawytscha*) populations express diverse early life history pathways that increase habitat utilization and demographic resiliency. Extensive anthropogenic alterations to freshwater habitats along with hatchery and harvest impacts have led to marked reductions in early life history diversity across much of the species' range. The recent removal of two Elwha River dams between 2011 and 2014 restored access to over 90% of the available habitat that had been inaccessible to Chinook salmon since the early 1900s. This provided an opportunity to investigate how renewed access to this habitat might affect life history diversity. As exotherms, egg-to-fry development, juvenile growth, and movement are influenced by water temperatures. We used spatially and temporally explicit Elwha River water temperature and Chinook salmon spawning location data, in conjunction with spawn timing, emergence, growth, and movement models, to predict observed timing and sizes of juvenile Chinook salmon captured in three rotary screw traps in the mainstem and two tributaries during four trap years. This effort allowed us to test hypotheses regarding Elwha River Chinook salmon early life history, identify potential problems with the data, and predict how emergence and growth would change with increased spawning in the upper watershed. Predicted Chinook salmon emergence timing and predicted dates that juveniles reached 65 mm differed by as much as 2 months for different river locations due to large differences in thermal regimes longitudinally in the mainstem and between tributaries. For 10 out of the 12 trap–year combinations, the model was able to replicate important characteristics of the out-migrant timing and length data collected at the three traps. However, in most cases, there were many plausible parameter combinations that performed well, and in some cases, the model predictions and observations differed. Potential problems with the data and model assumptions were identified as partial explanations for differences and provide avenues for future work. We show that juvenile out-migrant data combined with mechanistic models can improve our understanding of how differences in temperature, spawning extent, and spawn timing affect the emergence, growth, and movement of juvenile fish across diverse riverine habitats.

KEYWORDS

Chinook salmon (*Oncorhynchus tshawytscha*), life history diversity, dam removal influence, Elwha River, growth models, incubation models

1 Introduction

The salmon life cycle includes early freshwater life stages dependent on suitable stream habitat conditions (Quinn, 2018). These conditions are particularly important to salmonids because mortality tends to be high during these stages. As exotherms, their growth, survival, and movement are linked to stream temperature (Quinn, 2018). Understanding how stream temperature affects these processes is therefore fundamental to predicting freshwater survival of juvenile salmonids (Groot and Margolis, 1991).

The freshwater life stages of salmon have been dramatically impacted by anthropogenic activities that have disconnected, simplified, and degraded freshwater habitats (Nehlsen et al., 1991). These impacts are associated with the large declines over the last 150 years in Chinook salmon (*Oncorhynchus tshawytscha*) populations (e.g., Munsch et al., 2022). Dams and other barriers longitudinally disconnect upstream habitats that salmon occupied historically, reducing their access to the full diversity of stream temperatures expressed in these habitats, and therefore reducing life history diversity (Myers, 1998). For example, today there are fewer Puget Sound Chinook salmon populations dominated by the stream-type life history where juveniles rear a full year in freshwater before migrating to the ocean. This has been attributed in part to the construction of dams that prevent migration into cooler higher elevation reaches (Beechie et al., 2006).

Dam and barrier removal can allow for the reconnection of these habitats and the re-emergence of life history strategies that increase population resilience for salmon, steelhead, and other species (Greene et al., 2009; Brenkman et al., 2019; Munsch et al., 2023; Pess et al., In Press). The construction of two hydroelectric dams in the Elwha River, Washington, USA, in 1912 and 1927, completely cut off access to 90% of the watershed for Chinook salmon and other anadromous fishes (Pess et al., 2008). Removal of these dams between 2011 and 2014 provided a unique opportunity to see if life history diversity "re-awakened" and increased with the longitudinal re-connection of upstream and downstream riverine habitats and the resulting increased range of temperatures available during Chinook salmon egg incubation and freshwater juvenile growth (Munsch et al., 2023). Increased life history diversity in the Elwha River, post dam removal, has already been demonstrated for coho salmon (*O. kisutch*, Liermann et al., 2017; Munsch et al., 2023), bull trout (*Salvelinus confluentus*, Quinn et al., 2017; Brenkman et al., 2019), Steelhead (*Oncorhynchus mykiss*, Munsch et al., 2023; Pess et al., In Press), and Pacific Lamprey (*Entosphenus tridentatus*, Hess et al., 2021).

Differences in salmonid life history are typically initiated during egg incubation and the juvenile life stages (Connor et al., 2002). However, observing juvenile salmonids during this critical period can be challenging because individuals are often spread over and moving through a large and complex riverine network. Rotary screw traps, which collect migrating juvenile salmon as they move downstream, are present in many Pacific Northwest rivers and tributaries, with many enumerating out-migration of juvenile Chinook salmon. Observed patterns in juvenile Chinook salmon out-migration timing and sizes at these traps provide an opportunity to test hypotheses about, and advance our understanding of, juvenile Chinook salmon early life history (e.g., Zimmerman et al., 2015). However, these patterns are the product of multiple processes including spawn timing and location, egg incubation, movement, survival, and growth, all of which are regulated by temperature (Kaylor et al., 2021; Kaylor et al., 2022). Therefore, interpreting patterns in out-migrant timing and sizes requires combining our understanding of these biological processes along with spatially and temporally explicit estimates of water temperature upstream of the traps.

Extensive laboratory and field studies of these early life history processes have provided models that can be combined to integrate over these juvenile stages (e.g., Kaylor et al., 2021). The period between egg deposition and fry emergence from the gravel (incubation time) has been well characterized in the laboratory (e.g., Beacham and Murray, 1990; Geist et al., 2010; Steel et al., 2012) and is more certain than other stages since development is primarily dependent on temperature and egg size (e.g., Beer and Anderson, 1997). Models of juvenile salmonid temperature-dependent growth have also been well developed and are generally based on laboratory studies (e.g., Perry et al., 2015). However, factors such as habitat conditions, food availability, predation pressure, and competition introduce additional uncertainty when making predictions in natural settings (e.g., Al-Chokhachy et al., 2022). Juvenile or Chinook salmon movement downstream, ending in ocean entry, is less well understood. The Elwha River Chinook salmon population primarily follows the ocean-type life history strategy (Taylor, 1990b) where juveniles either migrate to the ocean soon after emerging from redds (nests) in late winter to early spring, or stay in freshwater for up to 2 to 3 months to feed before entering the ocean in late spring or summer. Factors linked to downstream movement include flow, light, and available habitat (Taylor, 1990a; Taylor, 1990b; Sykes et al., 2009; Apgar et al., 2021) as well as density dependence (Zimmerman et al., 2015; Apgar et al., 2021).

We used incubation and growth models to predict Chinook salmon emergence timing and growth trajectories for locations throughout the Elwha River based on spatially and temporally explicit estimates of spawning intensity and water temperature from 2018 to 2021. We then combined the incubation and growth models with a spawn timing and movement model to predict out-migration timing and sizes for juvenile Chinook salmon migrating downstream past three rotary screw traps in the Elwha River. We identified combinations of model parameters that provided plausible fits to the observed data for each trap and year and then looked for patterns in these parameters shared across traps and years. Where no combination of parameter values could explain the observed data, we examined the underlying assumptions, associated models, and the data—which provided an opportunity to critique our hypotheses and highlight opportunities for improved data collection. Finally, we discussed how the dam removals and continued expansion of adults into the upper river has increased the diversity of potential life history strategies and the effects that these new life history strategies may have on the Elwha River Chinook salmon population's persistence and resilience.

2 Materials and methods

2.1 Study site

The Elwha River is located on the Olympic Pennisula in Washington, USA (Figure 1) draining 833 km^2, 83% of which is in the Olympic National Park. Historically, the Elwha River is thought to have supported a Chinook salmon population of approximately 10,000 to 30,000 adults (Department of Interior, 1996; Pess et al., 2008) and was known for its large fish with reports of individuals weighing as much as 45 kg (Wunderlich et al., 1994). In 1912, the Elwha Dam was constructed at river kilometer (rkm) 7.9 (i.e., 7.9 km upstream of the river mouth). This completely blocked access to all habitat above the dam (~90% of the total habitat) for Chinook salmon and other anadromous fishes. Fifteen years later in 1927, the Glines Canyon Dam was installed at rkm 21. The dams also restricted movement of sediment and wood downstream, resulting in the simplification of the remaining accessible habitat below the Elwha dam (e.g., Pess et al., 2008). Starting in 2011 and ending in 2014, the two dams were removed, which restored access to the upper watershed, most of which was in pristine condition. For the period immediately preceding dam removal (1986–2010), the adult Chinook salmon returns averaged 2,827 fish, although this population was and still is heavily influenced by a hatchery program (Pess et al., In Press). Indeed, over the last four decades, an average of 2.4 million juvenile Chinook salmon per year have been released into the river (unpublished data) as part of a long-running hatchery program operated by the Washington Department of Fish and Wildlife (WDFW) since the 1930s. As a result, hatchery-reared fish have comprised over 90% of returning adults between 2009 and 2020 (Pess et al., In Press).

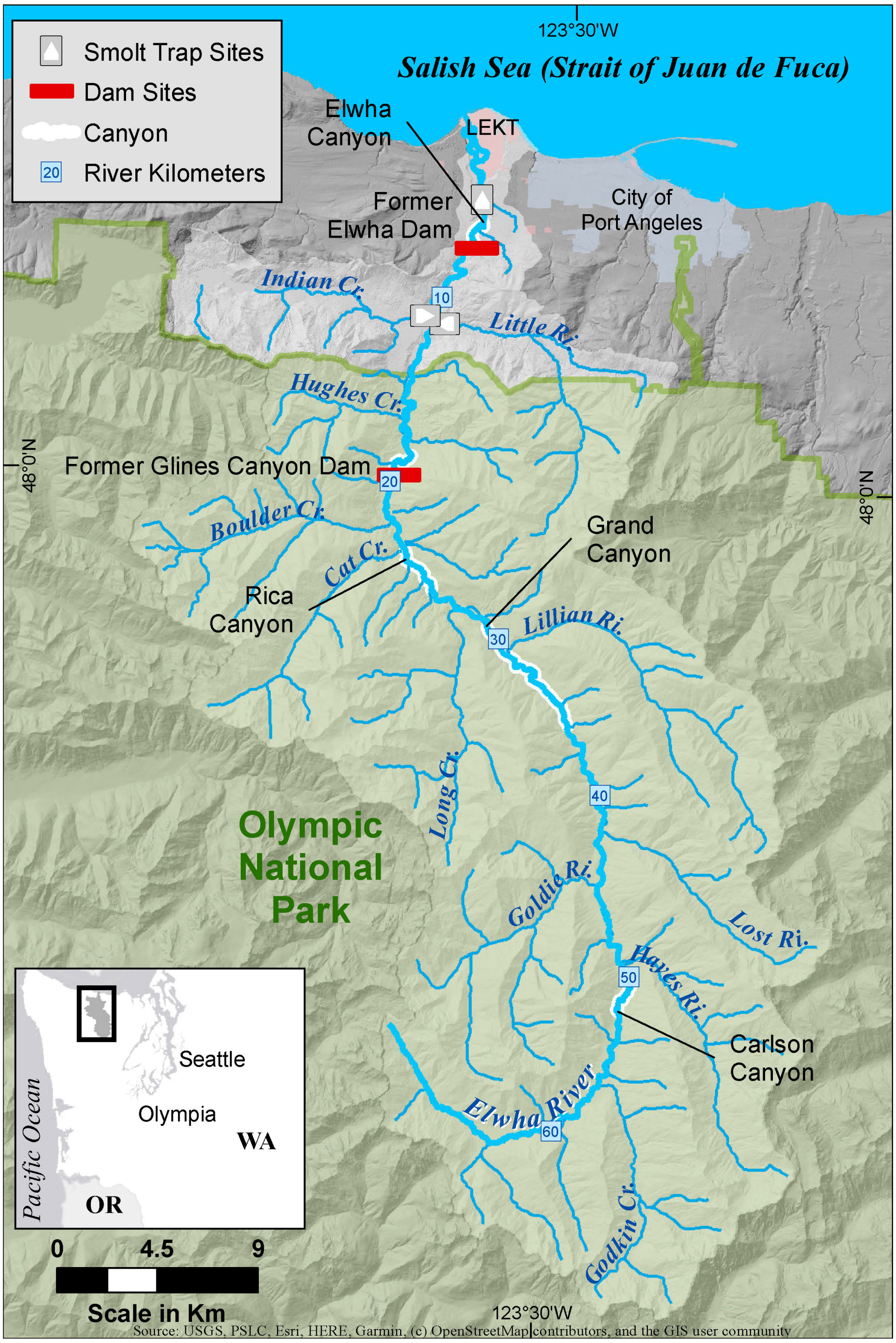
We focused on two study tributaries which enter the Elwha River mainstem across from each other at rkm 12.9, Indian Creek from the west draining 62 km^2, and Little River from the east draining 50 km^2. Little River is relatively steep (mean gradient ~3.5%), cold (mean yearly water temperature ~7.5°C, Washington Department of Ecology, 2016), shaded, and snow melt dominated with headwaters originating at 1,615 m. Indian Creek is lower gradient (mean gradient < 1%), has a broad floodplain, is warmer (mean yearly water temperature ~9.0°C, Washington Department of Ecology, 2016), and is heavily influenced by its source, Lake Sutherland at an elevation of 155 m. We refer to locations in the mainstem and tributaries using rkm, which is defined here as the distance upstream from where the mainstem enters the ocean or from where the tributaries enter the mainstem.

2.2 Data

2.2.1 Smolt trap data

We used data from three rotary screw traps that captured juvenile fish as they migrated downstream (McHenry et al., 2023b). One trap was located in the mainstem river at rkm 4.0, a second in Little River at rkm 0.2, and a third in Indian Creek at rkm 0.6 (Figure 1) (McHenry et al., 2023b). The mainstem trap [2.44 m (8') diameter] was located upstream of all hatcheries and downstream of the two tributaries. In both tributaries, smaller 1.22 m (4') diameter traps were used. Traps were generally checked daily, and mark–recapture efficiency trials were conducted every 1 to 2 weeks at each trap. For each efficiency trial, a group of age zero (0+) fish were marked with a stain (Bismarck Brown) and released 500 m and 100 m above the mainstem and tributary traps, respectively. For the tributary traps, most fish used in the efficiency trials were 0+ Chinook or coho salmon captured in the traps. Recapture probabilities (efficiencies) averaged approximately 15% using releases averaging 100 fish. For the mainstem trials, hatchery 0+ Chinook salmon were used, with most release groups consisting of 1,000 fish. Mainstem efficiencies were considerably lower, averaging 3%. For all traps, the majority of the recaptured fish arrived within a few days of release. The total number of fish migrating past the trap was estimated by adjusting the catches using the period and trap-specific efficiencies (e.g., Carlson et al., 1998). Approximately once a week at each trap, lengths (± 1 mm) and weights (± 0.1 g) were measured for a subset of up to 20 Chinook salmon. All traps were installed in January or February and typically fished through July. Catch of juvenile Chinook salmon often started immediately upon installation of the trap, suggesting that a portion of the out-migration had already occurred. Catch of Chinook salmon out-migrants at the time of trap removal was typically negligible.

In this paper, we limit our analyses to age zero (0+) fish that comprise the majority of the fish captured in the traps. We identify potential age one fish (1+) by fitting a cubic smoothing spline (smooth.spline in R with 4 degrees of freedom) to the logged length versus date relationship for each year and trap independently, and



Source: USGS, PSLC, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

FIGURE 1
A map of the Elwha River with the locations of the three rotary screw traps, the former dams (red rectangles), and other features discussed in the manuscript. The Lower Elwha Klallam Tribal (LEKT) reservation is shown in pink.

then identifying points with model residuals greater than log(1.5). On the un-logged scale, this translates to lengths that were greater than 1.5 times the predicted median length at a given date. This rule was developed based on visual inspection of the data. When plotting fish lengths against time, we also identified groups of large fish captured in the tributary traps that we believed were hatchery fish used in the efficiency trials that stayed above the traps long enough to lose their marks. The Bismarck Brown stain usually begins to fade after a week and hatchery fish are generally larger than natural origin fish. After discussions with field biologists and determining the timing of efficiency trials in which hatchery fish were used, we identified potential anomalous lengths and excluded them. These included all lengths measured at the Indian Creek and Little River traps on 6 April 2022, and all Little River fish in 2021 with lengths greater than 45 mm before May 1. We used the models described below to further assess the validity of these assumptions (see *Results*). In total, less than 4% of the length data was excluded.

2.2.2 Redd survey data

To describe the spatial distribution of Chinook salmon spawning activity, redd (nest) surveys were conducted by foot each year during the predicted period of peak spawning (McHenry et al., 2023a). Redds were identified based on differences in the substrate coloration and stream bed morphology produced by the redd construction process and/or the presence of adults (Johnson et al., 2007). The redd surveys extended from the mouth of the Elwha River to rkm 63.4 (Figure 1), and included side channel and larger tributary habitat (McHenry et al., 2023a). Redd surveys in the two study tributaries, Little River and Indian Creek, extend from rkm 0 to rkm 1.9 (McHenry et al., 2023a), which included most of the observed spawning extent. For each year, we aggregated the redds by reach, where mainstem reaches were defined by rkm (e.g., rkm 1, rkm 2, …), and the tributary reaches included the entire survey reach (rkm 0–1.9) (Figure 2).

The surveys were intended to describe spatial distribution (not abundance) and hence are timed to coincide with the peak of spawning based on historical averages and recent observations. Therefore, the spawn timing distribution is not captured in these surveys. However, spawning typically extends from the beginning of September to early to mid-October, peaking in mid- to late September (unpublished data).

2.2.3 Temperature data

During the study period (2018–2023), HOBO Water Temperature Pro v2 and TidbiT MX Temperature 400' data loggers (± 0.2°C) (Onset Computer Corporation, Bourne, Massachusetts, USA) were deployed in the Elwha River basin to measure average daily water temperature at a number of locations. Loggers were set to record hourly and were cabled underwater to large wood. Loggers were encased in sun shields to protect from solar radiation and downloaded quarterly. The temperature loggers were located throughout the spawning range of Chinook salmon in the Elwha River, from rkm 2.5 to rkm 42.5 in the mainstem and at rkm 0.3 in Indian Creek and rkm 1.1 in Little River, respectively. Due to logistical issues, including the COVID pandemic, there were no loggers that were recording for the entire period and there were periods when no loggers were recording. For this study, we used the available logger data and data from a site on the Quinault River (also on the Olympic Peninsula) to build a model that predicted mainstem water temperature within the spawning range based on

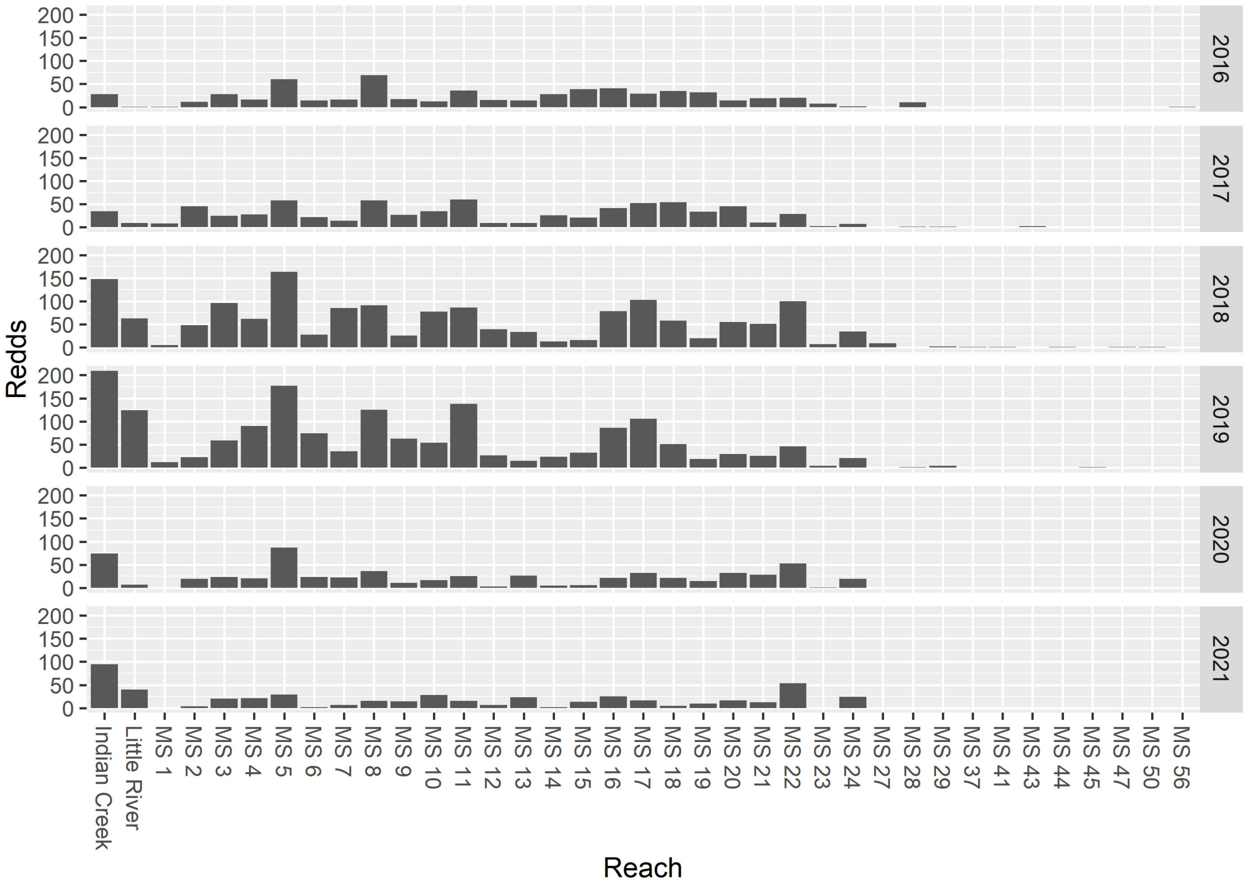


FIGURE 2
The total number of redds observed in 1-km mainstem reaches and in the two study tributaries, Indian Creek and Little River. The mainstem reach rkm X indicates the 1-km reach from river kilometer X–1 to river kilometer X.

date (between 2018 and 2023) and rkm. In addition, we filled in water temperature data in the sites in the two study tributaries (Little River and Indian Creek), using a model describing the seasonal temperature relationship between the two tributaries and a mainstem site. See Supplementary material Appendix A for details of how the temperature series were constructed.

2.2.4 Emergence size

The size at emergence of juvenile Chinook salmon varies considerably between and within redds, and between populations (Beacham and Murray, 1990). While we do not have direct estimates of size at emergence for Elwha River fish, we can infer size based on the observed distribution of egg weights and the estimated relationship between egg weight, temperature, and emergence size reported in Beacham and Murray (1990, Equation 11). Using an average egg weight, 246 mg, and standard deviation, 37 mg, based on measurements from 205 Chinook salmon examined at the WDFW Elwha River hatchery facility between 2015 and 2021 (unpublished data), a predicted average fry length of 35.9 mm was produced, for an average incubation temperature of 7°C. Predicted fry length changed slightly with changes in incubation temperatures, with 5, 6, 7, 8, and 9°C producing lengths of 35.7, 36, 35.9, 35.8, and 35.5 mm, respectively. Egg weight had a larger impact. Adding and subtracting one standard deviation from the mean egg weight, with an incubation temperature of 7°C, produced lengths of 35.1 and 36.7 mm. For the primary analysis, we used an emergence length of 36 mm but we explored the sensitivity of the results to this assumption in Supplementary material Appendix B. Emergence lengths in other studies were comparable to this value (e.g., Murray and Beacham, 1987; Geist et al., 2010).

2.3 Models

For each trap–year combination (12 in total), we sequentially applied the spawn timing model, emergence model, and growth model to produce estimates of emergence timing and juvenile length at date for different years and locations in the watershed. We then combined these models with the movement model to predict the timing and lengths of juveniles captured in the three rotary screw traps (Figure 3). Comparing these aggregate model predictions to the observed timing and lengths allowed us to identify potential problems with the model assumptions and describe combinations of spawn timing and movement model parameter values that best predicted the observations. Parameters for each sub-model are described in Table 1. We attempted to keep the models simple enough to use for inference, while allowing sufficient complexity to explain important biological and demographic processes. We acknowledge that there are many plausible explanations for the observed patterns, only some of which are accommodated by the models we used. We explored the sensitivity of our results to additional changes in the model form in Supplementary material Appendix B. For the incubation and growth models, we adopted the parameter and variable naming conventions used in the manuscripts where the models were developed.

2.3.1 Spawn timing

The spawn time distribution was assumed to follow a generalized beta distribution starting on September 1, peaking on September 18, and ending on October 7 (Figure 4A; see Supplementary material Appendix C). These dates are based on observations by biologists familiar with the river and represent an average timing across multiple years (unpublished data). To accommodate differences in spawn timing between years and across locations, we included an offset parameter, *offset*, that shifted the distribution earlier or later in time by up to 14 days.

2.3.2 Incubation

The length of the egg incubation period, D, was modeled using a model described in Beacham and Murray (1990, model 4) (Figure 4B).

$$log(D) = log(a) + b \times log(T - c)$$

where T is the average temperature during the incubation period. The parameters a, b, and c are estimated in Beacham and Murray (1990, Table 1). Because fish from an individual redd emerge over multiple days, we used a normal distribution centered on the predicted emergence date with standard deviation two, to spread the emerged fry across multiple days (e.g., Field-Dodgson, 1988). For the mainstem trap, with a diverse set of upstream temperature regimes, we divided the river into reaches (Figure 2), used reach specific temperatures to calculate the emergence times for redds from each reach and year, and combined the emergence times into a single aggregate emergence time distribution for each year, weighting by the relative number of redds in each reach. For each of the tributaries, we modeled incubation using a single temperature series since the spawning extent was relatively compact (rkm 0 to rkm 1.9). The end product for each year and trap was the proportion of total fish, P_t, that emerged on each day, t.

2.3.3 Growth

We used a length-based version of a juvenile Chinook salmon growth model, f_g, developed by Perry et al. (2015), which predicts length, L_t, at day t based on an initial length at day 0, L_0, and the

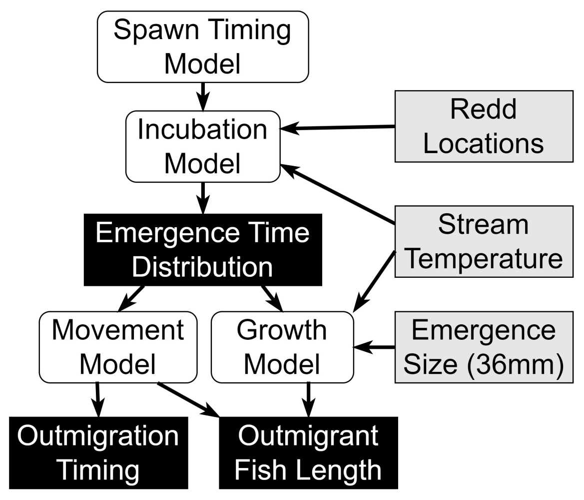


FIGURE 3
A diagram illustrating the different model components (white), input assumptions and data (gray), and model predictions (black).

TABLE 1 Description of the model parameters.

Parameter	Model	Source	Description
$d_1 = 9/1$	Spawn timing	Unpublished data	The first day of spawning
$d_2 = 9/18$	Spawn timing	Unpublished data	The peak of spawning
$d_3 = 10/7$	Spawn timing	Unpublished data	The last day of spawning
$v = 5$	Spawn timing	Unpublished data	Shape of the spawning distribution
offset	Spawn timing	Grid search	Shift in the median spawn timing
delay	Movement	Grid search	Days between emergence and the fry outmigrant pulse
M_{fry}	Movement	Grid search	The proportion of fry that leave in the fry pulse
M_0	Movement	Grid search	The minimum proportion of remaining juveniles that leave per day after the fry pulse
μ	Movement	By eye	The date at which proportion parr leaving is $(M_\mu + 1)/2$.
$\sigma = 10$	Movement	By eye	The rate at which the proportion of parr leaving increases
E_{tot}	Incubation	By eye	The total number of fry emerging above a trap for a given year that survive to the trap
$a = 32991.33$	Incubation	Beacham and Murray, 1990	Intercept, Model 4, table A.3
$b = -2.043$	Incubation	Beacham and Murray, 1990	Slope, Model 4, table A.3
$c = 7.575$	Incubation	Beacham and Murray, 1990	Offset, Model 4, table A.3
$b = 0.338$	Growth	Perry et al., 2015	The allometric growth exponent
$d = 0.415$	Growth	Perry et al., 2015	The increase in growth with temperature at low temperatures
$g = 0.315$	Growth	Perry et al., 2015	The rate at which growth declines as you approach the upper threshold
$T_L = 1.833$	Growth	Perry et al., 2015	Lowest temperature with non-zero growth
$T_U = 24.9183$	Growth	Perry et al., 2015	Highest temperature with non-zero growth
$a = 2.31329 \times 10^{-6}$	Growth	This study	The log–log length vs. weight relationship intercept
$c = 3.346022$	Growth	This study	The log–log length vs. weight relationship slope

Columns include the model (e.g., incubation), how the parameter value was set in the simulations (Source), and a description of how the parameter functions.

average temperature during the growth period, T (Figure 4C, see Supplementary material Appendix C for model details),

$$L_t = f_g(L_0, t, T) = \left(L_0^{cb} + d(T - T_L)(1 - e^{g(T-T_U)}) \frac{bt}{a^b 100} \right)^{\frac{1}{cb}}$$

The model parameters T_L and T_U (the minimum and maximum temperatures at which growth is positive), d and g (rate parameters), and b (an allometric growth exponent) were all estimated in Perry et al. (2015) (Table 1). The parameters a and c define the log–log relationship between lengths and weights and were estimated in this study based on captured fish measured at the three traps during the study period (Table 1). For the tributaries, we used the same temperature series that was used in the incubation model, while for the mainstem, we used temperatures for rkm 13, which is near the center of the redd distribution post dam removal, in an attempt to describe average conditions during migration to the trap.

2.3.4 Combined model with movement

To translate the predicted emergence times and growth trajectories into estimated out-migrant timing and size at the smolt trap, we modeled stream residence and migration past the trap. Juvenile movement is a complex process occurring across space and time. Here, we simplified the process to movement from above to below the smolt trap, combining all fish that emerged on a specific day above the trap into a single group.

The number of fish that emerged on day t_e was modeled as the predicted proportion of fish that emerged on that day, P_{t_e} (from the incubation model), times the total number of fish that emerged that season, E_{tot} (a model parameter).

$$N_{t_e,t_e} = E_{tot} P_{t_e}$$

Here, the first index on N indicates the emergence day for this group. Thus, $N_{t_e,t}$ represents the number of fish that emerged on day t_e that are above the trap on day t, where $t \geq t_e$. Day t represents Julian date (i.e., days since January 1 of the given trap year + 1). The value of $N_{t_e,t}$ was updated each day until the end of summer to reflect downstream migration past the trap,

$$N_{t_e,t} = N_{t_e,t-1}(1 - m_{t-t_e,t})$$

where the rate of movement past the trap, $m_{a,t}$, on day t is a function of the days since emergence, $a = t - t_e$, and the current day, t. Fish moving past the trap were therefore:

$$O_{t_e,t} = N_{t_e,t-1} m_{t-t_e,t}$$

The movement model assumed a fraction, M_{fry}, of the fish left as a pulse at a specified number of days, $a = delay$, after emergence. Probability of movement after the pulse was assumed to be a function of day, t, starting at a baseline migration rate of at least M_0 and increasing to 1 with a logistic form (Figure 4D).

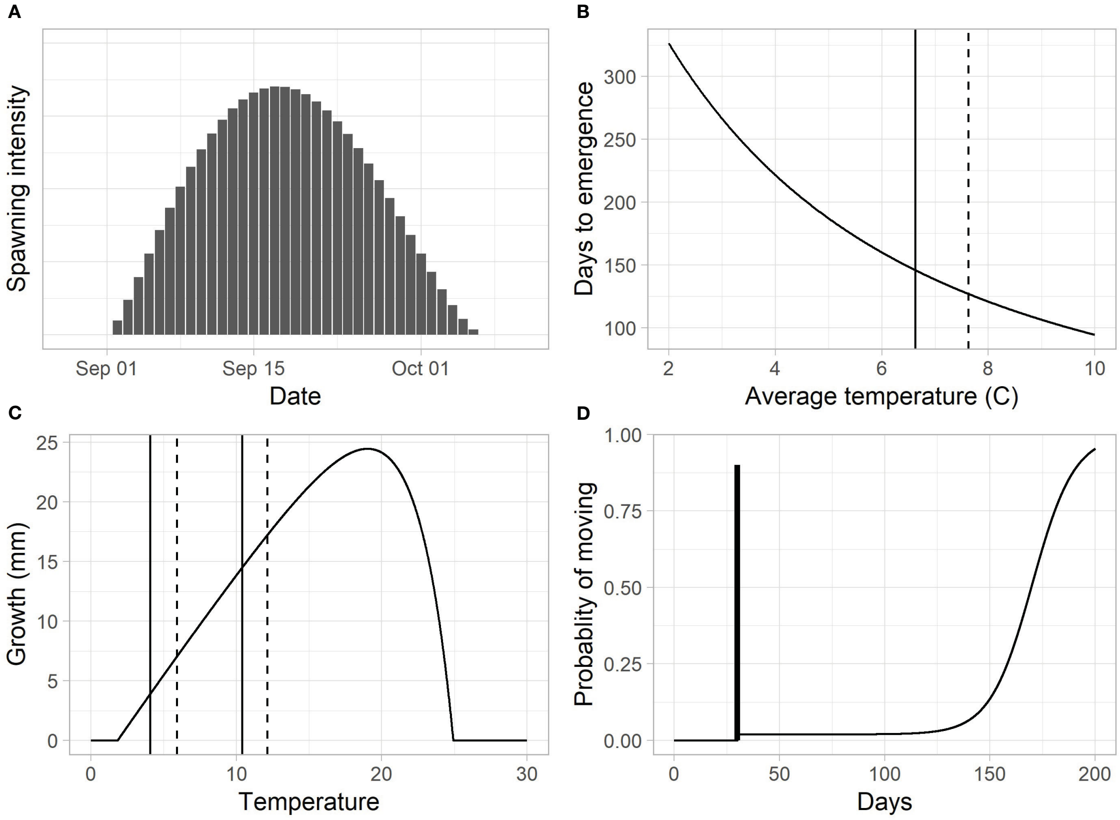


FIGURE 4
(A) The assumed spawn time distribution based on the generalized beta function. **(B)** Predicted emergence times for different average incubation temperatures (vertical lines = average incubation temperatures for the mainstem, solid, and Indian Creek, dashed). **(C)** Growth for a 40-mm fish over a 28-day period (vertical lines represent average temperatures in February and June for the mainstem, solid, and Indian Creek, dashed). **(D)** The proportion of fish above the trap that move past the trap per day. In this example, the dark vertical bar represents the pulse of fry (90%) leaving 30 days after emergence. The increasing function after day 30 represent the parr migration, with a rapid increase in out-migration at approximately day 150.

$$m_{a,t} = \begin{cases} 0 & \text{if } a \leq delay \\ M_{fry} & \text{if } a = delay + 1 \\ M_0 + (1 - M_0)\left(1 + e^{(t-\mu)/\sigma}\right)^{-1} & \text{if } a > delay + 1 \end{cases}$$

Here, μ regulated the timing of the increase in parr migration rate, and σ controlled how quickly the rate increased (Figure 4D).

Because simultaneously estimating mortality and the total number of fish that emerged would be difficult with these data, we modeled fish that would eventually survive to move past the trap.

Length for the group corresponding to each emergence day, t_e, was initialized at 36 mm ($L_{t_e,t_e} = 36$) and then updated daily thereafter using the growth model (see above), the temperature on that day, T_t, the length on the previous day, $L_{t_e,t-1}$, and a growth period of 1 day.

$$L_{t_e,t} = f_g(L_{t_e,t-1}, 1, T_t)$$

To create summaries that could be compared to the daily numbers and lengths of out-migrants observed at the traps, we summed across emergence day to get total out-migrants for each day t.

$$O_t = \sum_{t_e=d1}^{d2} O_{t_e,t}$$

Here, $d1$ and $d2$ are the first and last days that fish emerged for the given trap and year. We calculated the median predicted length of fish on each day.

$$L_t = median(rep(L_{\cdot,t}, O_{\cdot,t}))$$

Here, $rep(L_{\cdot,t}, O_{\cdot,t})$, is a vector with lengths for each of the O_t out-migrants on day t, where the length for fish that emerged on day t_e was replicated $O_{t_e,t}$ times. The vectors $L_{\cdot,t}$ and $O_{\cdot,t}$ represent all of the lengths or out-migrants for the different emergence days, predicted on day t.

2.4 Model evaluation

Because the models were deterministic and ignored many complexities of early life history, we used simple metrics to describe how well the predicted timing and sizes captured the observed values. For example, out-migration timing tends to occur in pulses regulated by factors such as patchy timing of redd construction, river discharge, and other physical habitat factors. Instead of trying to capture those pulses, we described more general characteristics that are less sensitive to small-scale patterns. While the simulation model produced a daily distribution of out-migrant lengths, we made no effort to realistically represent this variability and therefore focused on metrics based on the median predicted out-migrant length at each day. See Supplementary material Appendix C for further discussion about the model evaluation approach and method of parameter space exploration.

2.4.1 Model fit

We used four metrics to evaluate model agreement with the data. The first compared the predicted and observed date of transition from fry to parr migrants, the second and third compared predicted to observed fry and parr migrant lengths, and the final metric compared the observed and predicted proportion of out-migrants leaving between trap installation and the transition from fry to parr migrants. We focused only on the relative out-migrant timing (i.e., the shape of the curve) ignoring comparisons between total numbers of observed and predicted out-migrants.

Fry-to-Parr Transition (Δf2p): Ocean-type juvenile Chinook salmon tend to migrate downstream as fry soon after emergence or rear in the river for a few additional weeks or months before migrating as parr in late spring or summer (e.g., Zimmerman et al., 2015; Anderson and Topping, 2018). For the Elwha River trap–year combinations covered in this manuscript, the fry migrants outnumber the parr by at least 10 to 1, resulting in a sudden drop in out-migrants at the end of the fry migration. We use the number of days between the observed and predicted date of this transition as a measure of fit (*Δf2p*). The date of this transition, *f2p*, was estimated by smoothing the daily out-migrant series with a 7-day moving average and then finding the first date at which the smoothed series fell below 5% of the previous maximum value. Notice that using observed lengths to identify this transition was not possible due to large temporal gaps in the length data for some trap–year combinations.

$$\Delta f2p = \left| f2p_{pred} - f2p_{obs} \right|$$

Fry and Parr Length (ΔlenF, ΔlenP): We subtracted the log of the observed and predicted lengths of each measured fish during the fry migration period and parr migration period. The fry and parr migration periods were defined using the fry-to-parr transition calculated for the observed data, $f2p_{obs}$. The predicted out-migrant length for a specific day is defined as the median of the predicted sizes (see above). We took the mean of these differences to calculate the bias, and then took the absolute value of the bias, exponentiated the result, and subtracted this value from one to get a metric on the original scale. This meant that the bias was multiplicative. Therefore, predictions that were on average x times the observations would produce the same result as observations that were on average x times the predictions.

$$\Delta lenF = 1 - exp\left(\left| \sum_{i=1}^{N_{fry}} \left(log\left(L_{t[i]}\right) - log\left(L_{obs,i}\right) \right) / N_{fry} \right| \right)$$

$$\Delta lenF = 1 - exp\left(\left| \sum_{i=1}^{N_{fry}} \left(log\left(L_{t[i]}\right) - log\left(L_{obs,i}\right) \right) / N_{parr} \right| \right)$$

Here, $L_{t[i]}$ is the predicted median length on day $t[i]$ where $t[i]$ is the day of the i^{th} observed fry or parr length, N_{fry} and N_{parr} are the total number of observed fry and parr lengths, respectively, and $L_{obs,i}$ is the i^{th} observed fry or parr length.

Percent fry migrants (ΔpFry): For both the observed and predicted out-migrants, we calculated the proportion of juveniles that migrated past the trap between the installation of the trap and the transition from fry to parr migrants, *pFry*. We used the observed date of transition from fry to parr as described in the fry-to-parr transition metric above ($f2p_{obs}$). The fit metric was defined as the absolute value of the difference between the observed and predicted metrics.

$$\Delta pFry = \left| pFry_{pred} - pFry_{obs} \right|$$

2.4.2 Plausible parameter combinations

We defined plausible fits as those parameter combinations for which the differences between the observed and predicted values were less than parameter-specific tolerances. Specifically, a set of parameters was defined as plausible when the difference in fry-to-parr transition between the observed and predicted data, *Δf2p*, was less than 4 days, the absolute length bias for both fry and parr, *ΔlenF* and *ΔlenP*, was less than 10% (0.1), and the difference between the proportion of observed and predicted fry migrants, *ΔpFry*, was less than 2% (0.02). These criteria were derived by looking at fits and making a subjective decision about which fits appeared believable. We highlighted a specific parameter combination for plotting by minimizing the following objective function:

$$\frac{\Delta f2p}{4} + \frac{\Delta lenF}{0.1} + \frac{\Delta lenP}{0.1} + \frac{\Delta pFry}{0.02} + max\left(1, \frac{\Delta f2p}{4}\right) + max\left(1, \frac{\Delta lenF}{0.1}\right) + max\left(1, \frac{\Delta lenP}{0.1}\right) + max\left(1, \frac{\Delta pFry}{0.02}\right)$$

The last four terms of the expression penalize parameter values outside of the plausible parameter ranges (i.e., they are 1 within the plausible range and >1 outside of the plausible range).

2.4.3 Parameter exploration

The parameters for the emergence and growth models were taken from the respective papers and assumed fixed (Table 1). We used a grid search to explore possible parameter combinations for the spawn timing offset and movement model parameters primarily responsible for patterns captured in the fit metrics described above (*offset*, *delay*, M_{fry}, M_0). For each of these parameters, we chose a set (size = n) of values that spans a biologically reasonable range, and then examined all possible combinations of these values for the different parameters. The grid search parameters included the number of days between emergence and fry out-migration, *delay* (0 to 30, n = 31), the adjustment to median spawn timing, *offset* (−14 to 14, n = 29), the initial rate of parr migration, M_0 (0.001 to 0.01, n = 11), and the proportion of out-migrants that leave as fry, M_{fry} (0.905 to 0.995, $n = 10$). For all sets, we used equal steps except for M_0 where we used equal steps on the log scale ($10^{-(2 \ to\ 3\ by\ 0.1)}$). The total number of parameter combinations was $31 \times 29 \times 11 \times 10 = 98,890$, which was repeated for the 12 different trap–year combinations. The date at which parr migration increases in the summer, μ, and the total number of out-migrants, E_{tot}, were determined through trial and error using graphical comparisons of the observed and predicted out-migrants for each trap–year combination. The rate at which the parr migration increased, σ, was set to 10 for all trap–year combinations again based on graphical analysis. Because the fit metrics focus on the transition from fry to parr migrants and lengths, they were not as sensitive to these three parameters. For each trap–year combination, fits based on all parameter combinations were determined to be plausible or not plausible based on the criteria above, and the combination with the lowest value of the objective function described above was used to identify a single parameter combination for plotting. To explore the sensitivity of the results to different emergence sizes and growth rates, we repeated the analysis for three additional scenarios in Supplementary material Appendix B.

3 Results

3.1 Temperatures

Stream temperatures differed between years and reaches (Figure 5). Relative to the mainstem (rkm 13), temperatures in Indian Creek were 1 to 2°C warmer in the winter and 1 to 2°C cooler in the summer, with temperatures increasing earlier in the spring. Little River had similar temperatures to the mainstem in the winter, but was cooler in the summer by 1 to 3°C.

3.2 Emergence timing

Predicted emergence time varied by habitat type (mainstem vs. tributaries), reach, and year when the spawn time distribution was held constant (Figure 6A). Warmer stream temperatures in lower Indian Creek during incubation led to predicted emergence times that were approximately a month earlier than in Little River for the same spawn timing (Figure 7). There were similar differences between sites in the lower Elwha (rkm 2) and upper Elwha (rkm 42) mainstem sites. The predicted aggregate emergence time distribution for the Elwha mainstem, weighting by Chinook salmon redds per reach, fell in between Indian Creek and Little River distributions and tended to be more protracted relative to the tributaries or individual mainstem reaches. There were also predicted differences in emergence timing by year, with median emergence for the 2021 spawners (2022 out-migrants) predicted to occur close to a half of a month later than for the 2018 spawners (2019 out-migrants) (Figure 6A). Water temperature tends to decrease during the incubation period, which meant that eggs from redds constructed earlier were predicted to develop faster. This resulted in emergence time distributions that were broader than the spawn timing distributions (Figure 7).

3.3 Growth

Emerging Chinook salmon fry were predicted to experience different stream temperatures due to differences in emergence time and location. This led to differences in predicted growth rates (Figure 7). Differences in the date at which juvenile Chinook salmon were predicted to reach 65 mm were similar to differences identified in predicted emergence timing, although increasing

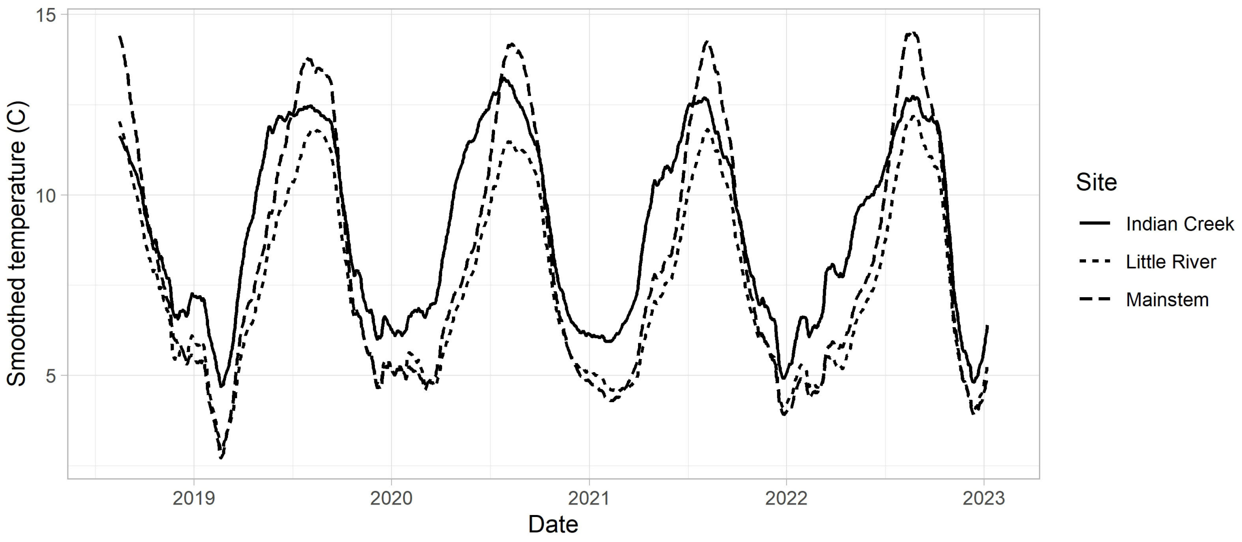


FIGURE 5
Temperature data for Indian Creek, Little River, and the mainstem site adjacent to the USGS gage (rkm 13, near the center of the redd distribution post dam removal). A 31-day moving average was applied to all series to improve visualization. See Supplementary material Appendix A for details of how these temperature series were prepared.

temperatures after emergence tended to result in narrower date ranges at which fish reach 65 mm (when compared to emergence dates) because earlier emerging fish grow slower and later emerging fish grow faster (Figures 6, 7). Predicted differences between Indian Creek and Little River were pronounced, with most Indian Creek juvenile Chinook salmon predicted to achieve 65 mm by the beginning of May while Little River juvenile Chinook salmon were predicted to reach this size primarily in June (Figures 6B, 7A).

3.4 Full model predictions

When the movement model was added to the spawn timing, incubation, and growth models, the combined model was able to explain the observed fish lengths and the timing of the fry-to-parr transition for most trap–year combinations (Figure 8; Table 2). Specifically, the grid search produced plausible parameter combinations for all but 2 years in Indian Creek (Figure 9). In most cases, there were many plausible parameter combinations. In fact, for 8 of the 12 trap–year combinations, the range of plausible *delay* values was more than 20 days (Figure 9). As the *delay* parameter increased, the plausible spawn timing shifted earlier (i.e., smaller *offset*) in order to explain the same out-migrant timing. For example, the observed timing and lengths of 2019 Little River out-migrants could be explained by a late spawn timing (*offset* = 14) and immediate fry out-migration (*delay* = 0) or early spawn timing (*offset* = −5) and a delayed fry out-migration (*delay* = 30). For some trap–year combinations, the fit to the length data also constrained the plausible set. For example, in 2022, the mainstem and Little River parr lengths could only be explained with earlier spawning and a longer delay between emergence and fry out-migration. In Indian Creek, there were only 2 years in which the grid search produced parameter combinations that satisfied the parr length criteria (2019 and 2021). However, if the growth rate was reduced by 25% to reflect food limited growth, there were plausible fits for all years (Supplementary material Appendix B). Even though there were often many plausible parameter combinations, there were some consistent patterns in the plausible sets across traps. For example, if *delay* was assumed to be constant across years, then the plausible spawn timings were later for juveniles in 2020 and earlier for those in 2022 for all traps. The decision to exclude some fish lengths that were inconsistent with the other length data (orange points in Figure 8) was supported by the model results. In almost all cases, the excluded points were far from the predicted lengths. For some trap–year combinations, it appeared that the trap was installed after significant numbers of fry had migrated past the trap (e.g., Little River 2020, Indian Creek 2021, and mainstem 2019 Figure 8). For trap–year combinations where it appeared that the traps were installed before substantial out-migration, the predicted and observed timing of out-migration initiation was not always consistent. In particular, in some years, it appeared that the observed initiation of out-migration occurred as much as a month after the predicted initiation (e.g., Little River 2019 and Indian Creek 2022, Figure 8). While we did not focus on timing of

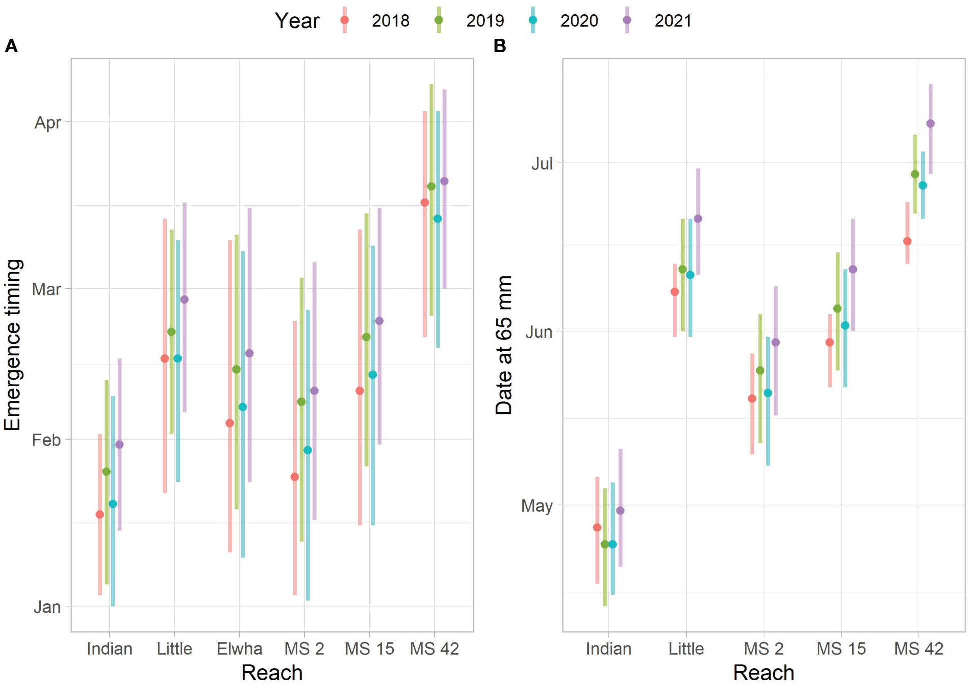


FIGURE 6
Predicted emergence timing and date at which fish have grown to 65 mm. **(A)** The 10th, 50th, and 90th quantiles for the predicted emergence time distributions for each reach and year. The Indian Creek (Indian) and Little River (Little) reaches represent the lower 1.9 km where most spawning occurs. The Elwha reach refers to the aggregate predicted emergence based on reach and year-specific temperature series and redd numbers. MS 2, MS 15, and MS 42 indicate mainstem reaches at rkm 2, rkm 15, and rkm 42 respectively. **(B)** The predicted dates at which fish have grown to 65 mm for fish emerging on the 10th, 50th, and 90th date quantiles (see left panel).

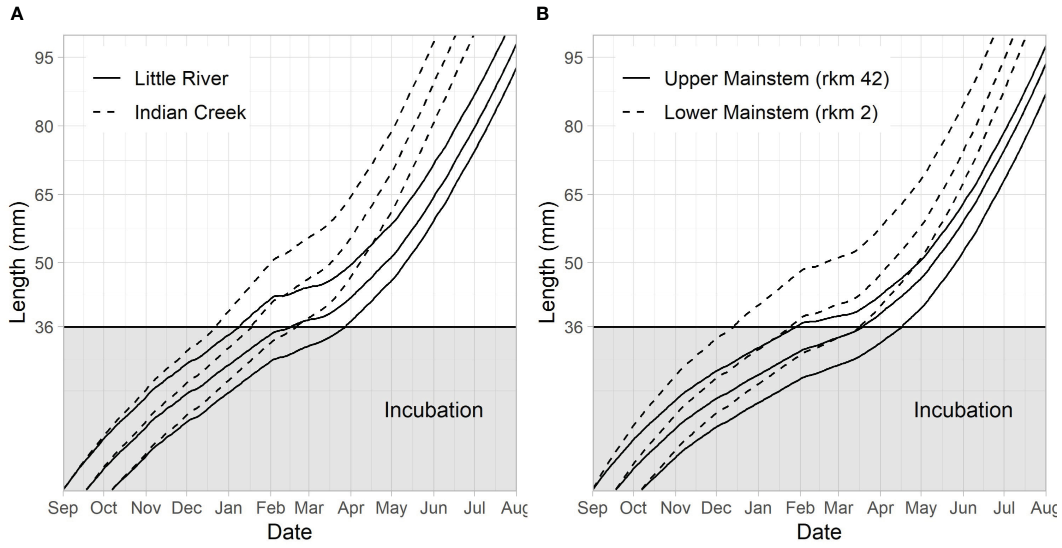


FIGURE 7
Embryo development and juvenile fish growth in 2018 from redds at the beginning (Sept 1), middle (Sept 18), and end (Oct 7) of the assumed spawn time distribution. The *y*-axis during incubation is the percent development of the embryo, with 100% development coinciding with a size of 36 mm (the assumed emergence size). Percent development at time *t* is defined as (degree days at time *t*)/(degree days at emergence)×100. **(A)** Compares trajectories for the two tributaries, Little River and Indian Creek. **(B)** Compares trajectories for a reach in the lower river (rkm 2) and a reach in the upper river (rkm 42).

the parr out-migration, using a single hand fit value for the parameter defining the end of parr migration, μ, the model approximately captures the shape of the parr migration for the different trap–year combinations (Figure 1 in Supplementary material Appendix D).

4 Discussion

The removal of two dams in the Elwha River increased the diversity of stream temperature regimes available to Chinook salmon (Figure 5), resulting in increased variability in predicted emergence timing and growth trajectories (Figures 6, 7). Predicted median emergence times and the date at which juveniles reached 65 mm differed by up to 2 months across locations within the watershed. We postulate that this diversity of emergence times and growth trajectories increases the chances that there will be juveniles that are well suited to year-specific conditions, resulting in higher population resiliency when compared to the pre-dam conditions (Greene et al., 2009; Schindler et al., 2010; Thorson et al., 2014).

This increased diversity of emergence times and growth trajectories may also result in the expansion of life history strategies that spend more time in the river rearing before ocean entry. Currently, there are very few natural origin juvenile Chinook salmon rearing above the traps past the fry stage, with fry comprising over 95% of out-migrants in most years (McHenry et al., 2023b) (Figure 8). The stream-type life history, where juveniles enter the ocean at age 1, is linked to colder rearing temperatures (Beckman and Dickhoff, 1998; Beechie et al., 2006) and may become more prevalent as spawning continues to expand into the upper watershed, characterized by colder temperatures. In addition, variable emergence timing and growth rates may provide more efficient utilization of the available rearing habitat through sequential use and size specific habitat preferences (Everest and Chapman, 1972). Attaining a larger size before leaving the river may be particularly important for population recovery in the Elwha River where estuary habitat is limited relative to other Puget Sound rivers reducing opportunities for growth before ocean entry. Campbell and Claiborne (2017), for example, found that in Puget Sound watersheds with little available intact estuary habitat, very few returning adult Chinook salmon had adopted the fry migrant strategy as juveniles, suggesting low marine survival of this life history strategy.

When the individual models were combined to predict out-migrant timing and lengths at the three screw traps, we found parameter combinations that satisfied all fit criteria for 10 of the 12 trap–year combinations (Figures 8, 9). While there were many plausible combinations of the *delay* and *offset* parameters for most trap–year combinations, if the *delay* parameter was assumed to be consistent across years, spawn timing was likely late for trap year 2020 fish and early for trap year 2022 fish (Figure 9). In general, it also appears that the delay between emergence and out-migration (*delay*) was smaller for Indian Creek than for Little River and the mainstem. This may be due to the short distance between the bulk of spawning and the trap, and high densities of juveniles resulting in density dependent processes that accelerated movements in Indian Creek.

Inconsistencies between the model predictions and observations provided opportunities to examine our model assumptions and data. In Little River, there was a pulse of large juvenile Chinook salmon around the beginning of April in both 2021 and 2022, which could not be explained by the emergence and growth models (Figure 8,

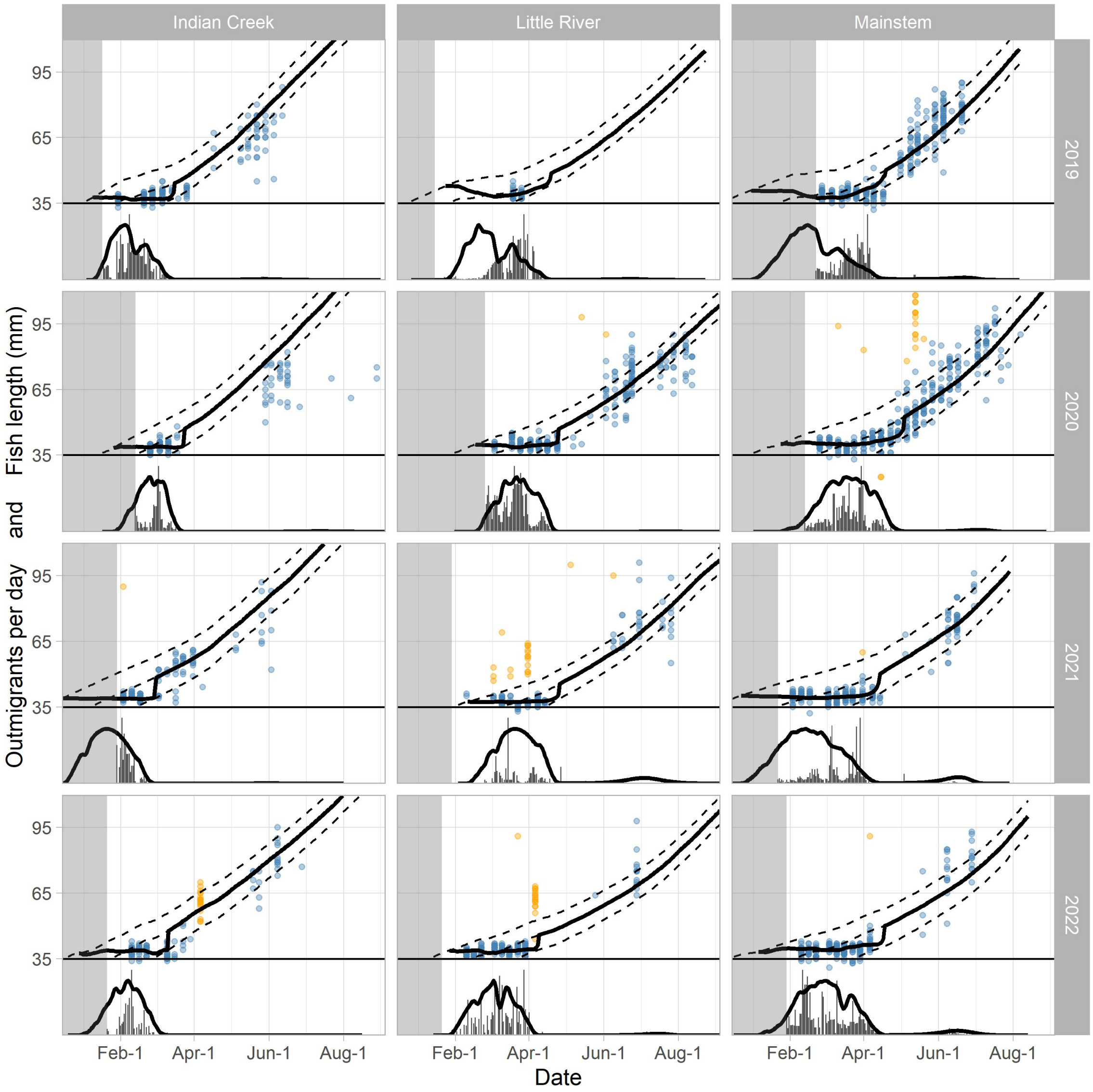


FIGURE 8
Observed and predicted out-migrant timing and lengths for the three traps and 4 years. Out-migrant timing is plotted below the solid horizontal line at $y = 35$, and the y-axis represents the daily number of out-migrants scaled by year and trap to fit within the available space. Out-migrant lengths are plotted above the solid line at $y = 35$ and the y-axis represents out-migrant length in mm. For both out-migrant timing and lengths, the thick black lines are the predictions corresponding to the best fit (black points in Figure 9). The dashed lines above $y = 35$ are the growth trajectories for fish emerging at the start, middle, and end of the predicted emergence time distribution corresponding to the best fit. The observed number of daily out-migrants is plotted as gray vertical bars (below $y = 35$) and the observed lengths for individual fish captured and measured in the traps are represented by points (above $y = 35$). The orange points are lengths that were not included when calculating the fit statistics due to discrepancies with the other length data (see *Materials and Methods*). The light gray region delineates the period before the trap was installed.

orange points). These fish may be larger hatchery fish released as part of an efficiency trial that stayed above the trap long enough to lose their Bismarck Brown mark (typically fades after 7–10 days). For example, in 2021, there were releases with 100 hatchery fish on March 9, 16, and 23 in Little River, which align with groups of longer-than-expected fish (Figure 8, orange points). These results suggest that alternatives to these hatchery fish or more permanent marks may be helpful.

For 2 years in Indian Creek, no plausible fits were found due to the model's tendency to over-predict parr lengths. There are a number of possible explanations. Indian Creek produces a large number of juvenile Chinook salmon in a small area (lower 1.9 km), likely due to high spawner densities (Figure 2) and stable incubation conditions resulting in high egg-to-fry survival. This creates the potential for intense density-dependent competition, which may result in slower growth. Warmer temperatures in Indian Creek during early growth (Figure 5) would also increase metabolic costs increasing the likelihood of food-limited growth (e.g., Myrick and Cech, 2002). Reducing the growth rate by 25% in Indian Creek improved the fit and resulted in plausible parameter combinations in all years (Supplementary material Appendix B), supporting but not confirming this hypothesis. Indian Creek may also be attracting smaller spawners, which would result in smaller eggs and therefore emergence sizes. However, reducing the assumed emergence size to

TABLE 2 The best-fit parameter combinations used for plotting the predictions in Figure 8.

Trap	Year	$delay$	$offset$	M_{fry}	M_0	μ	σ
Mainstem	2019	21	−4	0.945	0.0079	2019-08-08	10
Mainstem	2020	22	5	0.975	0.0032	2020-07-27	10
Mainstem	2021	21	−5	0.935	0.0020	2021-08-10	10
Mainstem	2022	20	−5	0.935	0.0016	2022-07-06	10
Indian	2019	5	9	0.975	0.0063	2019-06-06	10
Indian	2020	9	13	0.985	0.0010	2020-06-27	10
Indian	2021	11	−5	0.995	0.0010	2021-07-21	10
Indian	2022	9	−3	0.995	0.0010	2022-07-21	10
Little	2019	28	−6	0.975	0.0063	2019-07-09	10
Little	2020	17	7	0.995	0.0010	2020-06-18	10
Little	2021	8	12	0.905	0.0010	2021-06-01	10
Little	2022	13	−4	0.965	0.0032	2022-07-26	10

The *delay*, *offset*, M_{fry}, and M_0 values were chosen based on a grid search and the objective function is described in Materials and Methods. The σ value was set to 10 and the μ value was fit by eye using plots.

34 mm from 36 mm did not increase the number of years with plausible fits in Indian Creek (Supplementary material Appendix B). The conversion of the growth model (Perry et al., 2015) from weight based to length based may also be contributing to inconsistencies between the predicted and observed lengths. The length–weight relationship in salmonids tends to be different during the period immediately after emergence (Nika, 2013), which was not accounted for in our conversion. A careful exploration of the length–weight relationship in Elwha fish may produce more consistent results. Finally, smaller fry may be lost in the trap box through predation by larger captured fish, slipping through the screen, or becoming adhered to the rotating screen at the back of the trap box and being moved downstream. Fitting to the larger remaining fry lengths would then result in overestimating parr lengths. This has suggested further investigation with releases of marked recently emerged fry into the trap box.

The observed initiation of fry out-migration appeared to occur much later than predicted for some trap–year combinations (Figure 8). This was particularly evident in the tributaries and may have resulted from narrower spawn timing distributions for those trap–year combinations. This would make sense given that the tributary spawning reaches are much smaller and more homogeneous than the spawning habitat in the mainstem river. Additional redd surveys to better characterize the shape of the spawn timing curve may help explain these patterns.

The least understood part of the full model is the movement component. While there is a general understanding of ocean-type Chinook salmon movement during early life history (e.g., Taylor, 1990b), there are many possible and realized trajectories of juvenile fish through the river network over time, due to the many Chinook salmon life history strategies. We use a very simple movement model that combines all fish above the trap that emerged on a specific day, and then assumes the same growth rate and movement probabilities for this group over time. Fry migration is simplified to a single pulse a fixed number of days after emergence followed by a protracted date-based parr movement model, again, shared by all fish in a group. While this simple model can produce fits that agree relatively well with the data, there are clearly ways in which the model could be made more realistic. For example, the timing of the fry pulse could extend over multiple days, the delay could depend on distance to the trap, and movement could be cued off of changes in river discharge, water temperature or light (Taylor, 1990a; Taylor, 1990b; Sykes et al., 2009; Apgar et al., 2021). We had some limited success explaining patterns in the out-migrants using patterns in discharge, but these relationships were not sufficient to justify inclusion in the predictive model. We also tried a parr movement model based on days since emergence instead of date and found that fits to the length data tended to be less accurate. Age-based movement models tend to reduce the number of larger fish later in the season because the fish leave before reaching the larger sizes seen in the observed data (Figure 8). Density dependence has also been linked to juvenile Chinook salmon migration (Zimmerman et al., 2015; Apgar et al., 2021) and as more years of data become available, we should be able to investigate this hypothesis. While the movement model was simple, it still included four parameters that were not well defined by the literature or the data, resulting in a large set of plausible parameter combinations. Therefore, including additional complexity in the model will provide limited utility without additional information from the literature or data from the Elwha River to constrain the plausible set of models.

These results suggest a number of opportunities to further improve the full model. Spawn timing is not well characterized for Elwha River Chinook salmon since redd surveys are only conducted during peak spawning, which provides little information about the shape of the spawn timing distribution. Our current model reflects this with a fixed

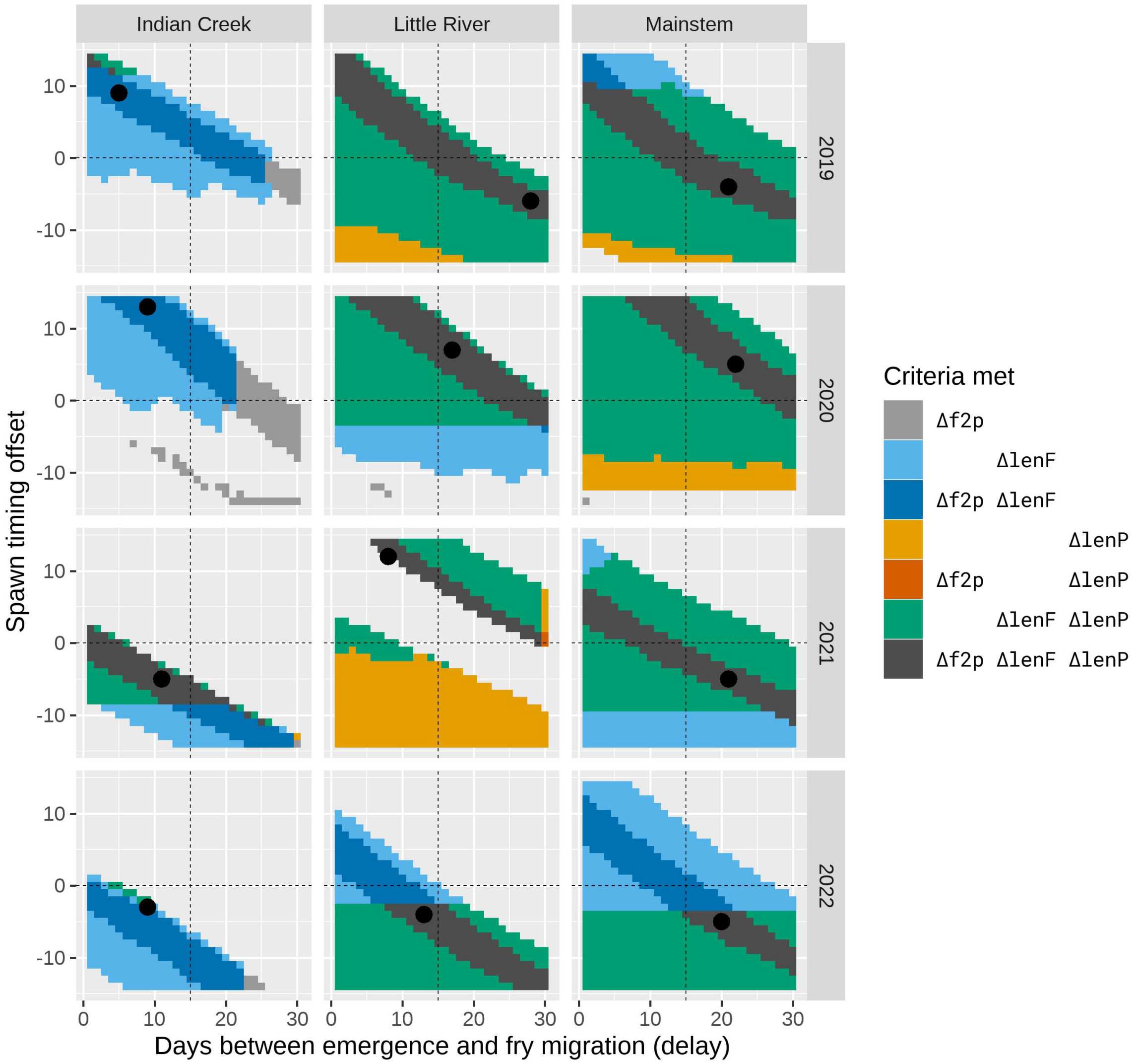


FIGURE 9
The combinations of the delay and offset parameters that resulted in plausible fits to the observed data as defined by the different fit criteria. The shaded areas represent combinations of the delay and offset parameters where at least one of the fit criteria Δf2p, ΔlenF, or ΔlenP was met and the criterion ΔpFry was also met. The dark gray area indicates that all criteria were met (i.e., plausible fits), and the black point identifies the parameter combination corresponding to the best fit as defined by the objective function in *Materials and Methods*. Other colors indicate parameter pairs where different combinations of the fit criteria were achieved (see the legend).

shape that is shifted in time using the *offset* parameter. Additional redd surveys, throughout the spawning period, would constrain the *offset* parameter, in turn providing more information about movement timing (e.g., the *delay* parameter). In addition, year- and location-specific data could be used to refine the spawn timing model with, for example, changes to the width of the distribution. The timing of adult entry into the river is estimated precisely every year using Imaging sonar (Denton et al., 2021). When combined with year-specific environmental data, such as flow and temperature, this may also inform the spawn timing distribution. The size and age of adult Chinook salmon affect the size of eggs (e.g., Gallinat and Ross, 2007) and thus fry (Beacham and Murray, 1990). Therefore, lengths collected during carcass surveys may allow for better explanation of trap and year differences in juvenile sizes, through expansion of the model to include year- and trap-specific emergence size. This is especially true for the tributary traps, where spawning is confined to a relatively small area, and therefore more easily characterized. The temperature data available during the study period was incomplete, with large gaps in the available series (Supplementary material Appendix A). Error introduced when filling these gaps (Supplementary material Appendix A) may have contributed to some of the inconsistencies between the predictions and observations. More recently, efforts have intensified to improve the consistency of these data, which will reduce this source of error. We ignored mortality in this work by modeling the fish that would eventually survive to move past the trap. This assumes that egg-to-out-migrant survival is consistent across locations and years. Violations of this assumptions could create additional errors in the model predictions. For example, in some years, the estimated number of Chinook salmon fry leaving Indian Creek is comparable to the estimated fry passing the mainstem trap (Pess et al., In Press).

However, the Indian Creek redds only comprise a small fraction of the total redds above the mainstem trap (Figure 2), and therefore are assumed, by the model, to produce a small percentage of the out-migrants passing the mainstem trap. This would only be true if mortality between the Indian Creek trap and mainstem trap was very high. An alternative hypothesis is that the egg-to-emergence survival for Indian Creek, with stable rearing conditions, is often much higher than the mainstem, where large winter flows may scour redds. Releases of marked fish from the Indian Creek trap that are later observed in the mainstem trap may help address this question, and may also inform the relationship between mainstem egg-to-fry survival and environmental covariates such as peak flow.

The Elwha River Chinook salmon population is dominated by hatchery fish with typically over 90% of returning fish traced back to the hatchery (Pess et al., In Press). While this illustrates the importance of the hatchery in maintaining the population, these high proportions may also have negative effects. Hatchery origin fish differ from natural origin fish in a number of ways relevant to recolonization. Hatchery practices may result in a shift in run timing counter to patterns observed in natural populations, owing to different patterns of selection in the hatchery vs. natural environment (Quinn et al., 2002; Tillotson et al., 2019; Austin et al., 2021). The spatial distribution of spawning may also be affected by hatchery programs (Ford et al., 2015), and may result in hatchery origin fish spawning in locations where the redds (nests) are more susceptible to environmental sources of mortality (Hughes and Murdoch, 2017). In the Elwha River, hatchery origin fish were released from a discrete location in the lower river whereas natural origin fish were spawned and fry emerged across a much a broader spatial distribution (Figure 2), potentially creating differences for olfactory imprinting and subsequent adult homing. Lastly, we have shown that diversity of thermal regimes contributes to juvenile life history diversity. In general, naturally spawned fish experience a greater diversity of temperature profiles across the landscape than fish reared in the more controlled hatchery setting. A narrowing of life history diversity associated with hatchery-rearing might alter ecosystem processes such as marine food web dynamics (Nelson et al., 2019), ultimately affecting patterns of smolt-to-adult survival.

Finally, prior to moving the primary mainstem rotary screw trap to above the state hatchery in 2019, there were a large number of captured out-migrant parr that were likely hatchery origin (Figure 11 in McHenry et al., 2023b). Hatchery origin fish rearing in freshwater may contribute to density-dependent movement (e.g., Zimmerman et al., 2015), growth (e.g., Crozier et al., 2010), and mortality for natural origin fish rearing below the hatchery. The increasing numbers of natural origin juvenile Chinook salmon produced above the hatchery since dam removal (McHenry et al., 2023b; Pess et al., In Press) may lead to more extensive and longer rearing above the hatchery, where natural origin fish would not be exposed to competition with hatchery fish. If this translated into larger natural origin fish leaving the river, then ocean survival may also increase, resulting in more natural origin spawners.

It may be tempting to view increases in habitat capacity and population abundance as the primary conservation benefit of dam removals. However, increasing the range of habitat types available to migratory fish may also be a crucial component of species recovery by promoting life history diversity. More diverse life history strategies buffer populations against episodic disturbances (Greene et al., 2009; Schindler et al., 2010; Thorson et al., 2014) and allow for adaptation in the face of climate change (e.g., Atlas et al., 2023), increasing population persistence and resilience. Therefore, conservation managers should explicitly consider opportunities to increase life history diversity when planning dam removals and other salmon habitat restoration actions. Mechanistic modeling, like the work described in this manuscript, can help managers predict how barrier removal and other forms of habitat restoration will affect the suite of life history strategies expressed by a population, moving beyond simple capacity models. In the Elwha River, the individual and combined models provided insight into how the varied thermal habitats available post dam removal translated into diverse early life history trajectories, and allowed for predictions of how these trajectories might change if spawner distribution shifted within the watershed. While using the emergence and growth models independently was useful, taking the additional step to integrate these predictions with a movement model and comparing the results to observed out-migrant timing and lengths allowed us to test the underlying hypotheses implicit in the models. Although agreement between predictions and observations does not validate the hypotheses, model failures provided opportunities for further work both in refining hypotheses (i.e., models) and in collecting better data. There are many smolt traps operated throughout the Pacific Northwest, capturing many different species and life history types. The type of modeling approach outlined here provides an opportunity to extract more value from this data and gain new understanding about the critical early life history stages of anadromous salmonids.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

We received US federal and state permits to work with the fish in this study. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

Concept Development, Analysis Writing: ML; Writing and synthesis: AF, GP, SM, and JA; Data collection, Site and biological expertise: MM, mT, JS, ME, and TB; GIS analysis, map and help with writing: RM. All authors contributed to the article and approved the submitted version.

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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.2023.1240987/full#supplementary-material

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Vegetation responses to large dam removal on the Elwha River, Washington, USA

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Large dam removal can trigger changes to physical and biological processes that influence vegetation dynamics in former reservoirs, along river corridors downstream of former dams, and at a river's terminus in deltas and estuaries. We present the first comprehensive review of vegetation response to major fluvial disturbance caused by the world's largest dam removal. After being in place for nearly a century, two large dams were removed along the Elwha River, Washington, USA, between 2011 and 2014. The exposure, erosion, transport, and deposition of large volumes of sediment and large wood that were impounded behind the dams created new fluvial surfaces where plant colonization and growth have occurred. In the former reservoirs, dam removal exposed ~290 ha of unvegetated sediment distributed on three main landforms: valley walls, high terraces, and dynamic floodplains. In addition to natural revegetation in the former reservoirs, weed control and seeding and planting of desirable plants influenced vegetation trajectories. In early years following dam removal, ~20.5 Mt of trapped sediment were eroded from the former reservoirs and transported downstream. This sediment pulse, in combination with transport of large wood, led to channel widening, an increase in gravel bars, and floodplain deposition. The primary vegetation responses along the river corridor were a reduction in vegetated area associated with channel widening, plant establishment on new gravel bars, increased hydrochory, and altered plant community composition on gravel bars and floodplains. Plant species diversity increased in some river segments. In the delta, sediment deposition led to the creation of ~26.8 ha of new land surfaces and altered the distribution and dynamics of intertidal water bodies. Vegetation colonized ~16.4 ha of new surfaces: mixed pioneer vegetation colonized supratidal beach, river bars, and river mouth bars, and emergent marsh vegetation colonized intertidal aquatic habitats. In addition to the sediment-dominated processes that have created opportunities for plant colonization and growth, biological processes such as restored hydrochory and anadromous fish passage with associated delivery of marine-derived nutrients may influence vegetation dynamics over time. Rapid changes to landforms and vegetation growth were related to the large sediment pulse in the early years following dam removal, and the rate of change is expected to attenuate as the system adjusts to natural flow and sediment regimes.

KEYWORDS

ecogeomorphology, sediment pulse, riparian vegetation, river restoration, drained reservoir, coastal vegetation, river delta, active revegetation

1 Introduction

Dam removal has occurred at an increasing pace over recent decades and is expected to continue as many aging dams cease to perform useful functions, and as the safety hazards, maintenance costs, and ecological consequences of keeping dams in place come to outweigh the benefits (O'Connor et al., 2015; Duda and Bellmore, 2022; American Rivers, 2023). Dam removal can trigger a range of responses in physical and biological components of river systems, driving new ecosystem dynamics and trajectories, including differing short- and long-term responses (Foley et al., 2017a; Major et al., 2017; Bellmore et al., 2019). Despite the ubiquity of dam removal, relatively few cases have been studied, and even fewer have been studied over a long period of time, including before, during and after dam removal (Bellmore et al., 2017; Foley et al., 2017a).

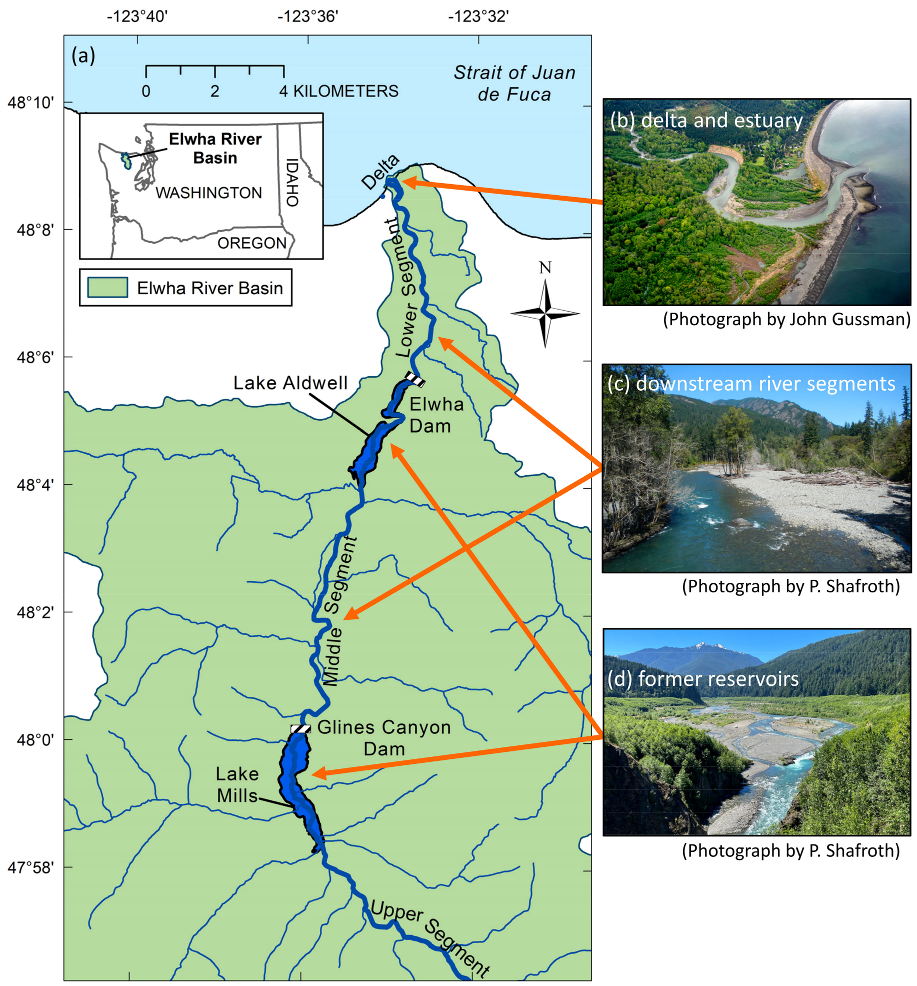
Riparian, wetland, and coastal vegetation may all change in response to dam removal (Shafroth et al., 2002), due to alterations of various physical and biological processes. One of the primary ways that dam removal affects vegetation is by changing the distribution, abundance, and character of landforms on which plants grow (Shafroth et al., 2002; Bellmore et al., 2019). In former reservoirs, water drawdown associated with dam removal exposes formerly submerged landforms that become available for plant colonization. In cases where a significant amount of sediment was trapped behind the dam, the mobilization, transport, and deposition of sediment downstream can trigger changes to active channels and near-channel bars, floodplain aggradation, or aggradation and new landform development in the river's delta (Pizzuto, 2002; Major et al., 2017). These kinds of changes can affect existing vegetation through burial or erosion/removal and provide opportunities for colonization of new plants via creation of new surfaces and landforms (Shafroth et al., 2002). The new surfaces and landforms may have environmental conditions that particularly favor early-successional, disturbance-adapted plant species, including weedy, non-native species (Shafroth et al., 2002; Tullos et al., 2016). Changes to flow regime associated with dam removal could also lead to vegetation changes over time, although we are unaware of any dam-removal case studies with significantly altered flow regimes (Foley et al., 2017a). Dam removal also restores connectivity along the river for organisms that were unable to pass through a dam in the up- or downstream direction (Bellmore et al., 2019). Seed or propagule dispersal of some riparian plants is accomplished by downstream transport in the river, a form of hydrochory (Nilsson et al., 2010). Dam removal can restore hydrochory, allowing seeds to be transported downstream past former dam sites. Transport and deposition of large wood past former dam sites may also influence vegetation via interactions with fluvial processes and landform dynamics (Francis et al., 2008; Naiman et al., 2010; Leung, 2019). Restored upstream movement of anadromous fish may lead to deposition of marine-derived nutrients on floodplains, potentially affecting growth of riparian plants (Helfield and Naiman, 2001; Quinn et al., 2018).

Ecosystem responses to dam removal may vary spatially along the river continuum – from former reservoir(s), along downstream river corridors, to deltas and estuaries. Most studies of vegetation responses to dam removal have focused on short-term colonization and growth of plants on formerly submerged surfaces associated with drained reservoirs (e.g., Orr and Stanley, 2006; Lisius et al., 2018; Ravot et al., 2020; Chenoweth et al., 2023). Others have examined specific aspects of vegetation in other parts of the river system, such as plant community composition and diversity (Schmitz et al., 2009; Brown et al., 2022). There have been no published reviews that synthesize results of vegetation change associated with dam removal in multiple riverine landscape positions.

The Elwha River (Washington, USA) is the site of two large dam removals that occurred between 2011 and 2014 and is the most studied dam-removal case study globally. The principal objective of the dam removals was to restore the Elwha's native anadromous salmon populations, but a secondary goal was to evaluate ecosystem responses to dam removal and the return of salmon (U.S. Department of the Interior and epartment of Commerce and Lower Elwha S'Klallam Tribe, 1994; Ward et al., 2008). Because most of the Elwha watershed is protected within a national park, ecosystem responses may be evaluated without the confounding influence of the various anthropogenic disturbances that occur in most American river systems (Duda et al., 2008). Moreover, whereas vegetation in the majority of the former reservoirs was actively managed through invasive vegetation control, and planting and seeding of native vegetation (funded as part of the dam removal; Chenoweth et al., 2011), the river reaches and delta were largely left to recover on their own. As a result, the Elwha dam removals offer a unique opportunity to assess how restoring natural fluvial processes affects riparian vegetation communities in a coastal temperate ecosystem. This work has important implications for biodiversity conservation as well as salmon recovery because coastal temperate riparian zones support diverse plant communities (Naiman et al., 1993; Naiman et al., 1998) and provide essential habitat functions for aquatic ecosystems (Gregory et al., 1991; Naiman and Decamps, 1997). There are more than 250 publications related to the Elwha dams and their removal (https://www.zotero.org/groups/4740476/elwha_bibliography), including studies of effects of dam removal on various aspects of the physical environment, and various terrestrial, aquatic, and marine communities. With respect to vegetation, previous research has examined ecosystem responses upstream, between, and downstream of the former dams, and within the former reservoirs (e.g., Brown et al., 2022; Chenoweth et al., 2023; Perry et al., 2023), but a comprehensive review of Elwha vegetation studies has not been conducted.

In this paper, we review and synthesize previous studies of vegetation responses to dam removal along the Elwha River, focusing on the important connections between fluvial processes and vegetation dynamics. We discuss vegetation dynamics in three major landscape positions along the river continuum (Figure 1): (1) the former reservoirs, (2) along the river corridor, and (3) in the Elwha delta and estuary. We gathered all available literature on Elwha River vegetation prior to and following dam removal, 39 sources in total (Table 1). Most of this literature focused on vegetation development in the former reservoirs following dam removal, but some sources examined vegetation along downstream river segments or in the river delta and estuary before and/or after dam removal. We also drew on published studies of geomorphic effects of the Elwha River dam removals, in order to place vegetation responses within the context of landform and sediment dynamics.

We created separate causal-loop feedback diagrams for each of the three major landscape positions to illustrate expected or hypothesized relationships between riparian vegetation and hydrology, sediment, large wood, and marine influences following dam removal (Figure 2), informed by prior reviews of dam removal



(b) delta and estuary

(Photograph by John Gussman)

(c) downstream river segments

(Photograph by P. Shafroth)

(d) former reservoirs

(Photograph by P. Shafroth)

FIGURE 1
(A) Map of the Elwha River study area. Inset map shows the location of the Elwha River Basin within the Pacific Northwest, United States. Areas where riparian and wetland vegetation were potentially affected by dam removal are labelled in the larger map: the river delta and estuary (delta), river segments downstream of and between the former dams (lower and middle segments), and the former reservoirs (Lake Aldwell and Lake Mills). The upper river segment used as a reference condition in some studies is also labeled. Photographs depict examples of these areas: **(B)** oblique image of the Elwha River delta and estuary on May 8, 2023, **(C)** oblique image of the Elwha River ~1.5 km downstream of former Glines Canyon Dam on August 22, 2014, and **(D)** oblique image of the former Lake Mills on July 11, 2022.

TABLE 1 Comprehensive list of publications on vegetation along the Elwha River, Washington, USA, before and after two dams were removed in 2011-2014.

Author(s), year	Title	Landform†	Pre/Post dam removal‡	Response variables
Acker et al., 2008	Effects of a natural dam-break flood on geomorphology and vegetation on the Elwha River, Washington, USA	corridor	pre	tree species basal area, stem density, age, mortality, regeneration
Baker, 2013	Elwha River revegetation project: 2012 Lake Aldwell seeding trials, M.S. Thesis	reservoir	post	native & non-native seedling density, cover
Brown and Chenoweth, 2008	The effect of Glines Canyon Dam on hydrochorous seed dispersal in the Elwha River	corridor	pre	seed species richness, abundance
Brown et al., 2022	Does large dam removal restore downstream riparian vegetation diversity? Testing predictions on the Elwha River, Washington, USA	corridor	pre/post	native & non-native plant species richness, composition
Calimpong, 2014	Elwha River revegetation 2013: a plant performance study, M.S. Thesis	reservoir	post	tree seedling survival, growth
Cendejas-Zarelli, 2021	The effect of large woody debris, direct seeding, and distance from the forest edge on species composition on novel terraces following dam removal on the Elwha River, WA, M.S. Thesis	reservoir	post	plant stem density, species richness, diversity, % non-native, composition
Chenoweth, 2007	Predicting seed germination in the sediments of Lake Mills after the removal of the Glines Canyon Dam on the Elwha River, M.S. Thesis	reservoir	pre	seedbank density; seed germination
Chenoweth et al., 2011	Revegetation and restoration plan for Lake Mills and Lake Aldwell	reservoir	pre	review: plant species composition
Chenoweth et al., 2022	Planting, seeding, and sediment impact restoration success following dam removal	reservoir	post	plant cover, species richness, stem density, composition, % non-native
Chenoweth et al., 2023	A review of natural and managed revegetation responses in two de-watered reservoirs after large dam removals on the Elwha River, Washington, USA	reservoir	post	review: native & non-native plant species richness, cover, stem density, composition,
Citron, 2017	Black cottonwood (*Populus trichocarpa*) nutrition in the dewatered Lake Aldwell reservoir on the Elwha River, Washington	reservoir	post	*Populus* foliar nutrients
Clausen, 2012	Riparian understory dynamics and relationship to dams on the Elwha River, Washington, M.S. Thesis.	corridor	pre	native & non-native plant species richness, composition
Cook et al., 2011	Effects of native plant species, mycorrhizal inoculum, and mulch on restoration of reservoir sediment following dam removal, Elwha River, Olympic Peninsula, Washington	reservoir	post	plant cover, growth, mycorrhizae; native & non-native species richness
Cortese, 2014	Mycorrhizal availability in the basin of Lake Mills and influence on colonization and growth of *Salix scouleriana* under drought stress. M.S. Thesis	reservoir	post	*Salix* growth, foliar N; mycorrhizae
Cortese and Bunn, 2017	Availability and function of arbuscular mycorrhizal and ectomycorrhizal fungi during revegetation of dewatered reservoirs left after dam removal	reservoir	post	*Salix* growth, foliar N: P, mycorrhizae
Cubley, 2015	Initial response of riparian vegetation to dam removal on the Elwha River, Washington. M.S. Thesis	corridor	pre/post	native & non-native plant species richness, composition
Cubley and Brown, 2016	Restoration of hydrochory following dam removal on the Elwha River, Washington	corridor	pre/post	seed species richness, abundance
Foley et al., 2017b	Coastal habitat and biological community response to dam removal on the Elwha River	delta	pre/post	plant species richness, composition
Hulce, 2009	Vegetation colonization and seed bank analysis of Lake Mills deltas: pre-dam removal analysis for post-dam removal insight. M.S. Thesis	reservoir	pre	plant & seed bank species diversity, composition
Johnson et al., 2023	Large wood supports Elwha revegetation by reducing ungulate browsing	reservoir	post	woody species browse intensity

(*Continued*)

TABLE 1 Continued

Author(s), year	Title	Landform†	Pre/Post dam removal‡	Response variables
Kane, 2018	Monitoring the influx of marine derived nitrogen and soil food webs of Northern Olympic Peninsula riparian zones. M.S. Thesis	corridor	post	δ15N abundance in foliage, soil, litter; plant parasitic & bacterivore nematode abundance, composition
Kane et al., 2020	Monitoring the return of marine-derived nitrogen to riparian areas in response to dam removal on the Elwha River, Washington	corridor	post	δ15N abundance in foliage, soil, litter
Kardouni, 2020	Forest restoration of the exposed Lake Mills bed: assessing vegetation, ectomycorrhizae, and nitrogen relative to riverbank lupine (*Lupinus rivularis*), M.S. Thesis	reservoir	post	tree seedling growth, foliar N, mycorrhizae; plant species richness, composition
Kardouni et al., 2023	Riverbank lupine's (*Lupinus rivularis*) influence on conifer growth, ectomycorrhizal colonization, and neighboring vegetation in coarse sediments left behind after dam removal	reservoir	post	tree seedling growth, foliar N, mycorrhizae; plant species richness, composition
Kloehn et al., 2008	Influence of dams on river-floodplain dynamics in the Elwha River	corridor	pre	forest stand age, composition, turnover
Labay, 2013	Impact of riverbank lupine (*Lupinus rivularis*) on grand fir (*Abies grandis*) ectomycorrhizal symbioses. M.S. Thesis.	reservoir	post	tree seedling growth, foliar N, mycorrhizae
McCaffery et al., 2018	Terrestrial fauna are agents and endpoints in ecosystem restoration following dam removal	reservoir	post	review: interactions between fauna & revegetation
McCaffery et al., 2020	Small mammals and ungulates respond to and interact with revegetation processes following dam removal	reservoir	post	plant cover; *Populus* & *Salix* browse intensity, height
McLaughlin, 2013	Engaging birds in vegetation restoration after Elwha dam removal	reservoir	post	tree density; avian scat distribution (seed dispersal)
Michel et al., 2011	Seed rain and revegetation of exposed substrates following dam removal on the Elwha River	reservoir	pre	native & non-native plant cover; seed germination
Morgan, 2018	Vegetation community development after dam removal on the Elwha River, M.S. Thesis	reservoir	post	native & non-native plant species richness, cover, composition
Perry et al., 2023	Coastal vegetation responses to large dam removal on the Elwha River	delta	pre/post	native & non-native plant species richness, cover, composition; community types, transitions
Prach et al., 2019	Spontaneous and assisted restoration of vegetation on the bottom of a former water reservoir, the Elwha River, Olympic National Park, WA, USA	reservoir	post	native & non-native plant species richness, cover, composition
Schuster, 2015	Vegetation colonization within exposed reservoirs following dam removal on the Elwha River, M.S. Thesis	reservoir	post	native & non-native plant species richness, cover, composition; soil nutrients
Shafroth et al., 2011	Vegetation of the Elwha River estuary	delta	pre	native & non-native plant species richness, cover, composition; community types
Shafroth et al., 2016	Effects of dams and geomorphic context on riparian forests of the Elwha River, Washington	corridor	pre	tree species importance, composition; community types; seedling abundance
Thomas, 2018	Riparian vegetation and the soil seed bank five years after dam removal on the Elwha River, Washington, M.S. Thesis	reservoir	post	native & non-native plant species richness, cover, composition; seed bank richness
Whisman, 2013	Revegetation of post-dam-removal riparian sediments in the Lower Elwha River, WA. M.S. Thesis	reservoir	post	tree & shrub seedling survival
Woodward et al., 2011	Predicting spread of invasive exotic plants into dewatered reservoirs after dam removal on the Elwha River, Olympic National Park, Washington	reservoir	pre	non-native plant population size, distribution

†reservoir=vegetation establishment in the former Lake Aldwell and/or Lake Mills; corridor=vegetation along the river corridor, upstream, between, and/or below the dams; delta=vegetation in the river delta and estuary at the river mouth.

‡pre=observations prior to dam removal; post=observations during and/or after dam removal; pre/post= comparisons of before vs during and/or after dam removal.

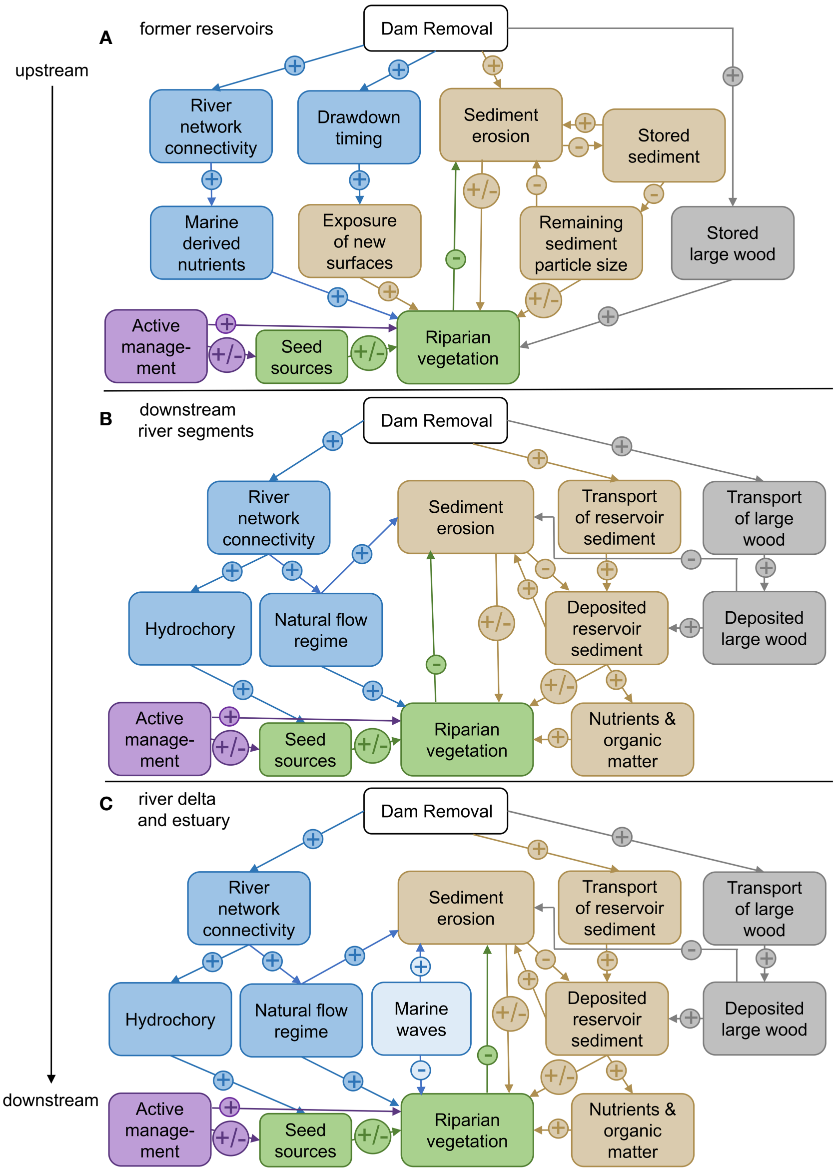


FIGURE 2
Causal-loop diagrams depicting cause-and-effect links and feedback loops influencing vegetation response to dam removal within **(A)** former reservoirs, **(B)** downstream river segments, and **(C)** coastal deltas and estuaries. The arrows indicate the direction of influence, and the plus and minus signs indicate whether the influence is positive (+; i.e., increases in the causal variable lead to increases in the response variable), negative (-), or positive for some plant taxa and negative for others (+/-). Sediment-driven processes are shown in brown, wood-driven processes are shown in grey, hydrology-driven processes are shown in blue, human-driven processes are shown in purple, and vegetation-driven processes are shown in green. The diagrams are loosely based on diagrams in Bellmore et al. (2019), modified to focus on vegetation responses.

effects on river systems (Shafroth et al., 2002; Foley et al., 2017a; Major et al., 2017). The structure of these diagrams was loosely based on diagrams of ecosystem effects of dam removal published in Bellmore et al. (2019). The locations of the different landscape positions relative to the former dam, the river mouth, and each other result in distinct roles of sediment, wood, and propagule transport downstream and marine-derived nutrient transport upstream at each landscape position.

In the review that follows, we (1) briefly summarize expected effects of dam removal on vegetation based on the causal-loop feedback diagrams in Figure 2, emphasizing changes that were particularly likely to occur in the context of the Elwha River dam removals, (2) describe observed sediment and landform dynamics following dam removal that were likely to influence vegetation, and (3) review vegetation responses to dam removal and post-dam-removal sediment and landform dynamics. For the former reservoirs, we also describe vegetation management activity and review vegetation responses to active management following dam removal. This review is intended to help guide future dam removal and ecosystem restoration efforts, and also to elucidate fundamental relationships between riparian vegetation and fluvial processes along a coastal temperate river.

2 Study area

The Elwha River flows 72 km from its headwaters in the Olympic Mountains to the Strait of Juan de Fuca, draining a total area of 833 km^2, >80% of which are within Olympic National Park. Average instantaneous discharge is 43 $m^3\ s^{-1}$. Two large dams were constructed for local hydropower along the Elwha River in 1913 (Elwha Dam, 32 m tall, 7.9 km from the river mouth) and 1927 (Glines Canyon Dam, 64 m tall, 21.6 km from the river mouth). The dams did not provide substantial flood control or water supply and, after 1975, regulated river flows were largely "run-of-the-river". However, the dams prevented upstream fish passage and restricted downstream transport of sediment and wood, impounding ~30 Mt of sediment within the reservoirs during the 84-98 years that the dams were in place (Randle et al., 2015). Approximately 45% of the stored sediment was fine sediment (silt and clay) and ~55% coarser sediment (Randle et al., 2015).

Both dams were removed between 2011 and 2014. In late May 2011, water levels in both reservoirs were reduced by approximately 4.5 m in preparation for dam removal, exposing a narrow band of the valley wall. Removal of the two dams began simultaneously in September 2011. Removal of the Elwha Dam was relatively rapid, completed in March 2012. Removal of Glines Canyon Dam was designed to be slower to allow the Elwha River to gradually erode the larger quantity of sediment impounded in the upstream reservoir delta. The reservoir pool was drained slowly over a period of 13 months (September 2011-October 2012) (Randle et al., 2015) and dam removal was completed in August 2014. Dam removal released ~20.5 ± 3.2 Mt of sediment downstream over the first five years (2012-2016) (Ritchie et al., 2018). More detailed descriptions of the dam removal process are provided by Randle et al. (2015) and Warrick et al. (2015).

The former reservoirs, Lake Mills (Glines Canyon Dam) and Lake Aldwell (Elwha Dam) (Figure 1), are located at 166 m and 57 m above sea level, respectively. When full, Lake Mills occupied 1.68 km^2 of Olympic National Park, flooding ~4.5 km of the former river (Duda et al., 2008). Lake Aldwell occupied 1.08 km^2 downstream of the Park boundary, flooding ~4 km of the former river (Duda et al., 2008). The forests around the former reservoirs are generally dominated by mature conifers [*Pseudotsuga menziesii* (Douglas fir), *Abies grandis* (grand fir), *Tsuga heterophylla* (western hemlock)], with thin bands of deciduous trees [*Alnus rubra* (red alder), *Acer macrophyllum* (bigleaf maple), *Populus balsamifera* spp. *trichocarpa* (black cottonwood), and *Salix* spp. (willow)] along the former shoreline (Chenoweth et al., 2022). Prior to dam removal, Lake Mills and Lake Aldwell held an estimated 23 ± 6 Mt and 7 ± 2 Mt of impounded sediment, respectively (Warrick et al., 2015).

River corridors downstream of the former dams included a ~10-km "middle segment" between the dams and a ~7.9-km "lower segment" downstream of the Elwha Dam site (Figure 1). Prior to dam removal, geomorphic surfaces along these river segments were composed of a mixture of developing and mature floodplains and terraces and infrequent gravel bars (Shafroth et al., 2016). Riparian forests were composed of a mixture of deciduous and coniferous trees, most commonly *A. rubra*, *A. macrophyllum*, and *P. menziesii* on the middle segment and *A. rubra* and *P. balsamifera* spp. *trichocarpa* on the lower segment (Shafroth et al., 2016). To evaluate effects of the dams, some pre-dam-removal studies compared vegetation responses in the middle and lower segments to a reference segment upstream of Lake Mills ("upper segment"; Figure 1). Low sediment supply while the dams were in place resulted in channel narrowing, incision, armoring, and channel bed coarsening downstream of the dams, particularly along the middle segment and upper portions of the lower segment, where there were fewer remaining sources of fine, unconsolidated sediment in channel margins and floodplains (Pohl, 2004; Draut et al., 2011). Reduced channel mobility and fluvial disturbance in turn resulted in older forest stand ages, reduced pioneer tree seedling establishment, and reduced native plant diversity downstream of the dams compared to upstream, particularly along the middle segment (Shafroth et al., 2016; Brown et al., 2022).

The river delta and estuary (Figure 1) are constrained by a levee on the west side constructed in 1964 and a second levee set back from the main channel on the east side, constructed in 1985 (Warrick et al., 2009). Both levees were raised approximately 1 m in 2010–2011 in preparation for dam removal, anticipating that bed aggradation due to the dam-removal sediment pulse could raise the water-surface elevations. The location of the main channel in the delta has changed repeatedly over time, resulting in dynamic coastal lakes along the shoreline created by abandoned channels. In particular, the predominant eastern channel was blocked by dike construction in 1950 and the western channel was redirected by levee construction in 1964. After levee construction, the channel still meandered considerably (Warrick et al., 2011), for example with lateral channel migration of several meters per year in the years immediately prior to dam removal (Draut et al., 2011). Channel movement in the lowermost river and delta, fed by sediment from eroding channel-margin bluffs and floodplains along the lower segment (Draut et al., 2011), maintained a mosaic of plant community types and stand ages, including younger riparian shrub-dominated communities and willow-alder forest, older mixed riparian forest, dunegrass communities at the tops of the beach fronts, and estuarine marsh vegetation at the margins of the coastal lakes (Shafroth et al., 2011). However, low sediment supply resulted in substantial and accelerating erosion east of the river mouth during the lifetime of the dams, with mean annual shoreline erosion of 0.9 ± 0.2 m per year from 1939 to 1990 and 1.2 ± 0.2 m per year from 1990 to 2006, resulting in loss of >8.7 ha of delta land surface between 1939 and 2006 (Warrick et al., 2009).

3 Former reservoirs

3.1 Expected effects of dam removal on vegetation in the former reservoirs

The draining of the two former reservoirs was certain to expose large areas of sediment where plants could become established and grow (Figure 2A). Several variables were expected to influence the details of natural, unmanaged vegetation succession and dynamics, including reservoir drawdown timing, distance from seed sources and seed banks, landform characteristics, and sediment texture (fine versus coarse) (Chenoweth et al., 2023). In addition, active management in the former reservoirs was aimed at promoting native vegetation colonization and growth (Chenoweth et al., 2023).

3.2 Sediment and landform dynamics in the former reservoirs

The exposed former reservoir areas provided extensive bare surfaces for vegetation establishment on three general landform types: (1) valley walls; (2) terraces (of variable elevation); and (3) dynamic floodplains and channels (Figure 3). The three landform types varied with respect to stability, slope, sediment texture, and elevation above the channel. Fine-textured sediments were predominant on the steep valley walls. Terraces of variable thickness and elevation above the channel formed as a result of sediment erosion, redistribution, and progradation within the former reservoirs during dam removal, and were modified by erosion and redeposition at lower elevations as the river responded to dam removal (Randle et al., 2015). These processes resulted in relatively flat, perched terraces, 6-18 m thick, topped with predominantly coarse sediments farther from the reservoir margins. Many of the terraces eroded away during high flow events in the first few years after dam removal (Ritchie et al., 2018). Finally, the lowest positions in the valley included dynamic braided channels and floodplains characterized by coarse sediments and extensive lateral mobility (Randle et al., 2015; Chenoweth et al., 2022).

3.3 Vegetation management in the former reservoirs

Four types of active management were implemented to influence revegetation in the former reservoirs (Chenoweth et al., 2011): 1) invasive vegetation control; 2) seeding of desirable plant species; 3) planting of containerized or bare root plants of desirable species; and 4) placement of large wood (hereafter, LW; e.g., tree boles, and boles with root wads) to create microclimatic complexity and protection from wind and herbivory for new plants.

Invasive vegetation control, which consisted of both chemical control and manual removal, started before dam removal in an effort to reduce seed sources of various species of concern (Woodward et al., 2011). Invasive vegetation control continued within the former reservoirs as sediments were gradually exposed, informed by annual invasive vegetation mapping efforts (Chenoweth et al., 2023). Planting of containerized plants began in November 2011 and seeding began in Fall 2012, except for a small seeding trial that occurred in Spring 2012 in the former Lake Aldwell (Baker, 2013).

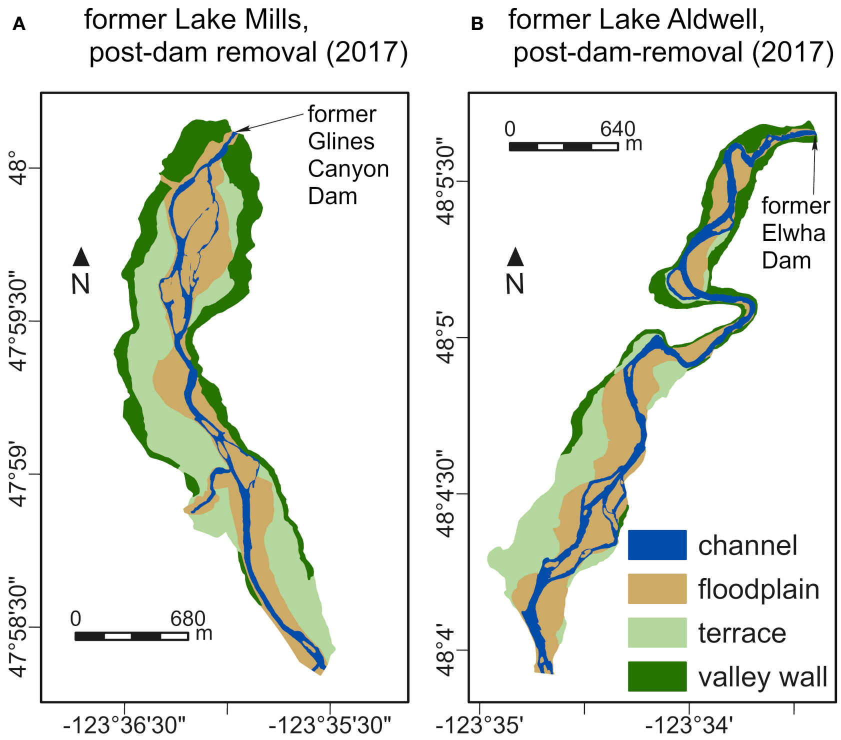


FIGURE 3
Cover by different landforms following dam removal in the former **(A)** Lake Mills and **(B)** Lake Aldwell along the Elwha River. Removal of Glines Canyon Dam was completed in 2014, and the Elwha Dam removal was completed in 2012. High valley wall surfaces were formed by initial, gradual drawdowns of the reservoirs. Terraces, varying in elevation, were formed by sediment erosion, redistribution, and progradation during dam removal. Low floodplain surfaces remained dynamic, with substantial, ongoing channel migration and sediment erosion, redistribution, and progradation. Polygons were drawn roughly from National Agriculture Imagery Program (NAIP) imagery taken on August 22, 2017. See Figure 1 for locations of the former reservoirs along the Elwha River.

In the former Lake Mills, 218,116 plants were installed, and 2,193 kg of seed were sown on 14.1 ha of the valley wall and 44.0 ha of terraces. Remaining areas were left to naturally revegetate, including 25.6 ha of valley wall landforms and 18.7 ha of terraces. In the former Lake Aldwell, 86,064 rooted plants were installed, and 716 kg of seed were sown on 16.7 ha, leaving 103.7 ha to revegetate naturally. Species composition and planting density varied by site and by year. Most of the plantings were trees and shrubs representing 60 native species (Chenoweth et al., 2022). The seed mixes varied but were composed primarily of nine native species (Chenoweth et al., 2022).

The Lower Elwha Klallam Tribe [Lower Elwha Tribe] and the Olympic National Park in 2012 and 2014 translocated 835 logs (log boles and logs with attached root-wads) by helicopter into the former Lake Mills onto the coarse-textured terraces formed during dam removal. The logs were arranged in single, parallel, and overlapping configurations (Chenoweth et al., 2023). Roughly two-thirds of the translocation area was planted and seeded.

3.4 Vegetation responses in the former reservoirs

Natural revegetation (i.e., passive revegetation) in the former reservoirs was studied during and 3-5 years after dam removal in plots along a series of transects on the three general landform types (valley walls, terraces, floodplains/channels) through areas that were not planted or seeded (Schuster, 2015; Morgan, 2018), and in "control" (untreated) plots along a separate series of transects through areas that had been planted and seeded (Prach et al., 2019; Chenoweth et al., 2022). Effects of planting and seeding (i.e., active revegetation) were examined in plots along the latter series of transects, in comparison to the "control" plots (Morgan, 2018; Prach et al., 2019; Chenoweth et al., 2022). Some studies differed with respect to plot sizes, years sampled, response variables, and other details, making comparisons among studies challenging in some cases (Chenoweth et al., 2023).

Within the unplanted portions of the former reservoirs, natural revegetation depended on sediment texture, landform, and the timing of landform development during reservoir drawdown (Figure 2A). The rate of natural revegetation was fastest on areas with fine sediment, such as valley walls and portions of terraces in the former Lake Aldwell, which tended to have finer sediment than the former Lake Mills because coarser sediments were preferentially trapped upstream in Lake Mills (Randle et al., 2015; Schuster, 2015; Morgan, 2018). On valley walls and terraces with fine sediment in Lake Aldwell, initial stands of *Juncus* spp. (rushes), *Carex* spp. (sedges) and *Equisetum* spp. (horsetails), likely germinated from *in situ* seed banks (Brown and Chenoweth, 2008), rapidly gave way to dense stands of *Alnus rubra* (red alder) interspersed with *Populus balsamifera* ssp. *trichocarpa* (black cottonwood) and *Salix sitchensis* (Sitka willow), which persist today and are self-thinning. On terraces with coarse sediment, natural revegetation was slow and, in some locations, still had relatively low plant cover six years after dam removal. However, one terrace landform in former Lake Mills, which formed in spring during initial dam removal, supported abundant black cottonwood and Sitka willow seedling establishment (Chenoweth et al., 2022). This establishment occurred during a drawdown hold period in May/June 2012 (Bountry et al., 2015), providing ideal conditions for the seedlings. However, when the drawdown resumed, the terrace quickly became perched, eventually ~18 meters above the final channel elevation. The tree seedlings eventually grew into woodlands with no cottonwood mortality observed in long-term monitoring plots established by the National Park Service (Chenoweth et al., 2022). On all terraces, bands of willow and cottonwood also formed in moisture-holding channels stemming from the valley wall. Open terrace areas not formed during the cottonwood and willow seed dispersal period (May-June) that were not seeded or planted continued to have low vegetation cover (Chenoweth et al., 2022) with sparse, drought-tolerant vegetation, including non-native annual grasses (e.g., *Vulpia myuros* (rat-tail fescue), *Aira caryophyllea* (silver hairgrass)), and biological soil crust (mostly bryophytes). Where larger plants and LW provided protection (Figure 2A), vegetation was denser (Cendejas-Zarelli, 2021). By 2016, an average of 13 native species had established per 100 m^2 on exposed new terraces in Lake Aldwell and Lake Mills (Figure 4). In the zone with dynamic channels and floodplains, bands of willow and cottonwood gradually established on stable gravel bar landforms, with herbaceous pioneer vegetation on less stable surfaces (Schuster, 2015; Morgan, 2018). Due to ongoing channel and floodplain dynamics, vegetation cover remained relatively low in these low-elevation parts of the former reservoirs.

Within the planted portions of the former reservoirs, effects of planting and seeding also varied with sediment texture and landform (Figure 2A), as well as among studies. In fine sediment sites, seeding reduced non-native frequency (Chenoweth et al., 2022) but not non-native cover (Morgan, 2018; Prach et al., 2019). Seeding also did not affect overall vegetation cover in fine sediment sites (Chenoweth et al., 2022). Planting trees and shrubs on fine sediments increased species richness in some studies (Chenoweth et al., 2022), but this effect was not detected in other studies (Morgan, 2018). Seeding and planting had the greatest effect on revegetation on the coarse-textured terraces (Cendejas-Zarelli, 2021; Chenoweth et al., 2022). Seeding increased vegetation cover relative to unseeded sites from 2012 to 2016 and affected species composition (Chenoweth et al., 2022). The most influential species seeded was *Lupinus rivularis* (riverbank lupine) (Morgan, 2018; Kardouni, 2020; Chenoweth et al., 2022). Planting trees and shrubs on coarse terraces affected species composition but did not significantly increase stem densities (Chenoweth et al., 2022), likely due to the low survival rate of plantings installed 2+ years after dam removal (Chenoweth et al., 2023).

Efforts to control invasive exotic vegetation focused on the more common non-native species of the region, such as *Phalaris arundinacea* (reed canary grass) and *Cytisus scoparius* (scotch broom) and were largely successful in that these species did not come to dominate the former reservoirs (Chenoweth et al., 2022). However, these control efforts were undertaken independently from vegetation monitoring and were not integrated into the monitoring

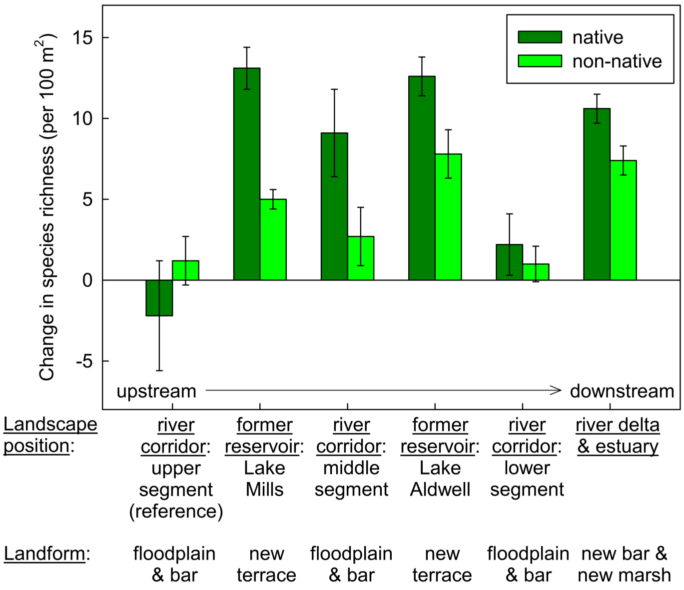


FIGURE 4
Change in mean native and non-native plant species richness in 100-m^2 plots between 2010 (before dam removal) and 2016-2018 (several years after the two dams were removed) at different landscape positions along the Elwha River. For river corridors, species richness was measured in 2017 on floodplains and gravel bars upstream of both former dams (upper segment) as a reference condition, between the two former dams (middle segment), and downstream of the former lower dam (lower segment) (Brown et al., 2022). For former reservoirs, species richness was measured in 2016 on terraces that formed during reservoir drawdown (Morgan, 2018). For the river delta and estuary, species richness was measured in 2018 on new river bars, river mouth bars, and intertidal aquatic marsh that formed from sediment eroded from the former reservoirs (Perry et al., 2023). Native species richness increased significantly between 2010 and 2017 on the middle river segment only (Brown et al., 2022). For the former reservoirs and delta, we treated mean species richness prior to dam removal as equal to zero, because these surfaces did not exist prior to dam removal, and, therefore, statistical analyses of temporal change were not possible. Error bars are one standard error of the mean. For consistency, we limited this figure to Elwha River studies that examined native and non-native species richness in 100-m^2 plots in 2016 or later.

plots in any consistent way. Their method of application by different field crews in different years and minimal documentation makes it a challenge to draw definitive conclusions about their effects on native vegetation trajectories. Initially, Lake Aldwell had more non-native species than Lake Mills, possibly due to (1) the higher levels of human development near the reservoir (Woodward et al., 2011) and (2) its relatively fine sediment, which promoted rapid colonization (Schuster, 2015). By 2017, this difference had largely disappeared due to non-native species establishment on the coarse sediments of Lake Mills (Morgan, 2018), such as the non-native annual grasses described above. Non-native species did not dominate vegetation on either of the former reservoirs.

Installations of LW were used in the former reservoirs to enhance revegetation efforts by creating favorable microclimates (i.e., "safe sites") for seedlings through shading and protection from wind and erosion (Figure 2A; Chenoweth et al., 2011; Calimpong, 2014). In Lake Mills, LW was associated with reductions in wind speed, soil temperature and evaporative stress (Colton, 2018), all of which can inhibit germination and contribute to plant mortality (MaChado and Paulsen, 2001; Wahid et al., 2007). Clusters of LW also likely enhanced seedling growth by impeding browsing by large ungulates (Johnson et al., 2023). At planting sites in Lake Mills, the presence of LW was associated with increased survivorship through the first growing season after planting (Calimpong, 2014). Plant diversity and species composition were also affected by LW. In Lake Mills, LW trapped wind-blown seeds, particularly of grasses and forbs, resulting in greater overall species richness but also increased representation of non-native species (Cendejas-Zarelli, 2021). In the Cendejas-Zarelli (2021) study, interaction effects were observed for LW and seeding treatments, as LW-associated increases in non-native species were most prevalent in unseeded areas, and the greatest increases in species richness were observed where seeding was paired with LW. In Lake Mills, LW also attracted avian seed dispersers, resulting in greater local abundance of native woody plants (McLaughlin, 2013; Cendejas-Zarelli, 2021).

4 River segments downstream of dams

4.1 Expected effects of dam removal on vegetation downstream of dams

River segments downstream of the dams were expected to become more dynamic in response to dam removal due to the effects of transport and deposition of large quantities of reservoir sediment and LW, and potential bed elevation changes (aggradation) as an expected sediment pulse moved downstream (Figure 2B). These processes were expected to promote channel widening, new bar formation, and sediment deposition, particularly fine sediment, on floodplains (Draut et al., 2011). Increased abundance of gravel bars, which experience frequent flood disturbance, was expected to support more pioneer riparian vegetation (Shafroth et al., 2002) and thus a younger overall forest community age structure (Shafroth et al., 2016). Where sediment deposition was significant, existing plants that were less well adapted to sediment burial were expected to be stressed or killed (Shafroth et al., 2002). Water transport of seeds (hydrochory) was expected to increase with dam removal (Figure 2B; Brown and Chenoweth, 2008), and along with gravel bar formation, was expected to increase downstream plant diversity (Clausen, 2012). Occasional, targeted invasive vegetation control and small-scale vegetation plantings occurred in the lower river segment, but effects could not be quantified (Brown et al., 2022).

4.2 Sediment and landform dynamics downstream of dams

Channel dynamics (largely associated with high sediment loads) during and after dam removal increased the abundance of young landforms downstream along the river, especially in the middle segment. An estimated 0.38 Mt and 0.98 Mt of sediment were deposited in the mainstem channel in the middle and lower segments, respectively, during the first five years of dam removal (2012-2016) (Ritchie et al., 2018). Widespread mainstem bed aggradation of 1-2 m and subsequent channel avulsion resulted in substantially increased channel width and braiding in the second year of dam removal (East et al., 2015). These processes, together with increased LW deposits (logjams, Leung, 2019), resulted in extensive, new bars along the mainstem channel (Figure 5) (East

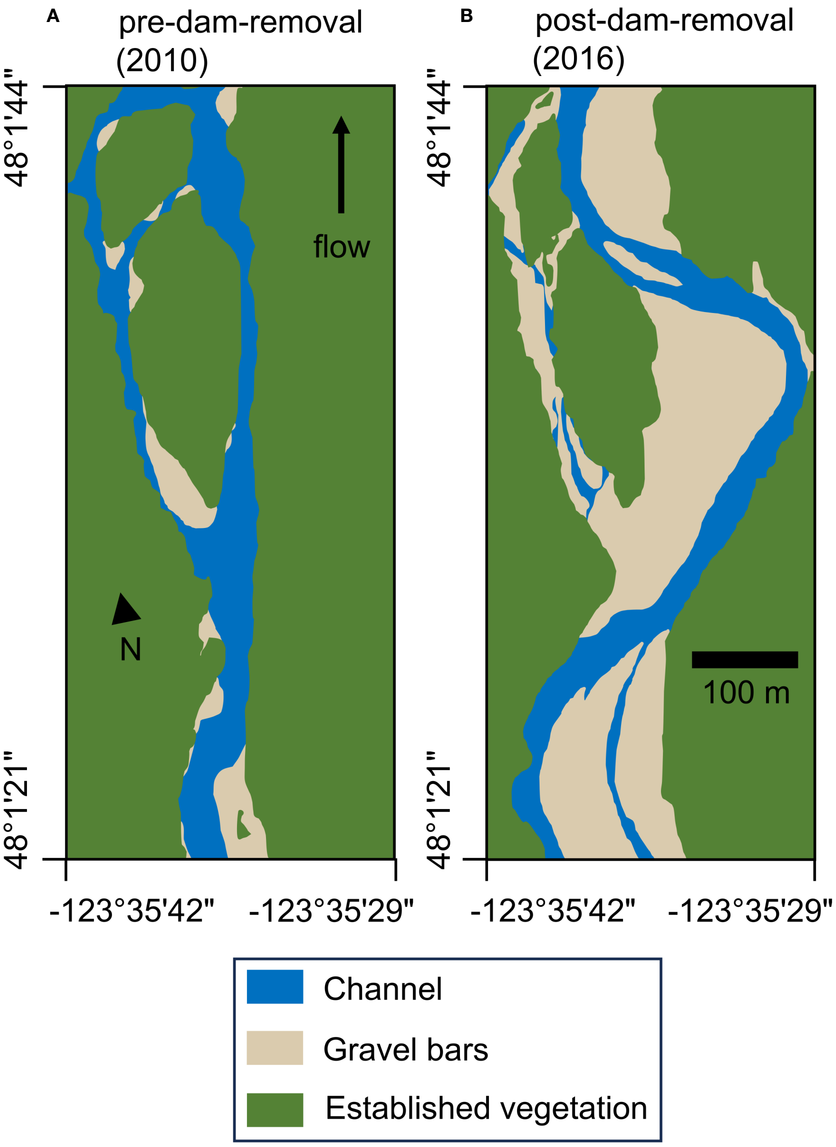


FIGURE 5
Change in cover by the channel, gravel bars, and established vegetation along an approximately 0.75-km reach of the middle segment of the Elwha River **(A)** before dam removal (2010) versus **(B)** after dam removal (2016). Polygons were drawn from imagery published in Ritchie et al. (2018). See Figure 1 for location of the middle segment of the Elwha River.

et al., 2015; Warrick et al., 2015). The initial downstream deposition included substantial fine (silt and clay) material (Draut and Ritchie, 2015) and most sediment deposited during the peak of the sediment pulse was sand and gravel, resulting in finer-textured channel beds and gravel bars compared to the armored, cobble surfaces that predominated prior to dam removal (East et al., 2015). The fine-textured, aggraded channels became incised, and some were abandoned between 2013 and 2017. On the lower river segment, channel width and braiding quickly returned to that of the dammed condition (East et al., 2018). However, on the middle segment, channel width and braiding remained higher relative to the dammed condition at least through 2017, probably because sediment was most limited along this segment when the dams were in place (Figure 5) (East et al., 2018).

In addition to the mainstem channel, established landforms along the river corridor also received substantial sediment deposition during dam removal. An estimated 0.24 Mt and 0.54 Mt of sediment were deposited on the floodplain on the middle and lower segments, respectively, during the first five years during and after dam removal (Ritchie et al., 2018). Mainstem bed aggradation redirected streamflow to floodplain side-channels even during low and moderate discharge, depositing a mean of 50 ± 38 cm of mainly fine sediment in floodplain channels, particularly along the middle segment, in the first two years of dam removal (East et al., 2015). Correspondingly, between 2010 and 2017, vegetation plots aggraded by 24 ± 8, 21 ± 16, and 17 ± 33 cm on bars, floodplains and terraces, respectively, on the middle segment, and by 61 ± 38, 35 ± 27, and 26 ± 42 cm on bars, floodplains and terraces, respectively, on the lower segment (Brown et al., 2022). Ten plots, mainly on the lower segment, aggraded by >50 cm.

4.3 Vegetation responses downstream of dams

Vegetation responses to post-dam-removal landform dynamics and sediment deposition along river corridors downstream from the dams were examined using field plot sampling on terraces, floodplains, gravel bars, and abandoned secondary channels. The plots were arranged along fifteen transects that spanned the river valley within the upper, middle and lower segments (Shafroth et al., 2016; Brown et al., 2022). These transects were repeatedly sampled before (2005, 2010) and after (2013, 2014, 2016, 2017) dam removal.

Native species richness on the middle segment increased by 31% during and after dam removal (2013-2017), as expected, partially mitigating what had been substantially lower species richness downstream of the dams compared to upstream prior to dam removal (Figure 4; Brown et al., 2022). By contrast, native plant diversity did not increase significantly on the lower segment during and after dam removal (Figure 4). Plant species composition on both the middle and lower segments also changed significantly on floodplains and bars during and after dam removal, but not on terraces (Brown et al., 2022). Herbaceous species changed the most in terms of both which species were most abundant, and which were significant indicator species for floodplains and bars (based on frequency and abundance), with fewer changes in shrubs and trees. Non-native species richness along the middle and lower segments did not significantly change following dam removal (Figure 4), while non-native species cover increased to a similar extent both upstream and downstream of the former dams (Brown et al., 2022).

Plant establishment on new gravel bars and fresh sediment deposits created during dam removal likely influenced changes in species richness and composition along the downstream river corridor (Figure 2B). New bars, varying spatially in elevation, flood disturbance, sediment texture, and overstory shade, can provide an array of niches and microsites suitable for establishment of different plant species. Likewise, fine sediment deposits on extant gravel bars and floodplains increase spatial variation in environmental conditions suitable for different plant species. These disturbed conditions are particularly suitable for establishment of early-successional plant communities, which were notably rare downstream of the dams compared to upstream prior to dam removal (Shafroth et al., 2016).

Changes in species richness and composition may also have been influenced by increases in hydrochorous seed dispersal (Figure 2B). Dams form a barrier to downstream seed transport, affecting downstream plant species occurrence and abundance (Nilsson et al., 2010). Prior to dam removal on the Elwha River, Glines Canyon Dam reduced species richness and abundance of floating and submerged seeds in the middle river segment by >80% compared to upstream of the dams (Brown and Chenoweth, 2008). After dam removal, seed abundance and richness in the middle segment increased by ~30x and ~6x, respectively, leading to higher seed abundance and richness downstream of the former dam than upstream (Cubley and Brown, 2016). This substantial hydrochory may have been supplied by a combination of seed produced by established upstream plant communities, seed produced by nascent plant communities in the former Lake Mills, and mobilization of seeds stored in former reservoir sediment.

Finally, some changes in plant community composition along the downstream river corridor may have been driven by negative effects of sediment burial on established plants (Figure 2B). On the lower river segment, native species richness was negatively associated with greater sediment deposition on terraces and bars, suggesting that high rates of sediment deposition on this segment may have reduced the frequency of some species (Brown et al., 2022). For example, sediment deposition on some lower segment terraces led to die-back of dense *Polystichum munitum* (western sword fern) stands and replacement by early-successional species. Negative effects of sediment deposition on some plants may have counterbalanced positive effects of sediment deposition on others better adapted to riparian sediment dynamics, perhaps explaining in part the lack of change in overall native species richness on the lower segment following dam removal (Brown et al., 2022).

5 Delta and estuary

5.1 Expected effects of dam removal on vegetation in the delta and estuary

Much of the sediment and LW stored behind the two dams was expected to be deposited in the river delta and nearshore (Czuba et al., 2011; Warrick et al., 2011), creating landforms that could be colonized by plants (Figure 2C). Where sediment deposition was significant, existing plants that were less well adapted to sediment burial were expected to be stressed or killed (Shafroth et al., 2002). Based on studies of sediment deposition in Pacific Northwest tidal wetlands, rapid sediment deposition in the delta had the potential to cause rapid vegetation change (Shafroth et al., 2011). Occasional, targeted invasive vegetation control and small-scale vegetation plantings occurred in the delta but effects could not be quantified (Perry et al., 2023).

5.2 Sediment and landform dynamics in the delta and estuary

Dam removal created abundant new surfaces suitable for riparian and wetland vegetation in the delta and estuary (Figure 6). Approximately 5.4 Mt of sediment were deposited in the delta and estuary in the first five years of dam removal (2012-2016) (Ritchie et al., 2018), forming new intertidal and supratidal river bars, river mouth bars, and beaches, as well as new intertidal aquatic habitats (Foley et al., 2017b; Perry et al., 2023). The total area of intertidal and supratidal surfaces increased by ~31.3 ha during this period, mainly seaward of the former shoreline, expanding the 97.5 ha pre-dam-removal sampling area for the delta and estuary by >30% (Perry et al., 2023). However, between 2016 and 2018, this trend reversed and the total area of intertidal and supratidal surfaces in the delta decreased by ~4.5 ha (Perry et al., 2023), as sediments at the river mouth were eroded and deposited further east along the shoreline (Warrick et al., 2019).

Surfaces in the delta and estuary that already existed prior to dam removal also received former reservoir sediments during and after dam removal. During the first five years of dam removal, an estimated 0.02 Mt of sediment were deposited within the pre-dam-removal delta and estuary, and what had been estuary area before dam removal was considered part of the lower river after 2012, as the new estuary developed 500 m farther seaward (Ritchie et al., 2018). Correspondingly, surface elevations in established emergent marsh, dunegrass, and riparian shrub communities in the delta and estuary increased by 31 ± 20 cm (range=2-67 cm) between 2007 and 2018 (Perry et al., 2023).

5.3 Vegetation responses in the delta and estuary

Vegetation responses to sediment deposition and landform dynamics in the delta and estuary were examined using (1) time series of aerial imagery to assess vegetation establishment on new surfaces and changes in cover of different vegetation types on older surfaces and (2) time series of field plot sampling to assess developing plant community composition on new surfaces and changes in community composition on older surfaces (Shafroth et al., 2011; Foley et al., 2017b; Perry et al., 2023).

By 2018, vegetation had established on 16.4 ha that had been unvegetated prior to dam removal, on both new surfaces in the delta and estuary and extant surfaces that aggraded, stabilized, and/or

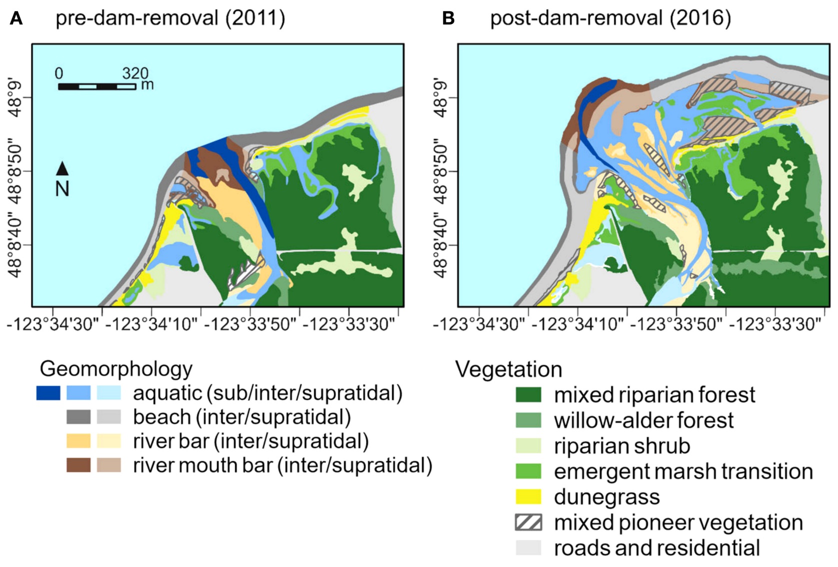


FIGURE 6
Change in vegetation and geomorphic surface cover in the Elwha River delta and estuary **(A)** before dam removal (2011) versus **(B)** after dam removal (2016). Geomorphic surfaces were separated into subtidal, intertidal, and supratidal areas based on elevations of mean lower low water and mean higher high water. New surfaces that formed in the delta and estuary following dam removal were colonized by mixed pioneer and emergent marsh vegetation. Polygons were drawn from aerial imagery; the figure is a modified version of a figure in Perry et al. (2023).

became protected from wave action during dam removal (Figure 2C; Perry et al., 2023). Surfaces that supported new vegetation tended to have been relatively stable in elevation for at least three years prior to vegetation establishment and were higher in elevation and farther from the new shoreline than unvegetated new surfaces. On-going channel migration and sediment reworking between 2013 and 2018 led to destruction and/or turnover of establishing vegetation on some new surfaces, especially during winter storms (Figure 2C). In particular, between 2016 and 2018, ~1.6 ha of new-surface vegetation reverted to unvegetated surfaces, as coastal erosion and sediment redistribution moved the outermost new river mouth bars and beaches inland towards the former shoreline. These trends of net shoreline erosion and loss of new vegetation have continued through 2022 (P. Shafroth, personal observation).

Vegetation development on stable new surfaces in the delta and estuary followed early-successional trajectories, with mixed pioneer vegetation (i.e., vegetation too young and undeveloped to be defined as a particular established community type on aerial imagery) on new supratidal beaches, river bars, and river mouth bars, and early-successional emergent marsh vegetation (i.e., communities dominated by obligate wetland species but with lower perennial, graminoid, and native plant cover and higher annual/biennial cover than well-established emergent marsh) in new intertidal aquatic habitats (Perry et al., 2023). Compositional differences between vegetation on new surfaces and well-established community types in the delta and estuary decreased over time following surface stabilization, as plant cover and species richness on new surfaces increased for graminoids, herbaceous forbs, perennials, annual/biennials, native species, and non-native species. By 2018, an average of 11 ± 1 native species had established per 100 m^2 on vegetated new surfaces (Figure 4). Further, nearly one hectare that initially established as mixed pioneer vegetation had matured into dunegrass communities and willow-alder forest discernible on aerial imagery, suggesting that given time, vegetation on persistent new surfaces will mature into typical, later-successional delta and estuarine community types.

By contrast, sediment deposition within plant communities that were already established in the delta and estuary prior to dam removal had few discernible effects on vegetation abundance or composition (Foley et al., 2017b; Perry et al., 2023). Contrary to expectations, negative effects of sediment deposition on plant survival and cover were not apparent. Most temporal changes in established community composition during and after dam removal likely reflected natural successional processes, including increases in woody cover, decreases in non-native species richness, increases in wetland adaptation (community-weighted mean wetland indicator value) in emergent marshes, and development of riparian shrub communities into willow-alder forest (Perry et al., 2023). However, decreases in *Leymus mollis* (American dunegrass) and increases in shrub cover in dunegrass communities east of the river mouth were not typical of natural dunegrass succession and may have been related to dam removal. The extensive new surfaces that formed seaward of the dunes in this portion of the delta shielded these dunegrass communities from wave action and salt spray to which they are adapted. This, perhaps together with changes in soil chemistry or texture caused by deposition of former reservoir sediments (Figure 2C), may have facilitated shrub establishment, growth, and competitive ability, altering community composition on the former dunes (Perry et al., 2023). Shrub cover continued to increase in these former dunegrass communities from 2018 to 2022 (L. Perry, personal observation).

Bare ground on new surfaces and on sediment deposits in established communities may have facilitated invasion by short-lived, disturbance-adapted non-native species in the delta and estuary. During and after dam removal (2014, 2018), 34 non-native species were observed in the delta and estuary vegetation plots that were not observed prior to dam removal (2007) (Perry et al., 2023). The majority were annual/biennial grasses and forbs. Over half of these species also occurred upstream along the Elwha River, suggesting that their propagules may have reached the delta via hydrochory following dam removal (Figure 2C; Brown et al., 2022; Perry et al., 2023). While one third of these new species were observed only in plots on new surfaces, the other two thirds invaded established community types, most often dunegrass communities, in addition to or instead of new surfaces. However, neither the proportion of total species richness in the delta that was composed of non-native species nor the number of non-native species per plot increased following dam removal, suggesting that local extinction of other non-native species was sufficient to counterbalance the increase in non-native annual/biennials.

6 Discussion

Our review of vegetation changes associated with dam removals on the Elwha River – the world's largest dam removal to date – was based on >35 publications covering vegetation responses in different landscape positions along the river and various before/after-control/impact studies, with and without active management (Table 1). Knowledge of vegetation dynamics is important not only for understanding plant communities, but also for better understanding other riverine ecosystem responses given the strong connections between vegetation, physical processes, aquatic and terrestrial habitats, and biota (Figure 2; Bellmore et al., 2019). Our review and synthesis provide new insights regarding the connections between fluvial geomorphic processes and vegetation responses and the effects of active management (e.g., weed control, vegetation planting), with implications and lessons that can help to inform dam removal monitoring efforts world-wide.

6.1 Connections between sediment, river morphodynamics, and vegetation following dam removal

In the case of the Elwha River dam removals, vegetation changes were primarily driven by processes related to the exposure, erosion, transport, and deposition of the large volume of sediment that had accumulated in the two reservoirs for nearly a century. These sediment-related processes connected the vegetation responses longitudinally (up- to downstream) in three different landscape contexts along the river: the former reservoirs, the river corridor, and the delta and estuary (Figure 2). In all three landscape positions, many plant species established on fresh sediment deposits (Figure 4), expanding vegetated habitat on new surfaces in the former reservoirs (Figure 3) and the river delta and estuary (Figure 6), and increasing species richness on floodplains and gravel bars along the river corridor between the two former dams (Figure 4). Sediment and landform dynamics during and after dam removal and throughout the affected parts of the Elwha River system underpinned the vegetation responses.

The connections between sediment dynamics and vegetation responses in multiple parts of a river system have not been reported in other dam-removal studies, though they are not surprising given the myriad relationships and feedbacks that commonly characterize fluvial geomorphic processes and riparian vegetation (Hupp and Osterkamp, 1996; Gurnell et al., 2016; Merritt, 2022). The large dam sizes and large volume of sediment released on the Elwha River (the most of any dam removal worldwide) led to the strong, system-wide signal. Virtually all other published studies of vegetation responses to dam removal have been associated with small dam removals and restricted to former reservoirs (e.g., Orr and Stanley, 2006). Geomorphic change downstream of small dam-removal sites, or large dam removals where the sediment release is deliberately limited, is typically minimal (Collins et al., 2020; Cashman et al., 2021; East et al., 2023), which translates to minor vegetation change. Also, riparian vegetation responses to dam removal have been studied much less than physical environmental variables or other biota such as fish or aquatic macroinvertebrates (Bellmore et al., 2017).

In natural riparian ecosystems, flood disturbance and fluvial dynamics drive spatiotemporal patterns, which have been described as a “shifting habitat mosaic” or “dynamic patch mosaic” (Stanford et al., 2005; Latterell et al., 2006). New patches of riparian vegetation are typically composed of pioneer species that establish on bare, moist sediments on landforms created by flood disturbance, such as gravel bars or low floodplains. Over time, landforms that support young stands of vegetation tend to aggrade, rendering them less vulnerable to destruction by future floods and providing conditions for vegetation to grow, further stabilize the landform, and facilitate establishment and growth of later-seral species (Naiman et al., 2010; Merritt, 2022). The character of the shifting habitat mosaic had been altered by the dams on the Elwha River (Shafroth et al., 2016).

The timeline of vegetation responses to dam removal on the Elwha River was closely related to the timeline of sediment and LW processes and dynamics (Ritchie et al., 2018; Leung, 2019). The pulse of sediment and LW caused the river corridor and delta downstream of the former reservoirs to be in a transport-limited state temporarily after dam removal began (particularly over the winter of 2012–2013), and then a sediment-supply-limited state beginning ~4-6 years after the start of dam removal (East et al., 2018). Surfaces on which vegetation can grow and persist need to be stable for months to years; thus, the transport-limited period when channels and near-channel landforms were unstable on the Elwha River (East et al., 2018) was characterized by conditions that were unfavorable for new vegetation establishment. During the ~6-month-long transport-limited period, significant geomorphic change occurred even in the absence of large peak flows. Rapid erosion and transport of reservoir sediment within the first three years following dam removal, often in the absence of high flows, has been documented in numerous cases (Wilcox et al., 2014; Foley et al., 2017a; Major et al., 2017), suggesting that the timeline on the Elwha River was not unique, although the sediment mass and response magnitude were larger than in any previous dam removal. LW transport and new logjam formation within the former reservoirs and in the two river segments and delta downstream likely interacted with sediment to promote the development of new fluvial surfaces where vegetation could establish near the main channel, in side channels, and in the delta (Figure 2; Fetherston et al., 1995; Abbe and Montgomery, 1996; Naiman et al., 2010; Leung, 2019).

Dam removal and the associated large disturbance event led to a large short-term increase in young fluvial surfaces that were colonized by pioneer vegetation, but in the longer term a return to more of a quasi-equilibrium, shifting habitat mosaic is expected. Over time on the new pioneer bars and former reservoir terraces and valley walls associated with dam removal, the importance of sediment-related processes should decrease relative to biological processes such as vegetation growth and plant community succession over decades to centuries (Latterell et al., 2006; Van Pelt et al., 2006). Conceptual models of ecological responses suggest that different potential trajectories could follow dam removal depending on variables such as the duration of downstream sediment effects, the abundance of non-native species, and whether other significant anthropogenic perturbations persist after dam removal (Bellmore et al., 2019).

6.2 Species composition considerations

The combination of new pioneer surfaces, sediment deposition and plant burial on extant surfaces, and expanded hydrochory was expected to influence vegetation community composition following dam removal along the Elwha River (Figure 2). For example, sediment burial was expected to reduce red alder survival and growth while new surfaces and sediment dynamics were expected to favor greater black cottonwood and willow establishment, potentially altering riparian forest composition and structure (Shafroth et al., 2002). Rather than declining, red alder increased in cover on bars and floodplains along the middle and lower river segments (Brown et al., 2022). Sediment burial had few large or lasting effects on downstream vegetation following dam removal (Brown et al., 2022; Perry et al., 2023), perhaps because typical burial depths (~15-60 cm; Brown et al., 2022; Perry et al., 2023) were insufficient to influence plants other than herbaceous species and woody seedlings (Lowe et al., 2010; Kui and Stella, 2016; Politti et al., 2018). As expected, however, cottonwood and willow established on new surfaces in the former reservoirs, on new gravel bars along the river corridor, and on new river mouth bars in the delta (Brown et al., Chenoweth et al., 2023; Perry et al., 2023). This was part of a broader trend of increased abundance of early-successional species from the former reservoirs downstream to the delta because of the increase in new, young landforms. Similarly, flushing of sediment from dams and associated deposition and bar development downstream promoted colonization of pioneer plants along the Kurobe River, Japan (Asaeda and Rashid, 2012).

The prevalence of disturbed pioneer habitat associated with dam removal has made potential invasion by non-native species a common management concern (Tullos et al., 2016). Along the Elwha River, pioneer surfaces created during and after dam removal were often invaded by non-native species, particularly weedy annuals (Schuster, 2015; Brown et al., 2022; Perry et al., 2023). However, early-successional native species were generally more abundant, and non-native species did not come to dominate pioneer vegetation in any of the three landscape positions, at least not within the first seven years during and after dam removal (Figure 4). Invasive vegetation control efforts in the former reservoirs may have reduced hydrochorous seed dispersal to downstream areas for at least some non-native species. The rapid, natural establishment of early-successional, native species also may have reduced opportunities for expansion of non-native species populations, emphasizing the benefits of local seed sources for disturbance-adapted native species in the context of dam removals (Figure 2).

In the longer term, vegetation dynamics and species composition might be influenced by the return of anadromous fish and corresponding deliveries of marine-derived nutrients (Figure 2). Nutrient subsidies from anadromous fish carcasses can affect riparian plant growth (Helfield and Naiman, 2001) and community composition (Mathewson et al., 2003; Bartz and Naiman, 2005; Wilkinson et al., 2005), with effects becoming evident within two decades (Quinn et al., 2018). In the years following the Elwha River dam removals, anadromous Pacific salmon (*Oncorhynchus* spp.) have returned to spawn above the former dams (Duda et al., 2021). Thus far there is limited evidence to suggest that riparian soils upstream of the former dams have been enriched with marine-derived nutrients (Kane et al., 2020), but marine-derived nutrients have been re-incorporated into freshwater and riparian food webs (Tonra et al., 2015). Returning salmon provide a seasonal food source for numerous mammal and bird species (Cederholm et al., 1989), many of which affect plant communities by disseminating marine-derived nutrients in their wastes (Ben-David et al., 1998; Hilderbrand et al., 1999; Helfield and Naiman, 2006). Animals that forage on salmon may also affect plant communities through zoochory. For example, salmon-supported bears (*Ursus* spp.) secondarily consume large quantities of fruit, and changes in salmon abundance may alter local bear distributions and patterns of seed dispersal (Harrer and Levi, 2018). Taken together with the observed effects of wildlife on revegetation in and around LW accumulations in the former reservoirs (Johnson et al., 2023), these findings illustrate the reciprocal roles that can be played by vegetation and wildlife in ecological restoration: wildlife benefit from restored habitats, and their activities in turn affect patterns of vegetation growth and restoration outcomes (McCaffery et al., 2018).

6.3 Managing vegetation in former reservoirs

The timing and duration of reservoir drawdown are important variables influencing vegetation trajectories in former reservoirs (Figure 2A; Shafroth et al., 2002). Slow reservoir drawdowns over several months are more likely to promote colonization by a variety of species (Chenoweth et al., 2023). On the Elwha River, timing the reservoir drawdown during *Salicaceae* (cottonwood and willow) seed dispersal led to rapid vegetation development on newly exposed landforms (Chenoweth et al., 2022). Given the ubiquity of cottonwood and willow taxa across the northern hemisphere and strong interest in restoring forests dominated by these genera (González et al., 2018), results from the Elwha River could help to inform management decisions in other dam removal contexts. The successful establishment of cottonwood despite the eventually deep water table and relatively rapid water decline was somewhat surprising, since these variables have been shown to limit cottonwood establishment in many other situations (Mahoney and Rood, 1998). However, Auble et al. (2007) also reported successful cottonwood establishment beyond these limits following a reservoir drawdown in Colorado. Relatively high annual precipitation along the Elwha River may have enabled survival of cottonwoods and willows even on landforms > 6 m above the alluvial water table.

Active management in the former reservoirs generally enhanced revegetation efforts. Inconsistencies in the results of seeding and planting may have been due to variations in conditions during plant establishment, such as those related to drawdown timing and moisture availability (Shafroth et al., 2002; Auble et al., 2007). Some inconsistency may also have been due to variations in monitoring methods, variation in sampling intensity on different landforms, differing years sampled, or discrepancies between planting and monitoring locations, such as in cases where plots established for monitoring planting success might have been only partially planted and included naturally-occurring vegetation (Chenoweth et al., 2023). Invasive vegetation control was largely effective, as evidenced by the fact that neither of the former reservoirs was dominated by non-native species, and these efforts were bolstered by other forms of active management, particularly seeding (Morgan, 2018; Cendejas-Zarelli, 2021). Similarly, seeding and planting efforts were bolstered by LW placement, as evidenced by the increased rates of survivorship observed in planting sites with LW installations (Calimpong, 2014; Johnson et al., 2023) and the increased species richness observed where seeding was paired with LW (Cendejas-Zarelli, 2021). Together, these findings point to the benefits of multiple forms of active management, undertaken in concert, for revegetating large areas exposed after dam removal.

The strong influence of sediment texture on natural revegetation in the former reservoirs (Schuster, 2015; Morgan, 2018; Prach et al., 2019; Chenoweth et al., 2022) suggests that considering sediment texture is important when planning active revegetation in former reservoirs following dam removal (Figure 2A). Seeding and planting efforts tended to be most effective and necessary on coarse sediments, where natural revegetation was more limited. The fact that fine sediment did not inhibit natural revegetation ran counter to pre-dam-removal predictions based on planting trials using dredged reservoir sediments in pots and raised beds (Chenoweth et al., 2011; Michel et al., 2011). This may have been due to artificial conditions that altered sediment characteristics or plant performance within the growing containers (Poorter et al., 2012; Kawaletz et al., 2014), suggesting that field experiments may be more useful for predicting revegetation success under different former reservoir conditions.

6.4 Monitoring vegetation responses to future dam removals

Studies of vegetation along the Elwha River before, during, and after two large dam removals captured many of the key responses and indicate methodological strengths and weaknesses that could provide insights when planning other dam-removal studies. Multiple factors led to a several year delay in the start of dam removals, which had the positive effect of providing more time and opportunity for pre-dam-removal data collection, including Before-After-Control-Impact study designs in some cases (e.g., East et al., 2018; Brown et al., 2022). These baseline data enabled more confident interpretations of dam-removal effects (e.g., Foley et al., 2017b; Brown et al., 2022; Perry et al., 2023); studies of future dam removals would benefit from similar pre-dam-removal data collection efforts. Some of the vegetation studies on the Elwha used similar sampling methodologies (e.g., Schuster, 2015; Morgan, 2018; Brown et al., 2022; Perry et al., 2023), which could facilitate future comparisons of vegetation in the different landscape positions along the river. In contrast, use of different methodologies complicated comparisons of multiple vegetation datasets in the former reservoirs (Chenoweth et al., 2023). We suggest that analysis of remotely sensed data (e.g., aerial imagery) to assess vegetation changes associated with dam removal along the Elwha River has been underutilized thus far (but see Perry et al., 2023). Assessments using unmanned aerial vehicles (UAVs; drones) could be particularly fruitful and have been used to assess changes in topography and vegetation in two small dam-removal case studies in New Hampshire, USA (Evans et al., 2022). Finally, given the close connections and interactions between fluvial geomorphic dynamics and vegetation dynamics on the Elwha, more interdisciplinary collaborations among physical and biological scientists could have strengthened the understanding and interpretations of vegetation responses. That said, monitoring on the Elwha River has been very successful largely due to effective collaborations within a diverse coalition of researchers and resource managers (Eitzel et al., 2023).

7 Conclusions

On the Elwha River, erosion, transport, and deposition of reservoir sediment were key drivers of vegetation responses to dam removal, from the former reservoirs to the river delta. Consistent with predictions made prior to dam removal, there was rapid revegetation of drained reservoirs; increased bar formation, hydrochory, and plant diversity in the river segment below Glines Canyon Dam; and colonization of new delta surfaces by emergent marsh and pioneer plant communities, an indication that dam removal has been effective thus far for restoring native plant communities. Comparing the dam-affected portions of the river with an upstream reference reach before and after dam removal led to the conclusion that the observed increases in species richness below Glines Canyon Dam were due to dam removal (Figure 4). However, plant species richness did not increase in the lower river segment (Figure 4), potentially due to burial-related mortality of some species and because this reach had more gravel bars and higher tributary sediment supply than the middle segment before dam removal. Non-native species did not come to dominate newly exposed or deposited landforms following dam removal on the Elwha River (Figure 4), another positive outcome. Active management (invasive vegetation control and planting and seeding) within the drained reservoirs may have reduced the abundance of target invasive species and may have limited downstream spread of invasive species onto newly formed river bar and delta surfaces. Plant communities may continue to change and diversify in the lower river segment as the river channel adjusts to a higher sediment supply post-dam removal. Our review covers the first 5-7 years after dam removal, but given the time required for forest succession, full understanding of recovery on the Elwha River will require long-term monitoring over decades.

As the frequency and scale of dam removal increases globally, detailed information about the ecological responses to past dam removals is needed to inform future research and management efforts. The differences in vegetation responses among river segments as well as among major landscape positions highlight the importance of understanding the unique setting of any dam removal. Factors such as reservoir sediment storage, the degree to which the dam altered the natural flow regime, constraints on channel migration, and surrounding land use can all affect vegetation dynamics. With most of its watershed contained within Olympic National Park, the Elwha River provided a unique opportunity to understand how vegetation responds to dam removal in a relatively natural, forested ecosystem. This allowed researchers to better isolate dam and dam-removal effects from other factors, such as urbanization, roadways, or agricultural development. Other systems may have more complex vegetation responses and higher risk of plant invasion after dam removal, such as the Klamath River, where large dam removal is currently underway. In contrast to the Elwha, the Klamath R. has a larger watershed that crosses several ecoregions with extensive agricultural development and grazing, as well as historic logging and mining (East and Grant, 2023). Going forward, it will be important to conduct multi-factorial studies to examine how dam removal interacts with other types of land use to anticipate and mitigate undesirable effects.

Author contributions

PS: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. LP: Writing – original draft, Writing – review & editing, Visualization, Project administration. JH: Writing – original draft, Writing – review & editing. JC: Writing – original draft. RB: Writing – review & editing, Visualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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A review of natural and managed revegetation responses in two de-watered reservoirs after large dam removals on the Elwha River, Washington, USA

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Large dam removals are increasing in frequency and the response of natural and managed revegetation is a critical consideration for managed restoration of dewatered reservoir landscapes post dam removal. The removal of two large dams on the Elwha River in 2011-2014 provides insight into reservoir revegetation. We review literature and datasets from 2012 through 2018, 1-6 years since reservoir dewatering, to compare pre-dam removal predictions on the Elwha to post-dam removal of natural revegetation, managed revegetation effects and invasive non-native vegetation response. Pre-dam removal hypotheses about natural revegetation did not predict species performance on reservoir sediments, seed rain patterns, or seed bank response. Sediment texture and landform affected multiple aspects of revegetation, including vegetation cover, species richness, woody stem densities and species composition. Reservoir drawdown timing influenced species composition and seedling densities. Predictions about managed revegetation effects were mixed. Planting trees and shrubs did not accelerate woody cover but did increase species richness. Seeding reduced non-native vegetation frequency and species richness, had no effect on vegetation cover on fine sediments, but increased vegetation cover on coarse sediments. Planting trees and shrubs during drawdown appeared to result in higher survival rates compared to plantings installed 1+ years post drawdown. Seeding *Lupinus rivularis* (riverbank lupine) on coarse sediments was successful and increased foliar nitrogen in planted conifers. Invasive non-native vegetation was correctly predicted to be more abundant in the Aldwell reservoir but did not preclude native species establishment in either reservoir, likely due to rapid establishment of native species and robust management that occurred before, during and after dam removal.

KEYWORDS

succession, invasive species, sediment texture, ecological restoration, riparian

1 Introduction

As more dams are being removed worldwide (O'Connor et al., 2015), more information is becoming available about the ecological consequences of dam removal and the outcomes of post-dam removal management strategies. Revegetation (natural or managed) of drained reservoirs is an important component of post-dam removal restoration, as the reservoir is often the part of the river most dramatically affected by dam emplacement and removal (Bellmore et al., 2019). Yet few data are available to describe vegetation responses in dewatered reservoirs, particularly following removal of large dams (O'Connor et al., 2015; Foley et al., 2017).

Revegetation of dewatered reservoirs is considered critical to successful restoration and is characterized by various biophysical interactions (Bellmore et al., 2019). Vegetation in former reservoirs provides habitat for upland and riparian fauna (Kelsey and West, 1998), and moderates erosion and stabilizes slopes (Riis et al., 2020), which is critical when lacustrine sediments are prevalent. Initial plant colonization after reservoir dewatering can be rapid, but it can take decades for mature forest vegetation to become sufficiently established to stabilize banks and terraces and fulfill other functions that enhance stream habitat (Shafroth et al., 2002; Orr and Stanley, 2006). Invasive plants represent a common management concern, as the initially bare, open nature of dewatered reservoirs makes them suitable for opportunistic pioneer species, many of which are non-native (Tullos et al., 2016). At some sites, non-native plants can colonize quickly and have an adverse effect on biodiversity and ecological condition (Orr and Stanley, 2006; Bellmore et al., 2019), but at many sites, natural (i.e., passive) revegetation results in a proportion of non-native species that is no greater than that found in typical riparian communities (Tullos et al., 2016). Diverse communities may develop (Ravot et al., 2020), but vegetation recovery might not result in a return to pre-dam conditions (Foley et al., 2017; Bellmore et al., 2019).

The objectives of this synthesis are to characterize revegetation trajectories in former reservoirs following the removal of two large dams on the Elwha River, and to consider how responses compare to hypotheses and predictions about revegetation generated prior to dam removal. Our synthesis is based on a review of literature and datasets. The main revegetation drivers were 1) biotic – the availability of species for colonization (e.g., distance from seed sources, seed banks, native species planting and seeding, invasive species), and 2) abiotic– the physical factors that affect plant growth (e.g., reservoir drawdown timing, sediment texture, geomorphic landforms, large woody debris placement). Finally, we discuss key lessons that may apply to other dam removal revegetation projects.

2 Study area and dam removal

The Elwha River drains 833 km^2 of forested mountain terrain, primarily in Olympic National Park in Washington state, USA (Figure 1; from Chenoweth et al., 2022). Two large dams were removed on the Elwha River between 2011 and 2014, exposing two former reservoirs. Elwha Dam, completed in 1912, was 33-m tall and impounded Aldwell Reservoir, which extended 4.8 km upstream from the dam (river km 7.9-12.7). Glines Canyon Dam, completed in 1927, was 64-m tall and impounded Lake Mills reservoir, which extended 3.8 km upstream from the dam (river km 21-24.8).

The upland vegetation surrounding the reservoirs are dense low-elevation coastal forests common in Western Washington, dominated by 100-300-year-old conifer species such as *Pseudotsuga menziesii* (Douglas-fir), *Abies grandis* (grand fir) and *Tsuga heterophylla* (western hemlock). Species characteristic of the understory are mid-to-late seral species such as *Polystichum munitum* (sword fern), *Gaultheria shallon* (salal), *Berberis nervosa* (dull Oregon-grape), *Linnaea borealis* (twinflower) and *Rubus spectabilis* (salmonberry). Common riparian vegetation that also was found in thin bands along the reservoir shorelines include *Alnus rubra* (red alder), *Acer macrophyllum* (bigleaf maple), *Populus balsamifera* ssp. *trichocarpa* (black cottonwood), and *Salix* species (Prach et al., 2019). Non-native, invasive species are present but are not common in the surrounding forest matrix (Woodward et al., 2011).

The two reservoirs contained an estimated 21 million m^3 of stored sediments at the start of dam removal (Randle et al., 2015; Warrick et al., 2015). In Lake Mills, where an estimated 16.1 million m^3 of sediment were stored, over half (56%) of the sediments were coarse-grained (sands, gravels, cobbles) and confined to the Lake Mills delta in the upper reservoir that was 24-27 m thick and 1.5 km long (Randle et al., 2015). Fine sediments comprised 44% of the total and were mainly composed of silt and clay with some fine sands (Mussman et al., 2008; Cavaliere and Homann, 2012). Fine sediments covered the valley bottom (2-14 m deep) and the valley

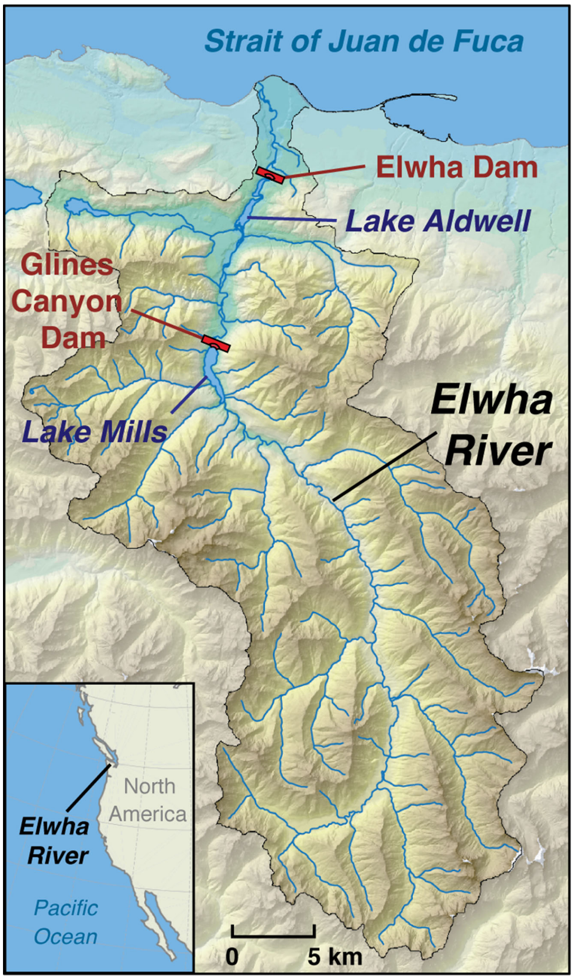

FIGURE 1
Map of the Elwha watershed, located west of Port Angeles, Washington, USA. The headwaters of the Elwha River reside 72 km within the Olympic Mountains where it flows south to north into the Strait of Juan de Fuca. Map illustrates the placement of the two former dams (in red); Elwha dam and Glines Canyon with former Lake Aldwell (river km 7.9-12.7) and Lake Mills (river km 21-24.8) labeled in purple.

walls (2 m deep). In Lake Aldwell an estimated 4.9 million m^3 of sediment were stored; 54% were fine-grained (silt and clay) and 46% were coarse (sands, gravel, cobbles; Randle et al., 2015). The Aldwell delta was estimated to be 6-8 m thick and 2.2 km long.

Initial drawdown of both reservoirs began in late May 2011 in preparation for dam removal. Power production ceased and the reservoirs dropped to the base of the spillway gates, a decrease of 4.5 m in water surface elevation, exposing a narrow band of uplands over a two-week period. Removal of the two dams and full reservoir dewatering began simultaneously in September 2011. Dam removal and reservoir drawdown was relatively rapid for the Elwha Dam, ending in March 2012. The larger dam, Glines Canyon Dam, was designed to be removed more slowly to allow for the Elwha River to gradually erode the Mills reservoir delta. The reservoir pool was drained slowly over a period of 13 months, September 2011-October 2012 (Randle et al., 2015). Glines Canyon Dam removal was completed in August 2014. The newly exposed valleys included channels, floodplains, terraces, and valley wall landforms (Figure 2; from Chenoweth et al., 2022). Because the channel and floodplain areas were especially dynamic following dam removal, most studies and management actions focused on the terraces and valley walls.

The phased removal of Glines Canyon Dam successfully eroded the Mills reservoir delta, re-depositing sediments into new terraces 2-10 m thick covering the valley bottom (Randle et al., 2015). These new deposits overtopped fine sediments, resulting in novel terrace landforms 6-18 m thick (Figure 2). Many of the terraces eroded away after dam removal was completed (Ritchie et al., 2018), but approximately 69 ha of terraces remained in 2016. Most of the terrace erosion occurred during high flow events in the first few years after dam removal. Erosion has continued since 2016 but with only minor loss of terraces (A. Ritchie, U.S. Geological Survey, oral personal communication, 2023).

3 Planting, seeding and invasive plant management (IPM)

Revegetation began simultaneously with dam removal in September 2011 and the initial 7-year revegetation effort ended in

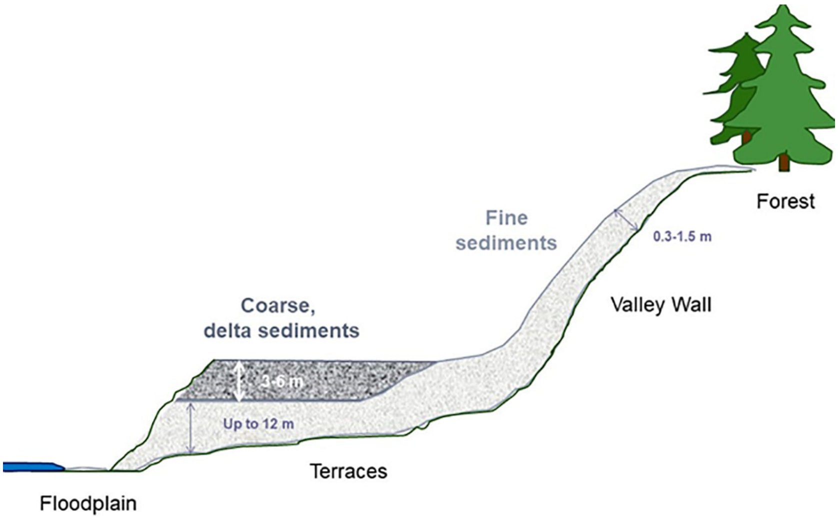

FIGURE 2
Stylized profile (not to scale) of the dewatered reservoir from forest edge to river. Fine sediments accumulated throughout the reservoir while the dam was in place. During dam removal, coarse sediments from the delta eroded and were redeposited as terraces on top of fine sediments. In the floodplain, the river eroded both fine sediments and terraces (Chenoweth et al., 2022).

the fall of 2018 (Chenoweth et al., 2011). Revegetation approaches included planting containerized plants and bare root plants as well as manual seeding. During the first year (November 2011-March 2012) only container plants were planted; no seed was sown except for a small seeding trial at Aldwell reservoir (Baker, 2013). Seeding the reservoirs began in the fall of 2012, one year after the start of dam removal. In the former Mills reservoir, 218,116 plants were planted, and 2,193 kilograms of seed were sown on 14.1 ha of the valley wall and 44.0 ha of terraces. A substantial area was left to naturally revegetate; 25.6 ha of valley wall landforms and 18.7 ha of terraces. In the Aldwell reservoir, 85,764 rooted plants were installed, and 716 kg of seed were sown on 16.7 ha leaving 103.7 hectares to revegetate naturally. Most of the plantings were trees and shrubs representing 60 species (Supplementary Table 1). The seed mixes varied but were composed primarily of nine native species (Supplementary Table 2). Average seeding rate was 183 seeds/m^2 on fine sediments and 488 seeds/m^2 on coarse sediments (Chenoweth et al., 2022). Species composition and planting density varied by site and by year.

A coordinated effort between Olympic National Park and the Lower Elwha Klallam Tribe was implemented to control invasive plants in the watershed several years prior to dam removal, continuing through 2018. Invasive species management occurred annually from spring through fall with species-specific control methods targeting the species of concern lists outlined in the Elwha Revegetation Plan (Chenoweth et al., 2011). As soon as the reservoirs were drained, the new lands were systematically mapped annually and treated within the same year, following the methods in Woodward et al. (2011). Treatments included the use of herbicides and mechanical removal. All areas were treated in both reservoirs including unplanted and unseeded areas.

The Lower Elwha Klallam Tribe and the Olympic National Park in 2012 and 2014 translocated 835 logs (log boles and logs with attached root-wads) by helicopter into the former Mills reservoir onto the coarse-textured terraces formed during dam removal. The logs were arranged in single, parallel, and overlapping configurations (Colton, 2018). Roughly two-thirds of the translocation area was planted and seeded.

4 Biotic drivers of revegetation

4.1 Distance from seed sources and seed banks

4.1.1 Predictions

The Elwha River reservoirs were large, with many newly exposed surfaces expected to be far from native seed sources, limiting revegetation (Chenoweth et al., 2011). Seed banks, an important source of new vegetation after disturbance, were predicted to be limited in density and species (Brown and Chenoweth, 2008; Michel et al., 2011).

4.1.2 Results

Prach et al. (2019) and Chenoweth et al. (2022) found distance from seed sources in the former Mills reservoir was a significant explanatory revegetation variable. Prach et al. (2019) determined that distance from the forest edge affected species composition in 2015, 2-3 years after reservoir drawdown. Chenoweth et al. (2022) further documented that distance from forest edge affected bare ground, species composition and species richness in 2016. However, both articles note that coarse-textured sediment, exclusive to terrace landforms, were predominantly located in the middle of the dewatered reservoir and, on average, farther from seed sources compared to the fine sediments covering the valley wall landforms. The interaction between landform, sediment texture and distance from forests was likely a contributing factor. On the coarse-textured terraces, Cendejas-Zarelli (2021) reported that as distance from the forest edge increased, diversity, species richness, and percent non-native species declined. However, plant abundance did not change significantly with distance. Instead, further distances favored wind-dispersed species and excluded plants with gravity and ballistic dispersal mechanisms.

The seed bank may have played a significant role in revegetation (Figure 3). Vegetation cover in the early years after dam removal was dominated by species commonly found in soil seed banks. The six most abundant species detected in pre-dam removal seed bank studies, including *Juncus* species (rushes), the most abundant seed bank species), *Carex deweyana* var. *deweyana* (Dewey's sedge), *A. rubra*, *Epilobium ciliatum* ssp. *ciliatum* (fringed willowherb), *Equisetum* species (horsetail), and the non-native *Mycelis muralis* (wall lettuce; Brown and Chenoweth, 2008), were common in the drained reservoirs.

4.2 Managed revegetation

4.2.1 Predictions

There were several hypotheses and predictions associated with managed revegetation. Chenoweth et al. (2011) predicted that planting and seeding native species would 1) minimize the abundance of non-native, invasive species, 2) accelerate vegetation growth (cover) relative to unplanted and unseeded areas, 3) increase native species diversity and richness, and 4) alter plant community composition.

4.2.2 Results

The four studies looking at the effects of seeding and planting in the former Mills reservoir (Morgan, 2018, Prach et al. 2019, Cendejas-Zarelli, 2021; Chenoweth et al., 2022) did not always have consistent results. However, most showed that seeding reduced non-native species relative frequency, species richness, or abundance on coarse sediments (Morgan, 2018; Cendejas-Zarelli, 2021; Chenoweth et al., 2022). Half of the studies showed that seeding and planting altered species composition (Morgan, 2018; Chenoweth et al., 2022), and one each showed that seeding or planting increased species richness (Cendejas-Zarelli, 2021; Chenoweth et al., 2022) as described below.

Chenoweth et al. (2022) assessed the effect of planting and seeding on species richness, relative frequency of non-native species, and species composition in 2016, using permutational multivariate analysis of variance and nonmetric multidimensional scaling (NMDS) ordinations. They found that planting increased native species richness while seeding significantly reduced the relative frequency of non-native species on both fine and coarse-textured sediments. Planting and seeding both altered species composition. They used the same analysis to assess the effects of seeding and planting on percent bare ground from 2013 to 2017. They found that seeding reduced bare ground in all years on coarse sediments with substantial reductions by 2016, but had no effect on fine sediments.

Using 60 100-m^2 plots on Lake Mills, including some sampled at the same locations as the Chenoweth et al. (2022) plots, with three treatments (seeding, planting + seeding, control) stratified across valley wall and terrace landforms, Morgan (2018) found that both seeded and seeded + planted plots had lower non-native species richness on terrace landforms with coarse sediments in 2017. Surprisingly, seeding (only) also reduced native species richness on coarse-textured landforms. Neither planting nor seeding affected percent cover. Using PERMANOVA analysis and NMDS, Morgan (2018) also found that treatment interacted with landform to significantly affect plant community composition. On valley walls, *A. rubra* was the most abundant species across all treatments; however, *Thuja plicata* (western redcedar), a planted species, was an indicator species for planted plots.

FIGURE 3
Juncus species, *Carex* species and other wetland plants quickly germinated from a seed bank in 2012. Photograph is from the east side of the former Mills reservoir, July 24, 2012. Photograph provided by Joshua Chenoweth.

Cendejas-Zarelli (2021) surveyed plants in seeded and unseeded plots on coarse sediment terraces with varying degrees of large woody debris (LWD) cover in Lake Mills in 2016. Each plot consisted of six 1-m^2 quadrats clustered around LWD or a 2 x 3-m plot without wood. She found that, in seeded areas, species richness and plant abundance increased and percent non-native species declined, results consistent with Chenoweth et al. (2022). She also found that large woody debris and seeding interacted to affect plant abundance, with greater abundance associated with single logs, and no difference where there was no large woody debris or clusters of logs.

Finally, Prach et al. (2019) assessed revegetation effects in 2015. This study measured species cover in 50-m^2 plots in the same locations sampled by Chenoweth et al. (2022) and analyzed the data using detrended correspondence analysis (DCA) and canonical correspondence analysis. The results of this work indicated that seeding and planting did not significantly affect the plant community in terms of overall species richness, non-native species richness or wetland species richness.

The most common species on seeded and planted + seeded plots on the coarse-textured terraces, where it thrived, was *Lupinus rivularis* (riverbank lupine), a seeded species (Morgan, 2018). *Lupinus rivularis* is a 30 to 150 cm tall pioneer species adapted to well drained sandy or gravelly soils and may grow as an annual, biennial, or short-lived perennial (Darris and Young-Mathews, 2012). As a legume, *L. rivularis* assimilates nitrogen (N) through N-fixing *Rhizobia* bacteria that form an endosymbiotic association in root nodules (Staniewski, 1970). Nitrogen fixing species such as *Lupinus* spp. can enhance N availability in nutrient-limited soils (Myrold and Huss-Danell, 2003). However, the dense herbaceous canopy created by *L. rivularis* may hinder facilitation through competition and negatively affect native seedling survival (Morris and Wood, 1989; Walker and del Moral, 2003), or alternatively, *L rivularis* may facilitate soil development and promote plant community recovery (Bishop, 2002; del Moral, 2007).

Kardouni et al. (2023) examined the effects of *L. rivularis* density on growth of planted conifers, specifically *P. menziesii, A. grandis*, and *Pinus monticola* (western white pine), and on neighboring plant species composition and ectomycorrhizal (ECM) root tip colonization, three years after planting on the Mills reservoir terraces. Dense *L. rivularis* increased foliar nitrogen in planted conifers without reducing growth, indicating nitrogen provided by lupine detritus is facilitating conifer growth. Dense *L. rivularis* cover also reduced herbaceous species richness compared to sparse stands of *L. rivularis*, which included a reduction in the non-native grasses *Holcus lanatus* (common velvet grass) and *Vulpia bromoides* (brome fescue). ECM root colonization increased in sparse plots and was lower on conifer roots in the medium and dense lupine plots.

4.3 Invasive plant colonization and management

4.3.1 Predictions

Non-native, invasive plant species were expected to dominate new landforms after reservoir drawdown with a more pervasive presence at the Aldwell reservoir due to its proximity to more developed areas with non-native plant populations (Woodward et al., 2011). Prior to dam removal non-native plant species were prioritized for control into three categories: primary species of concern, secondary species of concern, and species of concern that were not locally present but potentially could appear ("watch list"; Chenoweth et al., 2011).

4.3.2 Results

Invasive, non-native species of concern were not prominent in the Chenoweth et al. (2022) plots in any year. One species considered to be a secondary species of concern for management (Chenoweth et al., 2011) was significant in the plot data: *H. lanatus*. This species increased in frequency each year and was particularly abundant on fine sediments on the valley wall. It was never treated, as treatments were focused on primary species of concern (Chenoweth et al., 2011). Indicator species analysis by Morgan (2018) revealed that the Aldwell reservoir had relatively more non-native species as indicators than the Mills reservoir, such as *Lapsana communis* (nipplewort), *Leucanthemum vulgare* (ox-eye daisy), and *Agrostis stolonifera* (creeping bentgrass), consistent with pre-dam removal predictions (Woodward et al., 2011). None of these species were primary species of concern and consequently were not treated.

Targeted invasive species mapping surveys were conducted annually across both reservoirs following the methods outlined in Woodward et al. (2011). The Aldwell reservoir contained many more observations in all years compared to the Mills reservoir, as expected (Supplementary Figure 1). Plot surveys of non-native species confirmed these patterns: In 2013, Schuster (2015) found that the Aldwell reservoir had over four times greater non-native species richness (9 vs. 2 species per 100 m^2) and nine times greater non-native percent cover (9% vs. 1% in 100-m^2 plots) than the Mills reservoir. However, these differences were no longer statistically significant by 2014 due to an increase in non-native species richness and cover in Lake Mills and high variability in Lake Aldwell (Schuster, 2015). In the Aldwell reservoir there was a spike in observations of targeted invasive species in 2014 outside of the randomized plot surveys (Supplementary Figure 2). Management of targeted invasive species contributed to a rapid decline in observations from 2015-2017 (Supplementary Figure 2). Targeted invasive species remained rare enough to not be prevalent in any of the randomized plot studies in any year. In the Schuster plots, non-native cover gradually increased with time after dam removal on both reservoirs, and by 2016 was slightly higher on the Aldwell reservoir, and highest on valley walls compared to other landforms (Mills: 17% valley walls, 6% terraces, 2% riparian, Aldwell: 22% valley walls, 15% terraces, 3% riparian; Morgan, 2018). The proportion of total species that were non-native in 100-m^2 plots ranged from 21% on Aldwell valley walls to 38% on Aldwell terraces. In the Mills reservoir, non-native species cover was around 25% for all landforms. Hence, while non-native species were not dominant, they were certainly present, and warranted careful observation.

Phalaris arundinacea (reed canary grass) was particularly abundant in the Aldwell reservoir and its initial distribution suggests a seed bank may have been prevalent or seed was water-transported during reservoir drawdown. Active removal efforts likely limited the effect of primary species of concern and minimized their abundance, preventing direct competition effects on establishing native species.

5 Abiotic drivers of revegetation

5.1 Reservoir drawdown timing

5.1.1 Predictions

Reservoir drawdown timing was predicted to be an important variable for plant community succession (Shafroth et al., 2002). Spring drawdown was expected to recruit riparian species such as *Salicaceae* species as moist, bare soil availability would coincide with germination windows (Mahoney and Rood, 1998; Auble et al., 2007), while summer drawdown was expected to result in few naturally occurring species, particularly in areas far from seed sources (Michel et al., 2011). Fall and winter drawdown was expected to benefit natural recruitment across groups as it occurs during peak seed rain of important native species such as *T. heterophylla*, *P. menziesii*, *T. plicata* and *A. rubra* (Burns and Honkala, 1990). Reservoir drawdown variability spanning several seasons was consequently expected to provide opportunities for diverse species to colonize the newly exposed sediments.

5.1.2 Results

Reservoir drawdown timing affected several vegetation metrics. Naturally regenerating communities differed significantly with sediment exposure timing and among the two reservoirs in 2013; these differences persisted in 2015 (Werner, 2014). When combined with functional trait metrics from the TRY Plant Trait database (TRY Plant Trait Database (try-db.org); Kleyer et al., 2008; Kattge et al., 2011), drawdown timing-based differences in species establishment also translated to a difference in community-weighted functional trait metrics, with higher values of specific leaf area, seed mass, and maximum canopy height in the earlier-exposed soils.

As predicted, areas exposed during late spring were dominated by *Salicaceae* species. In the former Aldwell reservoir, areas exposed during the spring 2011 partial drawdown had a mean stem density of 71,200/ha in 2014, five times higher than areas exposed in fall 2011 through winter 2012 (13,600/ha in 2014). The dominant species in these sites were *P. balsamifera* ssp. *trichocarpa* (47,200/ha) and *Salix* species, largely *S. sitchensis* (Sitka willow; 20,020/ha). Fine sediment sites exposed in the fall and late winter/early spring in the Mills reservoir were dominated by *A. rubra*, constituting more than 50% of all stems by 2016 (Chenoweth et al., 2022).

Drawdown timing also affected species colonization of coarse sediments. Coarse sediment terraces exposed in late fall through spring were not readily colonized by *A. rubra*, even at sites directly adjacent to mature stands. In late spring of 2012, the erosion and re-deposition of the reservoir delta sediments occurred during the seed dispersal time of *Salicaceae* species while reservoir drawdown was on hold for 10 weeks beginning May 1st (Bountry et al., 2015). During this hold period, the newly formed terraces were inundated by multiple braided channels, allowing *P. balsamifera* (referred to without the subspecies name in all subsequent references) and *Salix* species to establish.

When reservoir drawdown resumed, over a 12-18-month period the river eroded down to the original river bed elevation, leaving a 12-ha terrace perched 16 m above the floodplain. Seedlings of *P. balsamifera* persisted despite the relatively fast, steep drop in the water table, and by 2017 the stem density was 9,600/ha with no mortality noted in the permanently marked sampling plots used in the Chenoweth et al. (2022) study. In contrast, in the 12 plots with coarse sediments located on terraces that did not form in late spring, mean stem density was only 300/ha, and nine of those plots had no woody stems or seedlings.

5.2 Effects of landforms and sediment grain size

Sediment texture was predicted to vary among landforms and reservoirs, with more coarse sediment expected to be trapped in the upstream reservoir (Mills). Coarse sediments (coarse sands, gravels, and cobbles) were predicted to be deposited during drawdown into high terrace landforms several meters above the water table, which was a concern for project managers, as they were predicted to create a water-stressed environment that would negatively affect revegetation (Auble et al., 2007; Chenoweth et al., 2011). Woody species were expected to colonize coarse-textured sediments, whereas fine-textured (silt and clay) lacustrine sediments were predicted to favor fine-rooted plants such as grasses and forbs (Grubb, 1986) and preclude the establishment of woody species, including a common early colonizer, *A. rubra* (Shafroth et al., 2002; Chenoweth, 2007; Chenoweth et al., 2011). Plant-growing trials using fine sediments dredged from Lake Mills indicated that fine lacustrine soils favored germination and establishment of native grasses over native forbs and *A. rubra* (Chenoweth, 2007; Chenoweth et al., 2011) and hampered germination of native shrubs and forbs as well as the potentially invasive non-native species *Cirsium arvense* (Canada thistle) and *Rubus discolor* (Himalayan blackberry; Michel et al., 2011).

5.2.1 Results

5.2.1.1 Post-dam removal sediments and landforms

Different landforms developed within the reservoirs, distinguished based on elevation above river channel, distance from river channel and forest edge, and average coarse particle size (Table 1). The main landform types include valley walls, where the original pre-dam geomorphology is still present, as well as terraces formed from reservoir sediment redeposited during dam removal, and the low elevation, dynamic channels, bars, and floodplains (hereafter 'riparian'), where fluvial process continue to shape channel morphology. Observations during and immediately after dam removal confirmed predictions that some landforms would be dominated by fine sediments and others by coarse sediments (Schuster, 2015; Morgan, 2018; Prach et al., 2019; Chenoweth et al., 2022). Generally finer sediments composed of

TABLE 1 Differences in elevation above river channel, distance from river channel and forest edge, and average coarse particle size among landforms and former reservoir beds observed in 2013 on the Elwha River, Washington, USA.

Reservoir	Landform	Average Elevation above Channel (m)	Distance (m)		Average Coarse Sediment Size (mm)
			River Channel	Established Forest	
Aldwell	Valley Wall	12.40 ± 2.02	114.03 ± 14.80	21.75 ± 3.51	1.11 ± 0.08
Aldwell	Terrace	6.28 ± 0.71	82.03 ± 15.59	131.20 ± 12.89	2.82 ± 0.63
Aldwell	Floodplain	1.22 ± 0.19	51.46 ± 18.48	102.47 ± 10.06	2.33 ± 1.15
Mills	Valley Wall	15.99 ± 3.18	242.82 ± 37.71	44.80 ± 8.32	2.63 ± 0.75
Mills	Terrace	7.31 ± 0.85	131.18 ± 18.39	150.07 ± 14.86	10.83 ± 2.36
Mills	Floodplain	1.89 ± 0.36	44.20 ± 8.29	287.59 ± 30.33	12.69 ± 3.65

Data are based on plots randomly stratified across landforms in five transects. Includes ± standard error (from Schuster, 2015).

silt and clay were found on valley walls, and coarser sediments composed of sand and cobbles were found on terraces and riparian landforms (Table 1, Schuster, 2015; Morgan, 2018). As predicted, the grain sizes were generally larger on the Mills reservoir than Aldwell reservoir (Figure 4). The finer sediments of valley walls and in Lake Aldwell had more organic matter and higher cation exchange capacity than the coarse sediments, and were associated with greater plant cover (Werner, 2014; Schuster, 2015; Morgan, 2018).

5.2.1.2 Effect of sediment grain size and landform on plant establishment, density, and growth

Predictions about which groups of species would colonize fine vs. coarse sediments were not consistently borne out. On fine

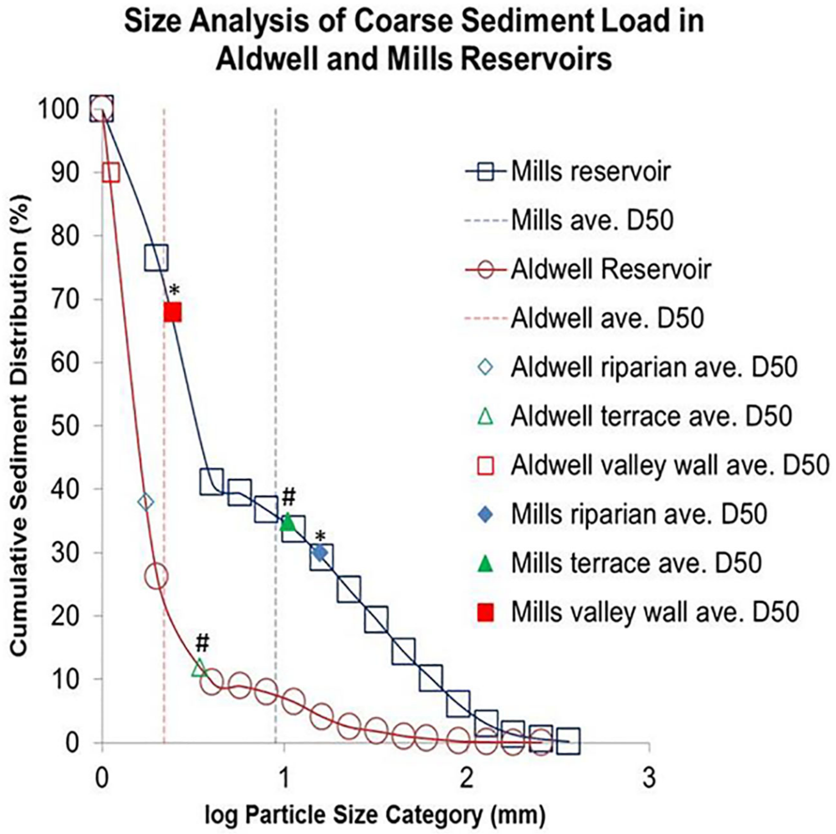

FIGURE 4
Log-transformed cumulative frequency curves comparing coarse sediment distribution between the Aldwell and Mills reservoirs along the Elwha River, WA. Sediment grain sizes were averaged between 2013 and 2014 for each reservoir. Grain sizes (x-axis) are plotted against the frequency in which they occur within each reservoir (y-axis). Squares, triangles, and rhombuses represent 2013-2014 landform average D50s (D50 - median grain size based on Wolman Pebble Counts). Asterisk denotes significance between the Mills valley walls and riparian landforms (p=0.001); number signs denote significance between the Mills and Aldwell terraces (p=0.003) (Schuster, 2015).

sediments, plant performance exceeded expectations. Within a year, herbaceous and woody plants covered fine sediments on valley walls and some terraces of Lake Aldwell. One species in particular, *A. rubra*, rapidly colonized fine sediments (Prach et al., 2019; Chenoweth et al., 2022), defying predictions. In 2012, nine months after the start of dam removal, mean density of *A. rubra* seedlings was 0.43 per m^2 (4,300 per ha) in unplanted plots. Seedlings successfully established, with the number of woody stems (>30 cm in height) increasing each year, reaching a peak of 1.4 per m^2 in 2015 before slowly declining to 1.1 per m^2 by 2017. *Populus balsamifera* and *S. sitchensis* also thrived, with mean densities of 0.7 per m^2 and 0.3 per m^2 by 2017. Although overall richness of woody species started low, with a mean of 3.5 species/50 m^2 in 2012, richness increased annually to a peak mean of 6.2 species/50 m^2 in 2017 (Chenoweth et al., 2022).

Woody species did not readily colonize coarse sediments except where draw-down timing matched establishment needs (Chenoweth et al., 2022). *Alnus rubra* was rare on coarse sediments, while *P. balsamifera* and *S. sitchensis* were present predominantly on one large terrace where the drawdown timing coincided with *Salicaceae* seed dispersal in May and June (Chenoweth et al., 2022). By 2016, mean densities of woody species on unplanted coarse sediments was 2,488 per ha compared to 26,882 per ha on unplanted fine sediments (Chenoweth et al., 2022). However, most of the stems in the unplanted terrace plots were counted in four plots located on the only terrace landform exposed during *Salicaceae* seed dispersal (Chenoweth et al., 2022). The remaining 10 untreated plots located on terraces that did not form during the May-June period had very few woody stems, with a mean of 360 stems/ha in 2016. Of those 10 plots, seven contained no woody stems at all.

Several studies found that plant species composition and richness were affected by sediment texture and landform (Schuster, 2015; Morgan, 2018; Prach et al., 2019; Chenoweth et al., 2022). Chenoweth et al. (2022) found that species richness was significantly higher on fine sediment landforms, with a mean of 23.4 species/50 m^2 compared to 15.4 species on coarse sediments. This is consistent with findings of Schuster (2015), who found that in the first year following dam removal, native plant species richness and percent cover were greatest on valley wall landforms. On valley walls, terraces, and riparian landforms respectively in 2013, the Aldwell reservoir had 28, 19, and 9 species and 102%, 48%, and 18% cover, while the Mills reservoir had 20, 4, and 4 species and 42%, 4%, and 3% cover in 100-m^2 plots; note that percent cover values can sum to more than 100% due to different layers of vegetation (Schuster, 2015).

The differences in plant diversity and cover among the two reservoirs was likely influenced by sediment texture. In 2013, the Aldwell reservoir had nearly twice as many native species per 100 m^2 as the Mills reservoir (21 vs. 11), and had four times greater native percent cover (62.5% vs. 14.6%) across all landforms. In the second year (2014), species richness and cover increased in the Mills reservoir and there was no longer a significant difference between the two reservoirs. By year four (2016), species richness had increased on the Mills reservoir terrace and riparian landforms, and cover had increased on both reservoirs, though more on the Mills reservoir, making the two reservoirs more similar. In 2016, on valley wall, terrace, and riparian landforms respectively, the Aldwell reservoir had 22, 13, and 19 species and 185%, 82%, and 14% cover, while the Mills reservoir had 21, 13, and 14 species and 146%, 24%, and 6% cover (Morgan, 2018). Because valley walls had finer sediment (e.g., more silt/clay and smaller cobbles) compared to other landforms, and the Aldwell reservoir had finer sediments than the Mills reservoir, Schuster (2015) and Morgan (2018) concluded that finer sediments were more favorable for plant establishment and growth, consistent with the findings of Prach et al. (2019) and Chenoweth et al. (2022).

Texture and landform also influenced planted material. Whisman (2013) and Calimpong (2014) tagged planted species in the former Mills reservoir to determine sediment texture effects on short and long-term rates of survival and growth. Whisman tagged 860 plants (5 species) installed on fine and coarse sediments in 2011-2012 during the first year of reservoir drawdown. Calimpong tagged 675 plants (5 species) installed on fine and coarse sediments in 2012-2013 during the second year of dam removal on landforms exposed for over one year prior to planting. In both studies, survival after the first growing season was high (>80%). In the Whisman study, mortality was higher on coarse sediments, with a statistically significant difference in survival rates of 88% compared to 92% on fine sediments. Calimpong also found survival on fine sediments and associated higher soil moisture was significantly higher (96%) compared to coarse sediment sites (92% and 88%). Olympic National Park continued to monitor a subset of the tagged plants through 2017 to monitor long-term survival rates (5-6 years). This included 688 of the Whisman plants, of which 180 were on fine sediments and 508 were on coarse sediments, and 456 of the Calimpong plants, all located on the coarse sediment terraces. Survivorship of the Whisman plants, planted while the reservoir was being drained, remained high, with a mean of 82% surviving past the 2017 summer, substantially higher than plants installed in 2012-2013, which had a mean survival of only 33% in 2017 (Supplementary Figure 2).

5.3 Large woody debris (LWD)

5.3.1 Predictions

Placement of large woody debris LWD was predicted to enhance managed and unmanaged revegetation by creating ‘safe sites’ for vegetation. LWD is used as a restoration tool to improve plant establishment by creating microenvironments that buffer temperature and wind velocities, provide shade, and enhance moisture retention in soils (Gray and Spies, 1997; Heinemann and Kitzberger, 2006; Calimpong, 2014; Colton, 2018). LWD adds perching sites for seed dispersers and may also protect vegetation by acting as a barrier against browsing ungulates (Harmon et al., 1986; Schreiner et al., 1996). Project managers predicted that LWD placement would result in higher plant abundance, diversity, and species richness.

5.3.2 Results

Colton (2018) investigated LWD with east-west orientation and reported reduced wind speed; high wind speeds increase heat and evaporative stress (Wahid et al., 2007). In addition to direct stress to the plant, wind speeds can also contribute to soil erosion. Colton (2018) also demonstrated a reduction in sediment temperatures, which can inhibit or slow germination as well as contribute to overall plant mortality (Covell et al., 1986; MaChado and Paulsen, 2001) but may prove beneficial in extreme environments where high temperatures can hinder plant establishment.

Cendejas-Zarelli (2021) examined the effects of the translocated LWD and direct seeding on species composition. Counter to predictions, there were no differences in mean plant abundance between plots with and without LWD. However, all plots containing LWD did have higher plant diversity and species richness when compared to open areas without LWD. Plant species richness increased most when seeding was paired with LWD treatments. A diverse array of wind-dispersed forbs and grasses contributed to increased Shannon-Weiner diversity and species richness in plots. Because LWD acts as an effective trap for wind-blown seeds, it led to an increase in windblown non-native species, particularly when unseeded. In addition, all woody plants dispersed by birds were found in plots containing wood, with the majority around elevated root-wads, which likely attracted avian species that deposit scat at LWD perch sites. Counter to our predictions, there were no differences in mean plant abundance between plots with and without LWD (Cendejas-Zarelli, 2021).

6 Discussion

Revegetation of the Elwha reservoirs after dam removal was rapid (Figure 5). On fine sediments (valley wall landforms), a rich assemblage of native species naturally colonized the reservoirs over a five-year period, often overwhelming planted sites. The rapid arrival and growth of predominantly riparian species such as *A. rubra*, *P. balsamifera* and *Salix* species exceeded expectations and resulted in a dense deciduous forest on valley walls. In contrast, revegetation was slower on coarse sediments (terrace landforms), likely due to moisture and nutrient limitations, although millions of slow growing *P. balsamifera* and *Salix* seedlings also colonized these landforms where reservoir drawdown matched moisture needs for germination (Mahoney and Rood, 1998). Results from the Elwha River corroborate previous work suggesting that drawdown timing can influence plant growth and survival as well as species composition and even community functional trait composition (Shafroth et al., 2002; Fukami et al., 2005; Auble et al., 2007). Timing the planting during or immediately after reservoir drawdown may also boost survival rates for many years compared to planting 1+ years post drawdown. It is unclear why survival rates were so much higher relative to later plantings but it may be due to the residual moisture that remained in the sediments as the reservoirs drained, creating favorable conditions for root growth in that critical first year of growth.

Contrary to expectations, invasive species did not dominate exposed sediments after dam removal, as has occurred in other dam removal studies (e.g., Lenhart, 2000; Orr and Koenig, 2006). This may have been due to active weed management of primary species of concern, rapid revegetation of areas with fine sediments by competitive native species such as *A. rubra*, and relatively harsh conditions on terraces with coarse sediments that slowed overall revegetation. The percentage of non-native species was similar to that of other dam removals (average 31% of species), while the relative abundance of non-natives (the highest of which was 22%) was slightly lower than in other dam removals (average 32%; Tullos et al., 2016). Over time, cover of non-native species gradually increased, largely comprising species that were not targets for removal. As expected, the Aldwell reservoir, which has larger amounts of nearby development and finer sediments, had relatively more non-native species than the more isolated Mills reservoir, consistent with studies showing the effect of human disturbance on non-native species invasion (Lázaro-Lobo and Ervin, 2021). One of the most problematic nonnative species in the Aldwell reservoir, *P. arundinacea*, is one of the most frequent management problems across many dam removal locations (Tullos et al., 2016). These results suggest that active management of species such as *P. arundinacea* can be effective after dam removal. However, monitoring the gradual increase of non-target nonnative species on the Elwha would contribute to understanding longer term invasive species dynamics following dam removal.

While the effects of seeding and planting were reduced on fine sediments due to the high cover of trees and shrubs, seeding and planting had a greater effect in coarse sediments, likely because natural recruitment was slower, with species richness and plant abundance metrics consistently lower compared to fine sediment landforms in all studies. Chenoweth et al. (2022); Cendejas-Zarelli (2021), and Morgan (2018) found significant reductions of non-native species in seeded sites, particularly on terraces with coarse sediments, but effects were weaker on valley walls with dense woody species.

Seeding *L. rivularis* was particularly successful on coarse sediments. Several studies in other environments have demonstrated the benefits of seeded *Lupinus* spp. in seral habitats, which include trapping seeds and leaf litter, creating microsites, reducing wind and water erosion, and increasing the establishment and survival rates of later successional woody species (Niederfriniger-Schlag and Erschbamer, 2000; Halvorson et al., 2005). Wind events alone can reduce leaf biomass by 36% in conifer forests (Kalma and Kuiper, 1966) and the presence of grass clumps and established shrubs have been demonstrated to decrease wind velocity by 70% and 40%, respectively (Mayaud et al., 2016). In the Elwha, moderate and dense stands of *L. rivularis* increased foliar N concentration in neighboring conifers. Increased foliar N levels can improve photosynthetic efficiency, increasing tree growth (Smethurst et al., 1986; Prietzel et al., 2008). As *Lupinus* spp. densities gradually decrease, their legacy facilitates soil development to promote plant community recovery (Bishop, 2002; del Moral, 2007). Though *L. rivularis* was associated with reduced species richness in the Elwha, non-native grasses were among the taxa suppressed. This may be important on coarse sediments that were not readily colonized by native species, leaving the site open and vulnerable to non-native species suited to open, dry conditions.

FIGURE 5
Photographs of the former Aldwell and Mills reservoirs on the Elwha River, Washington, USA. The Aldwell reservoir valley wall **(A)** in May, 2012, 2 months after full reservoir drawdown, **(B)** August 2013, 17 months after reservoir drawdown and **(C)** September 2016, 4 years post-drawdown. The Mills reservoir full valley showing floodplain, terraces and valley wall **(D)** April 2013, **(E)** August 2014 and **(F)** July 2017. Valley wall revegetation (upper margins in photograph) was rapid but significantly slower on terrace and floodplain landforms. Photographs provided by the National Park Service, available online at https://video-monitoring.com/construction/olympic/js.htm.

Comparisons of results among the different plot-based studies reviewed in this paper (Schuster, 2015; Morgan, 2018; Prach et al., 2019; Cendejas-Zarelli, 2021; Chenoweth et al., 2022) are complicated by inconsistencies in field methods and analytical approaches across the studies. For example, plot sizes varied among studies, which makes comparisons of some variables (e.g., species richness) challenging given the non-linear shape of species-area relationships (Dengler, 2009). Abundance measures were not consistent across studies, as some used percent cover (e.g., Prach et al., 2019) while others used other metrics such as relative frequency (Chenoweth et al., 2022). The extent to which the different landforms were sampled and the extent to which landform was incorporated into analyses also varied. Different years were sampled in the different studies, which makes it challenging to separate the possible effects of inter-annual variability associated with factors other than time since dam removal. In some instances, plots intended to monitor planting effects may not have been entirely located in a planted site. Planted sites were patchy, with planting staff instructed to plant clusters of vegetation in areas without obvious natural regeneration. As a result, a planted area may have only been partially planted with clusters surrounded by a matrix of naturally occurring vegetation. Randomized plots installed many years post-planting that are intended to sample a planted area could inadvertently sample a partially or completely unplanted site. This would result in species richness and diversity metrics with no relationship to planting effects. With more consistent sampling, results from the different studies would likely have been more consistent, however, our general conclusions would likely remain the same.

The placement of LWD appeared to increase richness and diversity, complementing the idea that structural diversity leads to biological complexity (Brown and Naeth, 2014). Using larger irregular surface topography such as cracks, rills, rocks, mounds, and depressions, studies have shown that these structures trap wind-blown seeds in early successional habitats, leading to increased seed deposition and ultimately increased germination of greater species (del Moral and Wood, 1993; Walker and del Moral, 2003; Jones and del Moral, 2005). However, contrary to predictions, plant abundance did not increase around LWD which is consistent with findings following the eruption of Mount St. Helens, where logs and boulders had negligible effects on plant establishment in seral post-volcanic habitats (Halpern and Harmon, 1983; Halpern et al., 1990). Since plant abundance did not differ significantly among wood and non-wood plots, it may indicate that seeds, albeit from fewer successful species, are dispersing to and germinating in open, coarse sediments. Studies in post-glacial habitats found that coarse surface sediments, similar to those that occur in the Mills reservoir, created favorable micro-sites for plant germination and establishment to occur (Jumpponen et al., 1999; Niederfriniger-Schlag and Erschbamer, 2000). Another factor was distance from the forest edge: As this increased, Shannon-Weiner diversity, species richness, and percent non-native species on unseeded plots declined. Seedlings of *P. balsamifera* and *S. sitchensis* were particularly abundant on terraces attributed to reservoir drawdown timing, which coincided with the height of both species' seed production (Bountry et al., 2015; Prach et al., 2019; Chenoweth et al., 2022).

Ungulate and other mammal browsing pressures are often a concern to revegetation efforts. Light browsing (uninterrupted growth types – see Keigley, 1997) was common, mostly from *Odocoileus hemionus columbianus* (Columbia black-tailed deer), but was never significant (growth interrupting) in any of the 6 years of data collection. Chenoweth et al. (2011) hypothesized that woody seedlings planted or naturally occurring immediately during reservoir drawdown would have time to establish before browsing pressures were high. Ungulate foraging patterns typically take time to shift from historic movements to new, previously unavailable landscapes (Nolte, 2003). Nearby herds of *Cervus canadensis roosevelti* (Roosevelt elk) did not begin regular movements into the reservoirs until 5-6 years after reservoir dewatering. During the first 5 years of light browsing impacts, plantings and naturally occurring vegetation established successfully, reaching average canopy heights above browse levels prior to the regular presence of *C. canadnsis roosevelti* herds (J. Chenoweth, National Park Service, personal observation). Johnson et al. (2023) found that plants on the Elwha that were fully surrounded by large woody debris (LWD) clusters experienced significantly less browse intensity than plants growing in the open or with LWD on one or two sides.

Overall, findings from the studies we reviewed suggest that rapid regeneration of native vegetation is possible within five years after dam removal under careful drawdown and weed management regimes, even in the absence of seeding and planting. However, seeding and planting lead to important benefits, such as increased woody species diversity (from planting) and reduced non-native species richness (from seeding), especially in relatively harsh environments where plant growth is slow. Findings from these studies also suggest that with weed control, it is possible to prevent invasive species from dominating newly exposed reservoirs. Forest succession can take decades to centuries to proceed (Van Pelt et al., 2006), and over the long-term, planting and seeding and non-native species composition may have increasingly important effects, so it will be important to continue monitoring to gain a full understanding of the long-term patterns of revegetation after dam removal.

7 Lessons for dam removal

- Fine (silt and clay-sized particles) sediments do not inhibit revegetation and species not typically considered viable on silt and clay soils may establish. Planting trials using fine sediments in pots and planter boxes did not successfully predict species performance (Chenoweth et al., 2011; Michel et al., 2011), likely due to the effects of the containers on fine sediment performance (Poorter et al., 2012; Kawaletz et al., 2014). Plant trials in pots or raised beds create a unique environment that likely alters fine sediment characteristics and does not successfully mimic field conditions.
- Timing of reservoir drawdown can influence the trajectory of revegetation. If possible, reservoir drawdown timing could be scheduled for specific species desirable to revegetation goals. The natural recruitment of riparian species will enhance riparian habitats, a common goal for large dam removals. Timing the drawdown during the seed rain of *Salicaceae* species may result in a robust recruitment of *Populus* spp. and *Salix* spp. Alternatively, if the reservoirs are surrounded by undesirable non-native species of concern with wind-dispersed seed adaptations, reservoir drawdown timing can be scheduled when these species are not setting seed. A slow drawdown over many months can open the newly exposed lands during many different seed dispersal periods, enhancing the diversity of seed available to colonize the new landforms. Slow drawdowns will also provide more moisture to newly germinated seedlings to boost survival.

- Planting timing matters. Planting during reservoir drawdown may provide new plantings residual moisture beneficial to short-term and long-term establishment and performance. Early planting also provides an establishment window for trees and shrubs before ungulate browsing patterns divert into the new landscapes.
- Seeding is an effective tool for minimizing non-native species abundance; it is more important in coarsely textured, high-stress environments or sites far from natural seed sources.
- Plot locations, long-term monitoring methods, and analysis approaches are important considerations. It is crucial to establish plots immediately after planting to ensure the plots encompass planted and/or seeded material. Locating and establishing control plots immediately after seeding and planting is also important to ensure the site was, in fact, not seeded or planted. Ensure plots are well monumented for easy relocation and use consistent monitoring approaches to ensure sampling can be repeated long-term. Use similar analytical approaches to enable straightforward comparisons across different studies.
- Plot-based monitoring combined with qualitative monitoring are essential for adaptively managing revegetation of dewatered reservoirs after large dam removal. A multi-year planting plan, invasive species management plan and monitoring effort that spans at least 5-year post dam removal would help ensure that vegetation establishment and early seral conditions are on a desirable trajectory driven predominantly by native species interactions that are not impaired by dense populations of invasive, non-native species.

Author contributions

JC: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. PS: Conceptualization, Writing – review & editing. RB: Visualization, Writing – original draft, Writing – review & editing. JH: Project administration, Writing – original draft, Writing – review & editing. JB: Writing – original draft. SC-Z: Data curation, Writing – original draft. CW: Writing – original draft. JS: Writing – review & editing. OM: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1268969/full#supplementary-material

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Riverbank lupine's (*Lupinus rivularis*) influence on conifer growth, ectomycorrhizal colonization, and neighboring vegetation in coarse sediments left behind after dam removal

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Introduction: Until recently, much of the Elwha River was inaccessible to anadromous fish species due to the Elwha and Glines Canyon dams. Dam deconstruction resulted in approximately 325 ha of formerly inundated lake beds devoid of natural riparian corridors or adjacent forests. Efforts to restore the vegetation have had varying success. Areas where fine sediments settled along the valley walls quickly regenerated, while coarse terraces were slower to revegetate from plantings and directed seeding. One seeded species, riverbank lupine (*Lupinus rivularis*), quickly established on the coarse-textured terraces. Riverbank lupine is a pioneering species that assimilates nitrogen (N) through N-fixing bacteria; thus, it enriches the soil with bioavailable N and organic matter upon decomposition.

Methods: The goal of this study was to investigate lupine's influence on conifer establishment in the coarse sediments of the former Lake Mills basin along the Elwha River. Conifers planted 3 years prior to the study in plots with different levels of lupine cover (sparse, medium, or dense) were measured for growth, foliar total nitrogen, and ectomycorrhizal (ECM) root colonization. Soil N, organic matter (OM), and surrounding plant community composition were also evaluated at this time.

Results: After 3 years, conifers did not statistically differ in height or basal diameter among differing levels of lupine cover. However, conifers in the medium- and dense-cover plots had significantly greater foliar N concentrations ($\beta = 0.25$, $SE = 0.08$, $p < 0.001$). The roots of conifers in the dense- and medium-cover plots had significantly less ECM colonization than those in the sparse-cover plots ($\beta = 0.14$, $SE = 0.03$, $p = 0.03$). No differences existed regarding soil total N or OM. Plant community composition differed among lupine cover classes (permutational multivariate analysis of variance (PERMANOVA), ($F_{(2,21)} = 2.02$, $p = 0.01$). Higher lupine cover resulted in lower species richness ($\beta = 25.9$, $SE = 0.61$, $p = 0.04$).

Discussion: Based on our findings, the inclusion of native lupine in coarse, N-limiting soils contributes to the N pools without reducing the growth of planted conifers, which may accelerate forest succession leading to closed canopies much faster than passive recovery.

KEYWORDS

companion planting, restoration, soil development, vegetation, cover crop

Introduction

The environmental impacts of dams on forest-river processes have been well documented (Hall et al., 2011; Reidy Liermann et al., 2012) and include alterations to aquatic animal populations, riparian vegetation, hydrology, and river deltas (Li et al., 1987; Jansson et al., 2000; Sharma, 2001; Perry et al., 2016). Damming rivers in the Pacific Northwest (PNW) obstructs many historic anadromous fish migration routes, leading to major species declines (Duda et al., 2008). Riparian and upland forests are inundated through the creation of reservoirs that impede downstream flow and sediment exchange and cause deeply channelized riverbeds that become disconnected from floodplains (Shafroth, 1999; Rood and Mahoney, 2000). Further, dams decrease the delivery of large woody debris from forests to riverine systems, which negatively affects floodplain, delta, and instream habitat complexity, and the nearshore environment (Andersson et al., 2000; Gregory et al., 2002). Inhibiting the passage of anadromous fish affects the overall health of riparian ecosystems by limiting the transfer of marine-derived nutrients to adjacent forests (Helfield and Naiman, 2001; Drake et al., 2002).

Until recently, much of the Elwha River Basin was inaccessible to sea-run fish due to the Elwha and Glines Canyon dams. These dams blocked access to 90% of the spawning habitat, impeded sediment transfer to the nearshore, and degraded stream and riparian habitat (Pess et al., 2008; Shaffer et al., 2008; Duda et al., 2011). Despite the environmental impact, the two dams operated with little regulation for over 50 years until the Federal Power Act (late 1960s–1970s) required the owner to license the dams with the Federal Energy Regulatory Commission (Sadin and Vogel, 2011). This required maintenance for structural integrity and construction of fish passageways (Service, 2011). The Elwha River Ecosystem and Fisheries Restoration Act was enacted in 1992, requiring dam removal to restore riverine habitats, native salmon runs, and other ecosystem processes (DOI (U.S. Department of Interior) et al., 1996; Winter and Crain, 2008). The costs/benefit analysis, combined with the potential to restore the Lower Elwha Klallam Tribe's salmon runs, began to sway public and political opinion in favor of dam removal (Gregory et al., 2002; Duda et al., 2008).

The deconstruction of both dams and lake drawdown was completed by 2014, restoring access to the upper river and marking the largest dam removal project to date in the United States. Given the unprecedented nature of the large-scale dam removal, there was considerable uncertainty about how the biota would respond to the dewatering of the two reservoirs, which were estimated to store ~21,000,000 m^3 of sediment prior to removal (Warrick et al., 2015; Major et al., 2017). A major concern was the impact on terrestrial and aquatic habitats of this increased sediment load (Pizzuto, 2002; Stanley and Doyle, 2003). During drawdown, coarse-grained terraces approximately 3.3 to 7 m thick formed along the Lake Mills bed above the Glines Canyon dam (East et al., 2015). These terraces, composed of unconsolidated sand, gravel, and cobble, resulted in novel landforms perched above the hyporheic zone and situated between the riparian and forest corridors along the Elwha River (Bauman and Kardouni, 2018).

Revegetating these landforms, a fundamental goal of the Elwha River and Ecosystem Restoration Project, required the restoration of river-forest processes and native communities while limiting the establishment of non-native species (DOI National Park Service, 2015). Revegetation plans were designed to promote rapid succession to native forests, thus limiting erosion, regulating water temperature, and providing critical habitats (Chenoweth et al., 2011). In the Lake Mills Basin of the Elwha River, 44.0 ha of newly exposed sediments were actively revegetated from 2013 to 2015. This included broadcasting 2,800 kg of native seed and planting 205,000 herbaceous and woody plants representing 64 species (Chenoweth et al., 2022). Conifers such as Douglas fir (*Pseudotsuga menziesii* Mirb Franco), grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.), and western white pine (*Pinus monticola* Douglas ex D. Don) were incorporated into the planting plan and are considered important indicators of forest recovery, as well as iconic species to the PNW forests (Franklin, 1988; Shafroth et al., 2002).

One seeded forb species, native riverbank lupine (*Lupinus rivularis* Douglas ex Lindl.), was included in the seed mix and thrived in the coarse sediments along the Lake Mills terraces (Chenoweth et al., 2022). As a legume, it assimilates nitrogen (N) through the endosymbiotic association with *Rhizobium*, a N-fixing bacterium (Staniewski, 1970). Myrold and Huss-Danell (2003) demonstrated that N-fixing species such as lupine can enhance N availability and organic matter in nutrient-limited soils (Halvorson et al., 1991). Riverbank lupine is an annual, biennial, or short-lived perennial that can grow up to 150 cm in height and acts as a pioneer species adapted to sandy or gravelly soils (Darris and Young-Mathews, 2012). The 2-to-3-year life cycle of riverbank lupine starts with a vegetative phase followed by seeding and senescence with subsequent grow-back periods by seeded progeny.

One of the most well-studied examples of lupine colonization was in plant successional studies conducted after the eruption of Mount Saint Helens in the Pacific Northwest region of the United States. *Lupinus lepidus* Douglas ex Lindl. was the first colonizing herbaceous plant and formed dense to patchy colonies within a decade after the eruption (del Moral et al., 1995). Its presence was shown to have both facilitative and inhibitory effects on invading plant species, where living colonies inhibited ruderal species, while dead lupine patches facilitated recruitment (Morris and Wood, 1989). Elsewhere at Mount Saint Helens, del Moral and Rozzell (2005) demonstrated that *L. lepidus* inhibited colonization of forbs in mature lupine colonies. However, older colonies demonstrated a subsequent increase in plant richness and diversity. Further, varying levels of lupine allowed different sets of species to be established, suggesting that variation in lupine abundance may lead to different successional trajectories (del Moral and Rozzell, 2005; del Moral, 2007). As lupine densities gradually decrease, it is hypothesized that their legacy will contribute to soil development and ultimately accelerate plant succession (Vitousek et al., 1987; del Moral, 2007). Therefore, developing our understanding of lupine during primary succession may be an important component of forest restoration projects given its adaptability, ability to facilitate the establishment of neighboring plants, and N-fixing capability (Bishop, 2002).

The planting of native tree seedlings with and into herbaceous cover is common in restoration; however, not all N-fixing herbaceous species facilitate the establishment of neighboring trees (Weidlich et al., 2020). Previous studies utilizing various *Lupinus* species have illustrated positive tree growth response and increased N acquisition (Prietzel et al., 2008; Mauer et al., 2013; Oldřich et al., 2013). Other projects have also shown that neighboring vegetation acts as “nurse plants” that moderate soil temperatures, increase water and nutrient availability, and promote microbial interactions (Bertness and Callaway, 1994; Raffaele and Veblen, 1998; Flores and Jurado, 2003). *L. lepidus* has also been reported to stimulate microbial activity in primary successional soils at Mount Saint Helens (Halvorson et al., 1991). Ectomycorrhizal fungi are key components of PNW forest soils, forming symbioses with conifers (Kranabetter et al., 2015). ECM fungi perform a variety of functions that contribute to the establishment, survivability, and resilience of planted seedlings (Massicotte et al., 1999; Smith and Read, 2008). Mature soils typically support diverse and abundant fungal communities essential to forest health (Balestrini et al., 2016). However, dam removal and deposition of coarser sediments may not be conducive to the formation of these symbioses, thus limiting tree establishment after dam removal (Cortese and Bunn, 2017). Therefore, lupine’s presence may facilitate soil development to promote ECM colonization of conifer roots, thereby supporting plant establishment and native plant community recovery.

In this study, we explored how varying densities of riverbank lupine affected the performance of planted conifers (Douglas fir, grand fir, and western white pine), ECM root colonization, soil N and organic matter (OM), and neighboring plant communities in coarse substrates on the exposed terraces of Lake Mills along the Elwha River. We hypothesized that greater lupine densities would result in greater conifer growth, foliar N concentrations, and greater ECM taxonomic richness and colonization. We also hypothesized that greater lupine densities would yield greater C:N, OM, and N content in coarse sediment. Finally, we hypothesized that plant species richness would be lower and community composition would differ in areas of greater vs. lesser lupine density. Documenting species interactions that accelerate succession by aiding the growth of conifers and the development of native plant communities and soils may help future projects that will have to manage the revegetation of coarse sediments left behind after dam removal.

Materials and methods

Study area

The field study was located in Olympic National Park (ONP) along the Elwha River at the location of the former Lake Mills reservoir behind the Glines Canyon dam (Figure 1). The dam was removed over the course of 3 years, and work was completed in 2014. Biologists at ONP and Lower Elwha Klallam Tribe implemented the Elwha River and Ecosystem Restoration Project, which had multiple restoration goals: establishing native vegetation to accelerate forest succession, controlling erosion, regulating water temperature, creating habitat, and limiting exotic plant invasion (Chenoweth et al., 2011).

The study area occupied multiple southwestern terraces approximately 1.6 km from the former dam (Figure 1). Conifers were grown in the greenhouse for 3 to 4 years, planted on the restoration site, and grew for approximately 3 years prior to our study in 2017. Areas where trees and shrubs were planted received 430 seeds per square meter from the ONP revegetation crew between 2013 and 2014. Seed mixtures contained a combination of 10 locally harvested and produced grass and forb species at the following quantities: common yarrow (*Achillea millifolium*; 44.2 kg), spiked bentgrass (*Agrostis exarata*; 4.0 kg), Suksdorf’s sagewort (*Artemisia suksdorfii*; 69.2 kg), Pacific brome (*Bromus pacificus*; 933.5 kg), sedges (*Carex pachystachya* and *Carex deweyana*; 202.4 kg combined), slender hairgrass (*Deschampsia elongata*; 75.1 kg), blue wild-rye (*Elymus glaucus*; 1,367.0 kg), Oregon sunshine (*Eriophyllum lanatum*; 70.1 kg), and riverbank lupine (*L. rivularis*; 59.5 kg; Chenoweth et al., 2022). Lupine was one of the few species that grew vigorously and spread to dominate many restoration areas. However, species were not seeded uniformly, and lupine was established at varying densities along the terraces (J. Chenoweth, per. comm).

Twenty-four plots (8 m × 8 m) were established to capture the range of lupine cover using the transitional zones where lupine is abundant in high to low densities along the western terraces of the Lake Mills reservoir bed (Figure 1). Plots were assigned by visual assessment based on relative cover and assigned one of three density classes: sparse, medium, or dense (eight plots each). Cover-class estimates of lupine abundance confirmed significant differences in the mean cover of lupine among density classes in 8-m^2 plots: dense = 76% (± 0.04%, medium = 58% (± 0.04%), and sparse (15% ± 0.02%) ($F_{(2,21)} = 72.94$, $p < 0.001$).

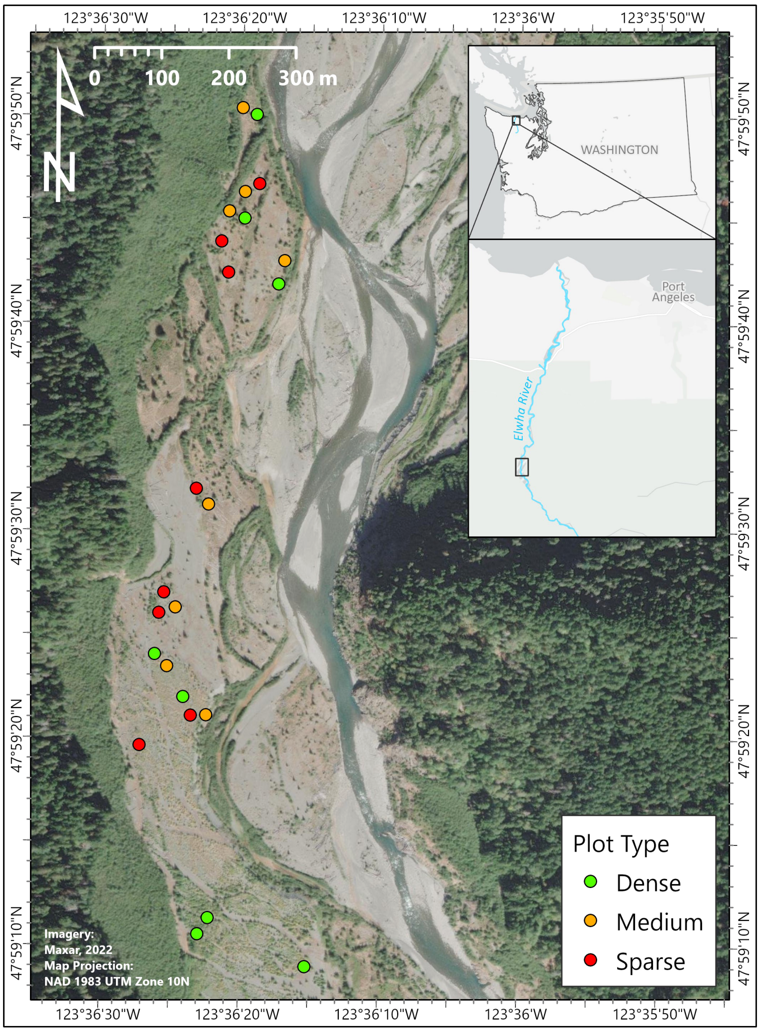

FIGURE 1
Western terraces formed after the drawdown of Lake Mills along the Elwha River located 22 river km from the mouth. This area was dewatered between 2012 and 2014 via the removal of the Glines Canyon dam. The multiple southwestern terraces were comprised of coarse sediment, sand, and cobble and were actively planted and seeded between 2013 and 2014 with study plots established in 2017. Twenty-four study plots represent three distinct densities of lupine: green = dense (76% lupine cover), orange = medium (58% lupine cover), and red = sparse (15% lupine cover). Map provided by Alex Harnick.

Each plot contained approximately 8–10 living conifers consisting of Douglas fir (*P. menziesii*), grand fir (*A. grandis*), and western white pine (*P. monticola*). After each plot was established, all living conifers were inventoried and numbered. From among the trees in each plot, three were randomly selected, yielding a total of 36 Douglas fir, 21 grand fir, and 15 western white pine. Each tree was assessed for its growth (height and basal diameter), foliar N, and ECM colonization. Soil N and OM and neighboring vegetation were also assessed (described below).

Conifer height, diameter, foliar N, and ECM colonization

Conifer height and basal diameter were measured in October 2018. Height (nearest cm) was measured from the ground surface to the top of the apical bud. Basal diameter (nearest mm) was measured approximately 2 cm above the soil surface using a mechanical caliper. At the beginning of the dormant season (October 2018) when foliar N concentrations had stabilized (Harrison et al., 2011), a small foliar sample (3–5 cm length) of the current year's growth was taken from each tree by clipping a branch tip. Samples were oven-dried for 1 week at approximately 45°C, ground to a fine powder using a mortar and pestle, and placed in a desiccant chamber for sample preservation. Foliar N concentrations were measured at the Western Washington University, Bellingham campus, using the Thermo Scientific Flash EA1112 Elemental Analyzer (Thermo Electron Corporation, Milan, Italy).

During growth and foliar tissue collection, root tips were excavated from each tree for ECM analysis. These sites were extremely rocky and difficult to sample with cores or probes. Therefore, sediments and rocks were removed with a spade to expose the conifer root system by carefully trenching approximately

50 cm from the base of each seedling to a depth of 25 cm and a width of 45 cm. Approximately three to five root segments that were 10–12 cm long and 1–3 mm in diameter were removed, placed in a plastic bag within a cooler, returned to the laboratory, and stored at 4°C until further processing (described below). At the same time, soil samples for N analysis were extracted (approximately 0.50 L) using a spade to a depth of roughly 18 cm adjacent to the roots of each tree.

Vegetation richness and community composition assessment

Vegetation composition was recorded in a circular, 2-m^2 quadrat centered on selected trees. All plant taxa were identified to species, if possible, and plant abundance was visually estimated by cover class: 1 (<1%), 2 (1% to 10%), 3 (11% to 25%), 4 (26% to 50%), 5 (51% to 75%), 6 (76% to 90%), and 7 (>90%). Species richness was expressed as the number of species accumulated across the three quadrats. All plants were identified to species using Hitchcock and Cronquist (1973) and Pojar and MacKinnon (1994). Species were classified as native or introduced (whether naturalized or not). Botanical nomenclature and nativity followed the plant profile descriptions outlined by the United States Department of Agriculture, PLANTS Database (USDA and NRCS, 2023). Species richness included all planted, seeded, or naturally recruited species within each quadrat. *L. rivularis* and any planted trees were excluded from the community-level analyses (described below).

Soil texture/particle size distribution

To account for the heterogeneity of the sediment, the soil-particle size distribution in each quadrat was assessed. Particle size-class data were collected at 10-cm intervals along two 1.6-m perpendicular transects per quadrat (36 counts per quadrat). The Wentworth scale was used to classify each randomly selected particle by length along the shorter axis (Wentworth, 1922; Supplementary Table 1). The median particle size in each quadrat was determined and assigned as a categorical variable from the Wentworth scale. The average length of each Wentworth size class was determined and assigned to the median of the particle count as a numeric value. Small particle sizes such as sands (0.13 to 1 mm) and silt (<0.13 mm) were not measured directly but were determined by rubbing the selected particles between finger and thumb, with silts being smoother to the touch than sands.

Soil organic matter and nitrogen

Soil collection for OM content was performed by taking the first 3 cm of sediment in four locations per quadrat and compositing them (n = 24; 250 g per composite sample). At the time of sampling, soils were placed in sealed bags after collection, and mass was determined pre- and post-drying. Samples were placed in a drying oven at 45°C for 1 week. Soil OM was measured using weight-loss-on ignition (Wang et al., 2001). Dried samples were weighed, then heated at 540°C for 5 hours in a Nanbei muffle furnace, and then weighed again to calculate OM content (%). After ashing, each sample was weighed to calculate the difference between dry and burned composites, indicating the OM (g) content of the soil sample. A portion of each composite sample was used to determine total N (%). Subsamples were ground to a powder with a Spex Mill grinder, and N content was determined with a Thermo Scientific Flash EA1112 Elemental Analyzer (Thermo Electron Corporation, Milan, Italy).

Ectomycorrhizal colonization and identification

In the laboratory, root tips were washed and placed in a Petri dish in autoclaved, distilled water. Roots were cut into 3-cm segments, and 100 randomly selected root tips per tree were scored for presence/absence of ECM (i.e., presence/absence of a fungal sheath; Simard et al., 1997; Massicotte et al., 1999). ECM colonization was expressed as the percentage of root tips with a fungal sheath. A 3-mm segment of ECM root tip was homogenized using a mortar and pestle, and DNA was extracted using appropriate buffers and filter columns provided by QIAGEN® DNeasy Plant Pro Kit per manufacturer's protocol (QIAGEN, Germantown, MD, USA). Approximately 10 ng of this DNA was used for PCR amplification using primers ITS1-F (5′ cttggtcatttagaggaagtaa 3′) and ITS4 (5′ tcctccgcttattgatatgc 3′; Gardes and Bruns, 1993). PCRs were based on the following concentrations for a 25-µl reaction: 12.5 µl of GoTaq® Green Master Mix (Promega, Madison, WI, USA), 0.25 µl of 25 µM of each primer, 11 µl of molecular grade water, and 1 µl of DNA template. Temperature cycling was accomplished using GeneAmp PCR System 9700, which allowed for a programmable Thermal Cycler Heating regimen (described in Bauman et al., 2022).

Positive PCR products were confirmed using gel electrophoresis and purified using a Wizard® SV 96 Genomic DNA Purification System (Promega, Madison, WI, USA). DNA concentration was quantified using a Thermo Scientific 2000 1-position Spectrophotometer (Thermo Fisher Scientific, Pittsburg, PA, USA) prior to sequencing. Sanger sequencing was performed using the Applied Biosystems ABI Prism 3730 DNA Analyzer (Retrogen Inc., San Diego, CA, USA). The DNA sequences were analyzed and edited using Retrogen Inc. software. To identify the fungus found on roots, internal transcribed spacer (ITS) sequences from samples were compared with those in the GenBank using the BLAST search (Altschul et al., 1997). The genus of each fungus reported in this study was based on the best matches of those in the GenBank with a >97% ITS sequence similarity as a threshold.

Statistical approach

Linear mixed-effects models (Zuur et al., 2007) were used to assess the relationships between relative abundance of lupine (cover class) and tree height (cm), tree basal diameter (mm), ECM root colonization (%), foliar and soil C:N, foliar and soil N (%), soil OM (%), species richness, and number of non-native species. Lupine cover class was the fixed factor in the model. Tree species and median soil particle size class comprised the random factors to account for varying genotypes and heterogeneity of substrate, respectively. In its simplest form, the linear mixed-effects model can be written as follows:

$$Y_{ijkl} = \mu + L_i + S_j + T_{(i)k} + \epsilon_{(ijk)l},$$

where Y is the response variable, L_i is the fixed effect of lupine cover class (dense, medium, or sparse), S is the random effect of median soil particle size class using the Wentworth scale, T is the random effect of tree species nested within the lupine cover class, μ is the true mean response among all experimental units, and ϵ is residual error.

Evaluation of mixed-effects model terms was performed using ANOVA tests and posterior predictive simulation to make an informed judgment on model fit using lme4: mixed-effects modeling with R (Gelman and Hill, 2006; Bates et al., 2015). The ANOVA tested for the significance of the fixed and random effects on each response variable ($\alpha = 0.05$). The Welch–Satterthwaite equation was used to calculate the approximate degrees of freedom. Significant ANOVA products were evaluated for differences among lupine cover classes using Fisher's least significant difference (LSD) pairwise comparisons. Fisher's LSD procedure reduces the risk of false-positive judgments when the number of planned comparisons is small, as in this study (Marcus et al., 1976; Keppel, 1991; Meier, 2006; Gamst et al., 2008). The posterior predictive simulation (predictive power %) of the model was examined by generating an ensemble of simulations (n = 1,000) and observing how often the model predictions fell within the inner quartile range of the observed data to examine model fitness (Gelman and Hill, 2006).

To assess parametric test assumptions, all data were examined for normality and homoscedasticity using the Shapiro–Wilks and Levene's tests, respectively. To achieve equal variance, transformations were performed on soil particle size (ψ; numeric class value squared) and ECM abundance (square root). Particle size gradation has a logarithmic scale ($\log_2$) since it doubles between each size class when expressed metrically as a length. Therefore, $\log_2$ was applied to the mean value for each particle bin level to produce ψ (Bunte and Abt, 2001). All statistical analyses were performed using the R Core Team (2013).

Permutational multivariate analysis of variance (PERMANOVA) was used to compare community composition among lupine cover classes. Planted trees and rare species (those with<1% cover) were excluded from the analysis. PERMANOVA was performed using the adonis function in the vegan package in R (Oksanen et al., 2010). The compositional variation among lupine cover classes was illustrated graphically with a non-metric multidimensional scaling (NMDS) ordination of a plot × species-abundance matrix using cover-class midpoints. The analysis was run with the metaMDS function in R using Bray–Curtis as the measure of dissimilarity (Oksanen et al., 2010). Plant species cover values were standardized via Wisconsin double standardization to improve results by equalizing emphasis among sample units and species. With the use of the indicspecies package, a multipattern analysis was used to identify the set of species with the highest association value with the perspective lupine cover classes using the multipatt function (De Cáceres and Legendre, 2009). A multi-level pattern analysis allowed species to be indicators of the three lupine cover classes by calculating an indicator value based on the product of the species' relative abundance and relative frequency within each plot. The significance was determined by $\alpha = 0.05$ for all analyses performed for this study.

Results

Conifer growth, foliar N concentrations, soils, and ECM colonization

Tree height was statistically similar among the three lupine cover classes: dense (35.7 ± 3.4 cm), medium (39.0 ± 2.4 cm), and sparse (33.0 ± 2.0 cm). Basal diameter followed the same non-significant trend when compared: dense cover (10.2 ± 0.6 mm), medium cover (9.7 ± 0.5 mm), and sparse cover (11.0 ± 0.6 mm). Foliar N concentrations did differ; conifers in dense- (1.8% ± 0.12%) and medium-cover (1.6% ± 0.09%) classes had higher concentrations of foliar N than those in sparse cover (1.3% ± 0.08%; $\beta = 0.25$, $SE = 0.08$, $p< 0.001$; Figure 2A).

Soil OM did not differ among the cover classes and averaged 0.02% ± 0.001%, regardless of the density. Similarly, total soil N did not differ statistically: dense cover (1.8% ± 0.11%), medium cover (1.6% ± 0.09%), and sparse cover (1.3% ± 0.08%). None of the response variables showed significant variation related to median soil particle size or tree species (random effects in the mixed models).

ECM root colonization was greater in plots with sparse lupine cover (0.31% ± 0.08%) than in plots with dense-cover (0.12% ± 0.05%) and medium-cover plots (0.12% ± 0.04%; $\beta = 0.14$, $SE = 0.03$, $p = 0.03$; Figure 2B). Nine fungal taxa were detected on conifer roots (Table 1). The most frequent were *Thelephora terrestris* and *Wilcoxina mikolae*. *Suillus luteus*, *Tuber pacificum*, *Hebeloma velutipes*, and *Rhizopogon* were also present, but less common. Non-ECM taxon included a pathogen (*Phialocephala* sp.) and two endophytes, one in the order Helotiales and the second a species of Leptosphaeria (Table 1).

Vegetation community composition

In total, we observed 49 plant taxa in plots, which included planted, seeded, and naturally recruiting species (Supplementary Table 2). Of these, 11 were grasses, 16 were forbs, and 22 were trees or shrubs. Plant species richness was greater in plots with sparse cover (28.5 ± 1.37) than in plots with medium cover (24.3 ± 0.89), while richness in plots with dense cover (25.2 ± 0.99) did not differ significantly from that of either sparse- or medium-cover plots ($\beta = 25.9$, $SE = 0.61$, $p = 0.04$; Figure 2C). The number of non-native plant species did not differ among the lupine cover classes.

An NMDS ordination illustrates a greater degree of compositional similarity between dense- and medium-cover plots

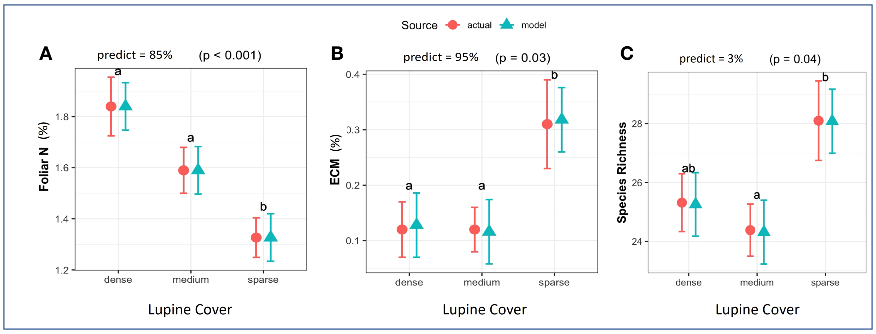

FIGURE 2
Response variables for which lupine cover class was a significant predictor in the mixed-effects models: **(A)** foliar N, **(B)** percent ectomycorrhizal (ECM) root colonization, and **(C)** species richness (mean number of species per 2-m^2 quadrat). The modeled intercept and standard error were included to offer a visual comparison of measured (actual) vs. predicted (model). At the top of each plot, the "predict" value (%) quantifies the predictive power of the model, and the *p*-value indicates model significance. Treatments that do not share the same letter are significantly different ($\alpha = 0.05$).

than between medium- and sparse-cover plots (stress = 0.12, k = 2; Figure 3). The separation of dense- and sparse-cover plots along NMDS1 is consistent with their compositional difference, as determined by PERMANOVA ($F_{(2,21)} = 2.02$, $p = 0.01$). *Vulpia* (VUPR) appeared associated with the sparse-cover plots, whereas *Aira* species (AICA and AIPR), hairy cat's ear (HYRA), Oregon sunshine (ERLA), and blue wild rye (ELGL) were associated with the dense-cover plots (Figure 3). Results of a multipattern analysis indicated that no species were indicators of the sparse lupine-cover plots, but wood groundsel (SESY) and black cottonwood (POBA) were indicators of the medium- and dense-cover plots (all $p < 0.05$).

Discussion

We documented lupine's ability to thrive in highly disturbed landscapes without reducing the growth of planted conifers. A direct benefit included an increase in foliar N concentrations among seedlings growing in the medium and dense lupine cover classes. An unexpected finding was the reduction of ECM on conifer roots in medium and dense lupine plots. In addition, areas of dense lupine cover had fewer, and a different composition of, species than did areas of sparse lupine cover.

TABLE 1 List of ectomycorrhizal (ECM) fungi sampled from the roots of three conifer species planted on the dewatered terraces of Lake Mills in the Elwha River Valley.

ECM taxa	Proportion	Function
Thelephora terrestris	0.56	ECM
Wilcoxina mikolae	0.16	ECM
Suillus luteus	0.05	ECM
Tuber pacificum	0.04	ECM
Hebeloma velutipes	0.03	ECM
Rhizopogon sp.	0.01	ECM
Phialocephala sp.	0.01	Pathogen
Leptosphaeria sp.	0.01	Endophyte
Helotiales	0.01	Endophyte

Nine taxa were identified, listed in descending order of occurrence (mean proportion of 100 randomly selected root tips per tree). Taxa were verified using DNA sequencing of the internal transcribed spacer (ITS) region of the fungal genome and compared to known sequences in GenBank.

There was no difference in tree height or diameter among the three lupine cover classes. This differed from Mauer et al. (2013), who demonstrated Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), and Scots pine (*Pinus sylvestris*) to have an increased height and collar diameter when sowed among three species of lupine (*Lupinus angustifolius*, *Lupinus albus*, and *Lupinus polyphyllus*) after a 5-year growing period. In our study, greater foliar N was correlated with greater cover of riverbank lupine—at concentrations well above those deemed adequate for conifers in the PNW (N > 1.25%; Radwan and Brix, 1986; Walker and Gessel, 1990). Scots pines also showed an increase in foliar N levels during the first decade of growth when lupine was present (Prietzel et al., 2008). N-fixation by both *Alnus incana* and *Lupinus nootkatensis* was incorporated into the foliage of birch trees after 20 years on degraded forest soils (Myrold and Huss-Danell, 2003).

We also demonstrated a significant reduction of ECM colonization on conifer roots in the medium- and dense-cover plots. One possible explanation for the decrease in ECM colonization is that conifers may reduce carbon allocation to their ECM symbiont when N is not limiting (Corrêa et al., 2008). Our results support other research illustrating that carbon transfer from the host plant to the fungal symbiont depends on the N status of the tree (Nilsson et al., 2005). Field studies have documented that nitrogen fertilization can directly reduce ECM growth and colonization rates on longleaf pine (*Pinus palustris*; Sims et al., 2007). Ostonen et al. (2011) demonstrated that as N deposition loads increased, ECM biomass decreased in stands of Norwegian spruce (*P. abies*). This phenomenon was also observed by Nilsson and Wallander (2003) where Norwegian spruce under N additions resulted in a 50% ECM reduction when compared to trees within non-fertilized plots. This finding supports hypotheses that speculate mycorrhizal relationships range from mutualistic to parasitic,

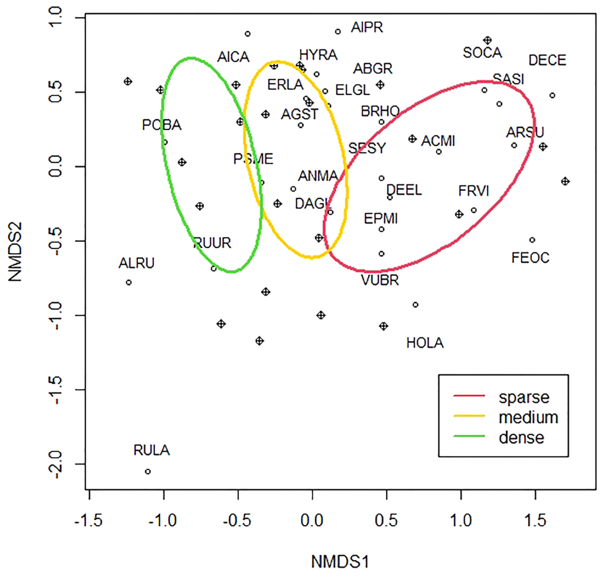

FIGURE 3
Non-metric multidimensional scaling (NMDS) ordination of plots representing the three lupine cover classes. Plant species centroids are represented by four-letter codes (see Supplementary Table 2 for the full names of species), and plots are represented by circles with crosses. Ellipses represent the 95% confidence intervals of plots within each lupine cover class.

depending on soil nutrient status (Johnson, 1993; Johnson et al., 1997). Therefore, we propose a new hypothesis that investing carbon in non-photosynthetic symbionts is more costly than acquiring N from neighboring N-fixers.

We found less ECM species richness on novel terraces. Of the taxa identified, *T. terrestris* and *W. mikolae* were the most abundant. Both of these species are noted as among the most ubiquitous greenhouse and field ectomycorrhizas symbiotic with grand fir, Douglas fir, and western white pine (Massicotte et al., 1999; Hilszczańska and Sierota, 2013). Rare species included *S. luteus*, *T. pacificum*, and a *Rhizopogon* sp., all considered prevalent in PNW forests (Dahlberg, 2001). In addition, the average root colonization was rather low (averaged 30% ECM root tips). Soil organic matter is important for mycorrhizal symbioses, and studies have shown that mycorrhizal infection increases with organic matter amendments (Baar and DeVries, 1995; Lunt and Hedger, 2003). This low rate of colonization and small species list likely reflect a soil environment insufficient to support functional mycorrhizas (Cortese and Bunn, 2017).

As nitrogen fixers, *Lupinus* species develop N pools via atmospheric N fixation, which become available to plants via the mineralization of organic N into ammonium (Vitousek et al., 2002; Robertson and Groffman, 2007). While this study illustrated lupine's ability to influence bioavailable N to neighboring conifers, we did not see differences in total soil N. In addition, we observed no differences when C:N and OM were compared among the lupine cover classes. The inability to detect differences in soil N may have been due to immediate bio-assimilation by conifers and neighboring vegetation coupled with N leaching in sediments with low water/nutrient holding capacity. We acknowledge that the measure of soil N was a single point-in-time measurement of total N, which could explain the lack of difference in soil N among lupine cover classes. Future work would benefit from the use of ion exchange resins, which integrate N availability over time (Qian and Schoenau, 2002). We noted that lupine litter-fall was abundant on the soil surface 4 years after seeding/planting; additional time may be needed to observe changes in the soil profile (Vitousek et al., 2002). In comparison, Halvorson et al. (1992) and Halvorson and Smith (1995) measured significant organic matter production and total increased N near the lupine's (*L. lepidus* and *Lupinus latifolius*) rhizosphere, 7 years after the Mount Saint Helens eruption.

With regard to the vegetation community, we found that species richness decreased in plots with abundant lupine. This was also documented following the Mount Saint Helens eruption; Morris and Wood (1989) demonstrated that Pacific lupine (*L. lepidus*) inhibited immediate colonization of forbs in the early years, while later studies demonstrated a subsequent increase in plant community species richness that was accelerated by the presence of lupine (del Moral, 2007). We also found compositional differences in plots with dense vs. sparse lupine cover, suggesting that lupine may influence the trajectory of community development during primary succession (del Moral and Rozzell, 2005). The increase observed in plant species in the sparse lupine plots included a few rare native and non-native plants; however, the non-native species count was not different among the cover classes, and neither species was in high abundance or a significant indicator of sparse cover class. Chenoweth et al. (2022) found that seeding herbaceous species (including lupine) on these coarse terraces deterred non-native species establishment. This is of particular importance in coarse, nutrient-poor substrates with the lack of canopy closure that creates an opportunity for the invasion of exotic ruderal (Shafroth et al., 2002; Tabacchi et al., 2005; Funk and Vitousek, 2007; Michel et al., 2011). Important to the overarching goal of accelerating forest succession, lupine's potential role as a beneficial cover crop may aid in the establishment of planted conifers while deterring non-native plant communities (Fierke and Kauffman, 2006; Peltzer et al., 2009; Urgenson et al., 2009).

Conclusion

The damming and the subsequent dewatering of Lake Mills created a phenomenal disturbance, leaving novel terraces void of ecological legacies. Similar to the post-eruption landforms colonized by lupine at Mount Saint Helens, seeded lupine in the Elwha River Valley was able to establish on the barren substrates. Important to restoration projects, lupine's cover did not impede conifer growth in the early years of planting. We acknowledge that we used natural variation in lupine density as a predictor of conifer performance and soil development; therefore, lupine density itself could be a response to variation in soils, vegetation, or other environmental features. Spatial variation in lupine abundance could be caused by or otherwise confounded with other environmental conditions that were not measured. Regardless, when comparing conifer growth within dense lupine cover, lupine canopies were not found to be detrimental.

Further, lupine's contribution to bio-available N promoted adequate foliar nitrogen concentrations that may contribute to greater growth in the subsequent years. It is not clear whether this increase in available N was the mechanism behind the inverse relationship with lupine and ECM root colonization; however, current research is further investigating this. This may be an explanation of tradeoffs: ECM fungi aid in nutrient uptake/growth in low lupine density cover, but N-fixation by lupine serves this function at higher densities.

This study also illustrates the challenges for revegetation in coarse sediments and the important function of a cover crop on sediment surfaces. Lupine OM contributions are an important attribute for the successional trajectory, given its biennial life cycle and ability to tolerate resource-limited soils. Although lupine did not contribute to an increase in soil carbon or OM, we hypothesize that lupine will contribute important carbon pools to the forest soil-building process after a decade of recovery, which may also lead to an increase in ECM fungal colonization and native plant recruitment. Importantly, this study also documented the benefits of including a locally native N-fixing species (riverbank lupine) in the Elwha River Restoration project, which can inform future practitioners when considering strategies of revegetation after dam removal. Based on our findings and corroborative literature, we recommend the inclusion of native lupine in highly disturbed, N-limiting soils to contribute to the N pools for native tree establishment. These attributes may accelerate forest succession leading to closed canopies much faster than passive recovery on coarse soils.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

JK: literature review, study design, data collection and analysis, and synthesis. MDL: DNA extraction and PCR. AL: DNA extraction and PCR, and literature review. JB: literature review, study design, data collection and analysis, synthesis, and project oversite. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1214117/full#supplementary-material

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Large wood supports Elwha revegetation by reducing ungulate browsing

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Introduction: The increasing number of dams approaching obsolescence drives a need for knowledge about riparian restoration associated with dam removal. Restoring woody vegetation on exposed reservoir beds following dam removal is essential to stabilizing sediment, reconnecting riverine and terrestrial systems, and providing future sources of shade, nutrients, and wood. Revegetation after dam removal on many rivers can be challenging due to rapidly drying sediment, low sediment nutrient content, and heavy ungulate browse pressure. Revegetation in Elwha River restoration, the largest dam removal to date, used large woody debris (LWD) to mitigate moisture and nutrient limitation but ungulate browsing has constrained woody plant growth in many coarse sediment deposits. We evaluated potential for LWD to reduce ungulate browsing following Elwha dam removal.

Methods: We studied LWD mitigation of browsing in the largest former reservoir and a comparable valley upriver with a natural floodplain. We measured browse intensity in randomly located plots stratified by four levels of LWD extent, from no LWD to complete LWD enclosure.

Results: LWD reduced browse intensity four-fold in the former reservoir, but only in plots fully surrounded by LWD. Partial LWD enclosure provided little browse reduction. We obtained similar results in the upriver valley, where browse intensity was somewhat lower except within wood clusters. Wood-mediated browse reduction was slightly greater in the former reservoir than in the upriver valley. Protection from browse was greatest for plant species preferred by ungulates.

Discussion: These results suggest forest restoration after dam removal can be expedited by surrounding young trees with large logs. Planting within LWD clusters or placing LWD clusters in restoration sites can facilitate establishment of forest islands in strategic locations. These forest islands can support dispersal of seeds and marine derived nutrients, reconnect established forest to the river, and potentially advance restoration by decades.

KEYWORDS

forest restoration, LWD, dam removal, plant growth, forest–river connection, deer, elk

1 Introduction

Rivers are vital to humanity and biodiversity (Lynch et al., 2023), but rivers are among the most imperiled systems on Earth (Dudgeon et al., 2006; Reid et al., 2019). Dams and impoundments are pervasive threats, impacting 60% of large rivers on Earth (World Commission on Dams, 2000) and all large river basins in the contiguous US (Graf, 1999). Dam removal is becoming widely recognized for efficacy in river restoration (O'Connor et al., 2015). Dam removal restores longitudinal connections in river systems, facilitating rapid responses by aquatic biota (Duda et al., 2021). Restoring lateral terrestrial–aquatic connections is slower and more challenging. Many dams sever connections between rivers and terrestrial systems by replacing lotic reaches with slackwater impoundments (Hjältén et al., 2016). After dam removal, reservoirs become open sediment deposits separating rivers from mature terrestrial habitats. Restoring mature habitats and vegetation on those sediments is at least challenging due to absence of structural legacies, rapid desiccation (Chenoweth et al., 2021), low sediment nutrient concentrations (Cavaliere and Homann, 2012), missing mycorrhizae (Cook et al., 2009; Cortese and Bunn, 2017), and herbivore browsing (Osei et al., 2015; McCaffery et al., 2020).

Restoring vegetation, habitat, and terrestrial–river connectivity is substantially more difficult for large dam removals than smaller projects because large dams and reservoirs create disproportionately large impacts. While small narrow impoundments may remain under the influence of adjacent stands of mature vegetation, large reservoir beds impose large distances separating active channels from mature vegetation. Restoring connections in small vs. large reservoir beds involves different processes and time scales. For example, the gap between an active channel and mature forest could be bridged by a single treefall on a narrow impoundment. Reconnecting river and forest across large reservoir beds requires growing forest on sediment deposits, which may take up to a century in boreal and temperate regions. Limited shade on large reservoir beds renders sediments prone to desiccation (Chenoweth et al., 2021), which further slows revegetation. Large reservoir sediment deposits are more distant from agents of ecological functions that support restoration, including litterfall, seed dispersers, and marine derived nutrient dispersers (McCaffery et al., 2018). Large rivers and river valleys support more complex channel dynamics, where extensive areas can be scoured and re-set to early successional seres (Collins et al., 2012). Similarly, revegetation in large reservoir beds may be impacted by disturbance regimes and patch dynamics that do not occur in smaller restoration projects. Relative effects of browse on revegetation following small versus large dam removals are unknown, due to limited study and complexity of confounding factors. Restoration site area, browser population abundance and seasonal distribution, adjacent habitat characteristics, alternative browser food sources, and exposure to predators may affect browse intensity in complex ways related to or independent of dam size. These issues are compounded by uncertainty: system responses to large expanses of sediment are unknown (Prach et al., 2019), with few prior large dam removals to serve as models. In summary, restoration following large dam removal is qualitatively distinct from small dam removals. Some lessons from small dam removals do not scale up simply to large projects, compelling a need to study large dam removals directly.

Restoring habitats and vegetation to dewatered reservoirs involves multiple challenges at several plant life stages (Table 1). Challenges at each stage must be overcome, culminating with browse mitigation during plant establishment and maturation stages addressed in this paper. First, plants must reach appropriate locations via active planting (Chenoweth et al., 2021) or seed dispersal by wind, water (Cubley and Brown, 2016), or animal vectors (Wang and Smith, 2002). Germination of dispersed seeds requires suitable sites and adequate moisture, which may be mediated by sediment texture (Osei et al., 2015), timing of reservoir drawdown (Muldavin et al., 2017; Chenoweth et al., 2021), or structures used by animal dispersers (McLaughlin, 2013). Plant establishment and growth require consistent sediment moisture, adequate nutrients, moderate temperatures, and protection from excessive herbivory (Maschinski et al., 2004; Heneghan et al., 2008; Osei et al., 2015). These needs can be addressed in part by planting adjacent to logs (Calimpong, 2014; Marangon et al., 2022), translocating large wood (McHenry and Chenoweth, 2015; Neilly and Cale, 2020), seeding nitrogen-fixing plants (Chenoweth et al., 2021), and inoculating with mycorrhizae (Hoeksema et al., 2010; Hawkins et al., 2015). Plant growth to maturity requires resources similar to establishment, with protection from herbivory becoming particularly important in systems with abundant browsers (Opperman and Merenlender, 2000; Peinetti et al., 2001; Zeigenfuss et al., 2002; Osei et al., 2015; Averett et al., 2017). Where intense browsing is not mitigated, plants can remain in an arrested growth form (Keigley, 1997) or become eliminated entirely (Opperman and Merenlender, 2000; Whyte and Lusk, 2019). Impacts of unrestrained browsing can persist for decades (Reed et al., 2021; Woodward et al., 2021).

Several interventions to mitigate vertebrate browsing have documented efficacy, including fencing, tree shelters, apex predator restoration, and large woody debris. Fencing can exclude herbivores (Opperman and Merenlender, 2000; Brookshire et al., 2002; Maschinski et al., 2004; Monks et al., 2023), but only if fences are maintained (Woodward et al., 1994). Fences can create undesirable impacts to connectivity (Jakes et al., 2018; Xu et al., 2021), and may contradict land management policies in some restoration sites. Tree shelters can increase woody plant survival rate substantially (Stange and Shea, 1998), but plastic residue may not be desirable in some sites. Reintroducing predators can restore riparian shrubs and forests by restoring "landscapes of fear" that reduce browse in riparian zones (Beschta and Ripple, 2008; Beschta and Ripple, 2010). Social and political factors may determine where this approach is practicable (Chapron et al., 2014; Richardson, 2023; Wakeling, 2023). Large wood can reduce ungulate access to plants, facilitating growth to maturity where otherwise browsing would exclude or suppress woody plants (Rooney, 1995; Schreiner et al., 1996).

Despite consistent efficacy of natural or placed large wood in mitigating browse impacts, this strategy has received limited attention in the restoration literature. Managing browse with

TABLE 1 Plant recruitment stages, mediating factors, and potential restoration interventions.

Stage	Mediating Factors	Interventions	References
Seed dispersal	Wind Water currents Animal abundance & behavior Sediment distribution	Drawdown timing LWD translocation Active seeding & planting	Nathan and Muller-Landau, 2000 Wang and Smith, 2002 Shafroth et al., 2002 McLaughlin, 2013 Cubley and Brown, 2016 Prach et al., 2019 Chenoweth et al., 2021
Germination	Sediment distribution Seed predation Sediment moisture Microhabitat suitability	Drawdown timing LWD translocation Active planting	Shafroth et al., 2002 Schmitz et al., 2009 Michel et al., 2011 Nakamura et al., 2012 McHenry and Chenoweth, 2015 Muldavin et al., 2017 Chenoweth et al., 2021 Brown et al., 2022
Establishment	Sediment erosion Sediment moisture Nutrients Soil biota Soil organic matter Mycorrhizae Temperature Invasive plants Herbivory	LWD translocation, LWD clusters, Mycorrhizal inoculation Lupine seeding Invasive species removal Supplemental watering	Maschinski et al., 2004 Orr and Koenig, 2006 Orr and Stanley, 2006 Heneghan et al., 2008 Hoeksema et al., 2010 Michel et al., 2011 Cavaliere and Homann, 2012 Nakamura et al., 2012 Kim et al., 2014 Hawkins et al., 2015 Horner et al., 2016 McHenry and Chenoweth, 2015 Muldavin et al., 2017 Lisius et al., 2018 McCaffery et al., 2020 Chenoweth et al., 2021
Maturation	Light intensity Soil moisture Soil properties Nutrients Mycorrhizae Herbivory	LWD translocation LWD clusters Mycorrhizal inoculation Lupine seeding Fencing Carnivore reintroduction	Shafroth et al., 2002 Brookshire et al., 2002 Montgomery and Abbe, 2006 Heneghan et al., 2008 Beschta and Ripple, 2010 Hoeksema et al., 2010 Collins et al., 2012 Hawkins et al., 2015 Chenoweth et al., 2021

Vegetation restoration involves multiple factors during all four stages in the table, but the focus of this paper is the single factor of browse during establishment and maturation stages. The table includes other stages, factors, and interventions to set browse in context and to facilitate cross-disciplinary understanding.
Intervention descriptions and additional citations are in the body of the article.

large wood has been reported in fewer than 25 articles in the last 30 years, based on work on four continents. Just two articles addressed wood-mediated browse reduction in riparian systems (Matney et al., 2005; Muldavin et al., 2017). By comparison, more than 500 articles were published in the same period on limiting browse by other means or measuring its impacts in sites on six continents. Similarly, only 22 of the 306 unduplicated sources in the USGS Dam Removal Science Database (Duda et al., 2018) addressed vegetation responses to dam removal. Of those 22, just 5 considered large wood, and only one (McCaffery et al., 2020) mentioned the potential for large wood to reduce browse. The discrepancy between efficacy and attention to wood-mediated browse reduction may reflect a dearth of large wood in most forests and rivers, following centuries of large wood removal (Rooney, 1995; Wohl, 2014). We worked to address this discrepancy in forest restoration associated with dam removal.

We studied ungulate browse on woody plants in recently exposed sediments in broad valleys along the Elwha River, site of humanity's largest dam removals to date (Ritchie et al., 2018). Our goal was to determine whether large woody debris (LWD) can protect young woody plants from ungulate browsing. Initial observations suggested six hypotheses regarding effects of browsing and large wood on riparian restoration (Table 2). We focused on two in work reported here (Table 2, hypotheses 3 and 4). Our primary hypothesis was that browse intensity would be inversely proportional to extent of large wood enclosure. Our secondary hypothesis was that LWD-mediated browse reduction would be proportional to species preferences by ungulate browsers. We evaluated these hypotheses in two valleys along the Elwha River: the recently exposed reservoir bed directly above the largest dam removal and a comparable valley upstream of both of the Elwha's former dams and reservoirs. The two valleys represent opposite

TABLE 2 Hypotheses regarding browse pressure on woody plants growing in coarse sediments in the two study areas, drained Mills reservoir and Geyser Valley floodplain.

1	Browse intensity will be high in both areas, except in dense stands on fine or perennially wet sediments.
2	Browse intensity will be greater in Geyser Valley, due to continuous ungulate use, smaller valley area, and more extensive cover habitat.
3	LWD reduces exposure to browsing ungulates. Browse intensity will be lowest on plants fully enclosed by LWD, intermediate on plants adjacent to one or more logs, and greatest on plants distant from LWD.
4	LWD-mediated browse reduction will be greater for plant species preferred by ungulate browsers than for species less preferred.
5	Differences in browse intensity (hypothesis 2) will decrease over time as Mills restoration proceeds and LWD accumulates on the former reservoir.
6	Without LWD- or predator-mediated browse reduction, intense browsing will impede riparian forest restoration following dam removal over short and long time scales. (Integration of hypotheses 1–5.)

The study areas are described in Section 2.2 and compared in Table 3.

ends in a riparian restoration continuum. Vegetation in the drained reservoir was early successional, growing in substrates recently exposed to a receding water table, dispersing seeds, desiccating wind and insolation, and herbivory. The upstream valley contained a diverse successional vegetation mosaic resulting from long exposure to those factors and episodic flooding throughout the Holocene (Acker et al., 2008; Warrick et al., 2011; Brown et al., 2022). By working in the two valleys, we hoped to derive insights regarding browse impacts and LWD mediation from early years to late stages in riparian restoration.

2 Study area and restoration background

2.1 Study system

The Elwha River drains the largest basin in the Olympic Mountains, a coastal range in northwestern Washington State (Figure 1). The river flows north 72 kilometers from snowbound headwaters to the Strait of Juan de Fuca. Eighty-three percent of the Elwha's 833 km^2 basin lies within Olympic National Park (Duda et al., 2008), which has protected it from many anthropogenic stressors and simplified interpretation of ecosystem responses to restoration. The lower basin contains a mosaic of public, private, and Lower Elwha Klallam Tribal lands. The basin has a maritime climate, characterized by wet mild winters and warm dry summers. Conifers dominate most of the basin, particularly Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Mixed conifer–hardwood stands occur in many areas, where red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and black cottonwood (*Populus balsamifera*) intersperse with conifers. Floodplains contain vegetation mosaics (Kloehn et al., 2008), including mature forests and young stands of alder, cottonwood, and willows (*Salix* spp.; National Park Service (NPS), 1996). More information about the Elwha basin is in Duda et al. (2008).

Two large hydroelectric dams on the Elwha obstructed passage of sediment, wood, and aquatic biota for nearly a century, during which 21 million m^3 (± 3 million m^3) of sediment accumulated in the two reservoirs (East et al., 2015). The 32 m tall Elwha Dam was built in 1910–1913 at river kilometer (rkm) 7.9 and impounded the 120-ha Aldwell reservoir. The 64 m tall Glines Canyon Dam was built in 1927 at rkm 21.4, impounding the 172-ha Mills reservoir. Both dams were in the traditional territory of the Lower Elwha Klallam Tribe, who opposed the dams, suffered from their impacts, and initiated the process leading to dam removal (Mapes, 2013; Brewitt, 2019; Mauer, 2021). Most (76%) of the impounded

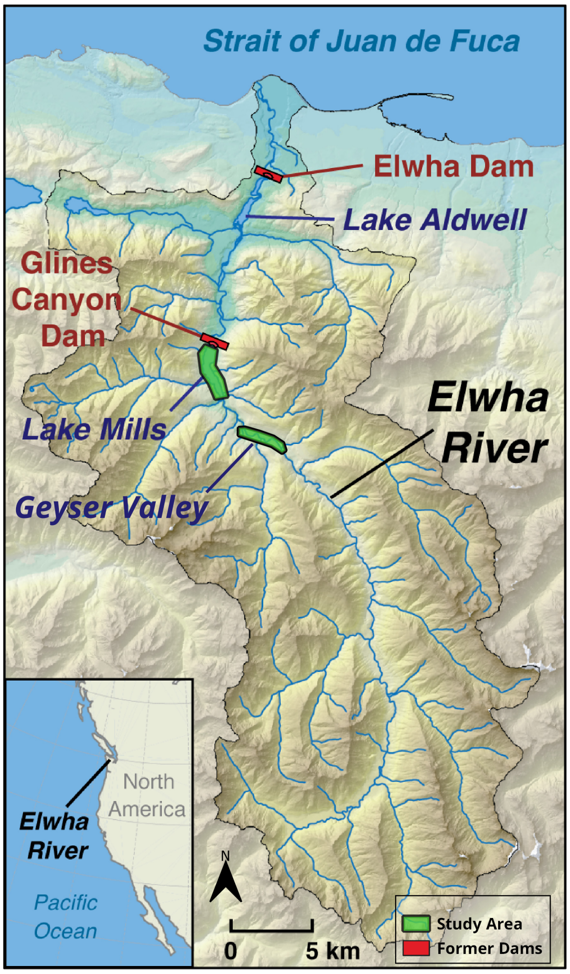

FIGURE 1
Map of the Elwha River basin, including locations of former dams and study areas in Geyser Valley and the former Mills reservoir. Map by CJ, modified from original at: https://www.usgs.gov/media/images/map-elwha-river-state-washington.

sediment was in the larger and upper Mills reservoir (East et al., 2015). Both dams were removed in a phased process from 2011 to 2014. In the five years following the start of dam removal, 65% of the impounded sediment eroded from the former reservoirs (Ritchie et al., 2018). The residual sediment deposits provide substrates targeted for forest restoration (Prach et al., 2019).

2.2 Study areas

Our two study areas share similar environmental and contextual factors, but differ in several characteristics relevant to browse exposure and large wood distribution. Table 3 summarizes these similarities and differences.

The dewatered Mills reservoir bed is the largest restoration site associated with the Elwha River Ecosystem Restoration project (Figure 1). The Mills reservoir accumulated 16 million m^3 (± 3 million m^3) of sediments during the 84 years following dam construction (East et al., 2015). The river eroded most (65%) of this sediment in the five years since dam removal started, of which 90% was transported to the coast and 10% was redistributed within the reservoir bed and downstream river locations (Ritchie et al., 2018). The river and its active floodplain occupy 37% of the Mills reservoir bed (Prach et al., 2019), where chronic disturbance impedes woody plant establishment. One fifth (19%) of the Mills reservoir bed consists of steep slopes along the valley wall, covered by fine lacustrine sediments that now support dense stands of young cottonwoods, alders, and willows (Prach et al., 2019). Water retention by fine sediments supported growth of woody plants, and those stands rapidly exceeded the reach of ungulate browsers. The remaining 44% of the former Mills reservoir bed consists of valley bottom and terraces covered by coarse sediments (Prach et al., 2019). Poor moisture retention in the coarse sediments causes drought stress in woody plants, which occur sparsely and grow slowly during the dry growing season (Prach et al., 2019; Chenoweth et al., 2021). Most large wood in the valley is

TABLE 3 Comparison of the two study areas, the drained Mills reservoir and Geyser Valley floodplain.

Characteristics	References
Similarities	
Land designation: Olympic National Park, federal wilderness	National Park Service (NPS), 1996
Valley area: Mills 172 ha, Geyser Valley 157 ha	Prach et al., 2019, Trejo et al., 2019
Valley floor elevation: Mills 130–182m, Geyser Valley 220–245m	
Adjacent forest overstory: conifers exceeding 100 years age	Shafroth et al., 2016; Chenoweth et al., 2021
Dominant early successional species: *Salix, P. trichocarpa, A. rubra*	Shafroth et al., 2016
Ungulate browsers: Roosevelt elk, Columbian black-tailed deer	McCaffery et al., 2020
Low ungulate predation risk, 100 years (wolf extirpated, few cougars)	Beschta and Ripple, 2008
Differences	
Mills drained reservoir	
More dynamic channel configuration	East et al., 2015
Initial condition lacked vegetation	
Oldest habitats date to 2011, start of dam removal	
Most LWD distributed in single pieces	Leung, 2019
Current ungulate browsing is new, dating to start of dam removal	
Active revegetation, including 45 tree and shrub species	Chenoweth et al., 2021
Geyser Valley	
Channel configuration more stable, with episodic flooding	Acker et al., 2008
Diversity of vegetation patch types and ages	Shafroth et al., 2016
LWD distributed in both single pieces and jams	Leung, 2019
Long continuous history of ungulate browsing	
Extensive and diverse ungulate cover habitats and structures	
No active revegetation	Chenoweth et al., 2021

The two valleys also share or differ in many other characteristics.
Characteristics below are relevant to browsing and riparian restoration.

distributed as single logs or stumps, resulting from upriver transport, hydraulic excavation from eroding sediments, or active translocation (McHenry and Chenoweth, 2015; Leung, 2019).

Geyser Valley is the largest unconstrained reach above the dams and reservoirs (Figure 1). Although the dams prevented anadromous fish from reaching Geyser Valley for a century, it was not otherwise directly impacted by the dams. The valley extends from rkm 27.3 to 31.1, and is separated from the dewatered Mills reservoir by the 1.2 km long Rica Canyon. Geyser Valley spans 1.57 km^2, an area comparable to the former Mills reservoir. The valley's geomorphology and vegetation have been shaped by a history of disturbance by high flow events (Acker et al., 2008). High flows influenced valley sediment distributions, disturbed riparian vegetation, and deposited or redistributed large wood. Similar to other Pacific Northwest rivers with "natural wood regimes" (Wohl et al., 2019), large wood in Geyser Valley is distributed as both individual logs and in multi-log jams. Log jams and spatial variation in disturbance history have generated a mosaic of successional seres (Abbe and Montgomery, 1996; Collins et al., 2012). Geyser Valley is considered a model for post-dam removal restoration of the dewatered Elwha reservoir beds, with particular relevance to the first restoration goal stated below.

Elwha valleys support large populations of Roosevelt elk (*Cervus elaphus roosevelti*) and Columbian black-tailed deer (*Odocoileus hemionus columbianus*; McCaffery et al., 2020). Elk winter in valleys and migrate to higher elevations as snow melts in late spring (Jenkins et al., 2015). Deer remain in valleys throughout the year. Ungulate browsing strongly affects valley forest patch structure and dynamics, tree recruitment, and woody plant architecture in Olympic National Park (Schreiner et al., 1996; Beschta and Ripple, 2008), including Elwha riparian forests (Woodward et al., 1994; McCaffery et al., 2020). Browse intensity, measured as fraction of the previous year's growth, was high in both study areas. Annual browse intensity (years 2015–2018) on all woody species averaged 48.1% on the Mills reservoir and 84.2% in Geyser Valley (calculation based on data in McCaffery et al., 2020, Supplementary Material).

2.3 Reservoir revegetation

The Elwha revegetation and restoration program was designed to achieve three goals on the dewatered reservoir beds: restore native forest, stabilize residual sediment, and minimize spread of invasive exotic species (Chenoweth et al., 2011). The revegetation program lasted six years beginning concurrently with dam removal, using a combination of active seeding, active planting of woody species, passive approaches, and untreated control sites (Chenoweth et al., 2021). Early monitoring showed rapid growth of naturally dispersed cottonwood, alder, and willows in dense stands on fine sediments (Prach et al., 2019; Chenoweth et al., 2021). Subsequently, active planting focused on coarse sediments where low moisture retention slowed early plant establishment (Chenoweth et al., 2021). Recently, natural establishment of cottonwood and willow seedlings on some terraces has been extensive. The planting program included more than 205,000 woody plants of 64 native species (Chenoweth et al., 2021). Active revegetation was not conducted in the active floodplain.

Vegetation monitoring results showed that woody plant establishment was slower on coarse sediments, attributed to moisture and nutrient limitation (Calimpong, 2014; Schuster, 2015; Prach et al., 2019). Moisture limitation presumably resulted from rapid water percolation through coarse sediments, likely compounded by high wind exposure on reservoir terraces. The revegetation program attempted to mitigate drought stress and reduce wind exposure by translocating LWD from accumulation sites along the reservoir perimeter to coarse sediment terraces (McHenry and Chenoweth, 2015). Most translocated logs were placed individually in an east–west orientation, to maximize shaded sediment area on the north side (McHenry and Chenoweth, 2015). Although potential impacts of browsing were acknowledged (Chenoweth et al., 2011), the revegetation program did not implement measures to limit browsing.

3 Materials and methods

3.1 Sampling design and methods

We measured browse intensity on young woody plants on coarse sediment terraces in the former Mills reservoir and coarse floodplain sediments in Geyser Valley. We restricted sampling to early successional habitats with woody plants growing within reach of ungulate browsers. We collected data during late April–May in 2018 (Mills) and 2019 (Geyser Valley). We measured recent browse on plants within or adjacent to four LWD configurations: no LWD, adjacent to single logs, between two parallel logs, and fully enclosed within LWD clusters.

We sampled woody plants using a stratified random design with strata defined by the four LWD configurations. Large woody debris was abundant in the Elwha valleys (Ritchie et al., 2018), but log clusters were less numerous than individual logs. To ensure balanced sampling among LWD configurations, we used a stratified design anchored on LWD cluster locations. Relative to each LWD cluster, we located the nearest single log, the nearest pair of parallel logs, and the nearest area free of LWD within a 10 meter radius. Although LWD usually is defined as any wood exceeding 10 cm diameter and 1 m length (Gurnell, 2013; Gregory et al., 2017; Wohl, 2017), we restricted sampling to logs at least 50 cm above the ground and 5 m long to ensure wood structures were large enough to function as partial barriers to ungulates. At each sampling site, we delineated a 5 m × 1 m plot oriented parallel to the largest log. We used an elongated plot shape to ensure all plants in LWD plots were close to LWD. We placed plots without LWD in random orientations. In the Mills valley, we sampled 140 plots: 42 plots in areas without wood, 35 plots adjacent to individual logs, 33 plots between parallel logs, and 30 plots within wood clusters. In Geyser Valley, we sampled 128 plots: 32 plots in each of the four LWD configurations. Within each plot, we recorded the total number of stems and the number of recently browsed stems on each woody plant.

3.2 Data analysis

We calculated aggregate browse intensity for plants in each plot as the ratio of browsed stems to total stems. We normalized browse percentage data using an arcsine transformation. Then we compared mean browse intensity among the four LWD configurations within each valley using analysis of variance on transformed browse intensity values. We identified configuration-specific differences in browse intensity using a Tukey multiple comparisons test.

We compared effects of study area on LWD mediation of browse using two-factor analysis, with site and LWD plot type as factors. We fit the model without an intercept to obtain site-specific browse means. We included a site × plot interaction term to evaluate whether LWD-mediated browse effects differed between the two study areas.

We compared browse intensity among the plant species selected by ungulates with high, medium, and low intensities. We classified plant species into one of the three browse selection categories using Supplementary Data in McCaffery et al. (2020). We rated species in McCaffery et al. (2020) with annual browse intensities exceeding 66% as strong selection: bigleaf maple (*Acer macrophyllum*), Douglas maple (*Acer glabrum*), Nootka rose (*Rosa nutkana*), red-osier dogwood (*Cornus sericea*), thimbleberry (*Rubus parviflorus*). We rated species with annual browse intensities between 34% and 66% as moderate selection: black cottonwood, willows, western red cedar, bitter cherry (*Prunus emarginata*), oceanspray (*Holodiscus discolor*), and serviceberry (*Amelanchier alnifolia*). We rated species with annual browse intensities of 33% or less as low selection: Douglas fir, western hemlock, grand fir (*Abies grandis*), salmonberry (*Rubus spectabilis*), and western white pine (*Pinus monticola*). We evaluated ungulate selection preference in the context of LWD configuration using two-factor analysis of variance with two LWD levels: LWD clusters and sites without LWD. We evaluated proportionality of wood-mediated browse reductions using the selection × LWD interaction term. We conducted all analyses using R (version 4.3.1; R Core Team, 2023).

4 Results

Our plots on the Mills reservoir bed contained 931 plants of 19 tree and shrub species. Our Geyser Valley plots contained 784 plants of 14 species. Woody plant densities were similar among plots in the two valleys: 1.4 plants/m^2 in Mills and 1.3 plants/m^2 in Geyser Valley.

In both valleys, browse rates differed substantially and significantly among LWD configurations (Mills: $F_{3,136} = 20.5$, $p < 10^{-10}$; Geyser Valley: $F_{3,124} = 8.8$, $p < 10^{-4}$). Differences in browse rates among LWD configuration types were largely due to lower browse rates within clusters than other wood configurations. Mean browse rate in LWD cluster plots was several-fold lower than in plots without LWD. In Mills, mean browse rate within clusters was four times lower than in open plots (0.135 vs. 0.541, $p < 10^{-7}$; Figure 2). In Geyser Valley, mean browse rate within clusters was 2.5 times lower than in open plots (0.16 vs. 0.40, $p < 10^{-4}$; Figure 3). Mean browse rates within wood clusters also were substantially lower than plots associated with single logs or two parallel logs (Tukey's *q*: $p \leq 0.0004$ for Mills, Figure 2; $p \leq 0.001$ for Geyser Valley, Figure 3).

The mean browse intensity was greater in Mills than Geyser Valley ($F_{2,260} = 701.7$, $p < 10^{-15}$), and differed among LWD configurations as described above ($F_{3,260} = 30.4$, $p < 10^{-15}$). There was a small but significant interaction effect between site and LWD plot type ($F_{3,260} = 2.675$, $p = 0.048$), implying LWD-mediated browse reduction was greater in Mills than Geyser Valley.

On the Mills reservoir bed, reduction in browse intensity within wood clusters was disproportionately greater for species preferred by ungulates than for less preferred species, mostly conifers (species × LWD interaction term: $F_{6,890} = 2.55$, $p = 0.0308$; Figure 4). Reduction in browse intensity was intermediate for species with moderate selection. In Geyser Valley, differential reduction in browse intensity relative to ungulate preference could not be concluded with confidence. Analysis of browse intensity on plants with intermediate and low ungulate preference was equivocal (species × LWD interaction term: $F_{1,376} = 0.020$, $p = 0.58$; Figure 5). Plant species preferred by ungulates were almost entirely absent (0.2%) from Geyser Valley samples.

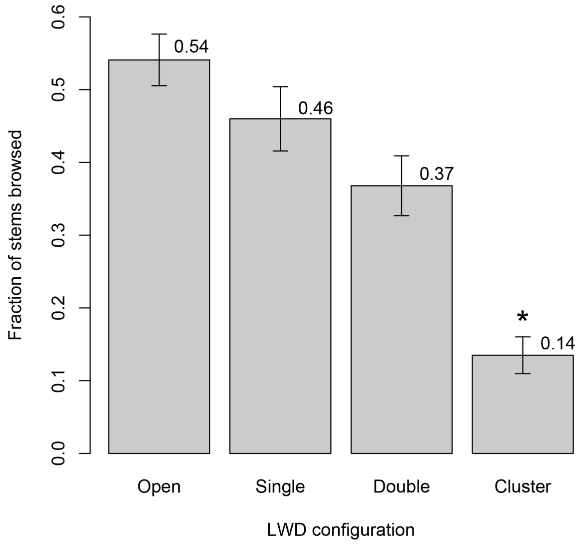

FIGURE 2
Browse intensity on woody plants growing in coarse sediment terraces on the drained Mills reservoir bed. Labels on the horizontal axis refer to large wood characteristics associated with each of four plot types. "Open" plots were at least 10 meters from any LWD. "Single" plots were adjacent to one log. "Double" plots were aligned between two parallel logs. "Cluster" plots were fully surrounded by LWD. All woody debris used to determine plot types stood at least 50 cm above ground level. Values on the vertical axis are mean browse rates, expressed as fraction of stems browsed relative to all stems produced within the previous year. Bar heights are mean per-plot browse rates, and error bars are +/− one standard error. The asterisk (*) indicates mean browse rate in cluster plots was significantly lower than all other wood categories. Mean browse rate in "Double" plots was significantly lower than "Open" plots, but the difference with "Single" plots was not significant.

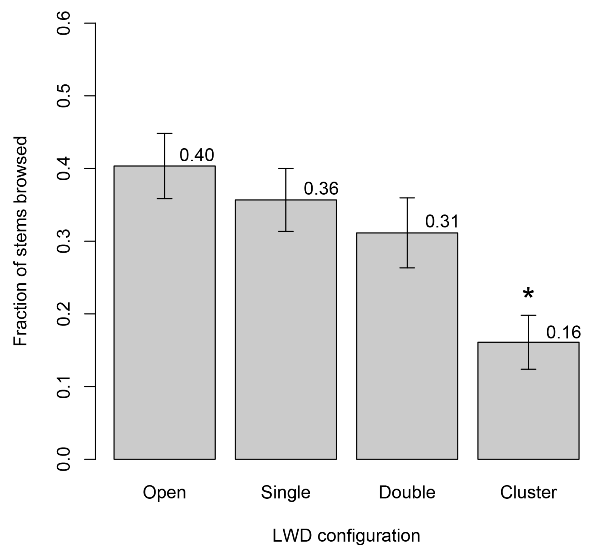

FIGURE 3
Browse intensity on woody plants growing in coarse sediments on the Geyser Valley floodplain. Labels on the horizontal axis refer to large wood characteristics associated with each of four plot types. "Open" plots were at least 10 meters from any LWD. "Single" plots were adjacent to one log. "Double" plots were aligned between two parallel logs. "Cluster" plots were fully surrounded by LWD. All woody debris used to determine plot types reached at least 50 cm above ground level. Values on the vertical axis are browse rates, expressed as fraction of stems browsed relative to all stems produced within the previous year. Bar heights are mean per-plot browse rates, and error bars are +/− one standard error. The asterisk (*) indicates mean browse rate in cluster plots was significantly lower than all other wood categories. Mean browse rate in other wood categories did not differ significantly from each other.

5 Discussion

5.1 Key results

We found that large downed wood can substantially reduce browse intensity on young trees and shrubs, but only when wood surrounds the plants. Relative to plants without LWD protection, mean browse intensity on plants enclosed by wood was lower by a factor of 4 and 2.5 on the former Mills reservoir and Geyser Valley, respectively. Browse intensity was slightly but significantly lower where wood sheltered plants on two sides. Mean browse intensity was marginally lower adjacent to single logs, but not significantly different from areas without LWD. In areas with heavy browse pressure, wood clusters can facilitate woody plant growth to maturity instead of arrested growth forms (Keigley, 1997) that do not achieve restoration objectives (Figure 6).

Wood-mediated browse reduction was similar in both study areas, but overall browse intensity was greater in Mills than Geyser Valley. This result contradicted our second hypothesis (Table 2) and results in McCaffery et al. (2020). These differences merit confirmation with further study. If correct, they suggest browsing is likely to slow plant growth throughout post-dam removal restoration, but browse intensity may decrease slightly as restoration proceeds. Conversely, these results suggest wood-mediated browse reduction may be greatest in the early years following dam removal, when rapid plant growth is most important. Strong reduction in browse within LWD clusters throughout the restoration process appears to be unequivocal.

Wood-mediated protection was greater for plant species preferred by ungulates. On the former Mills reservoir, the

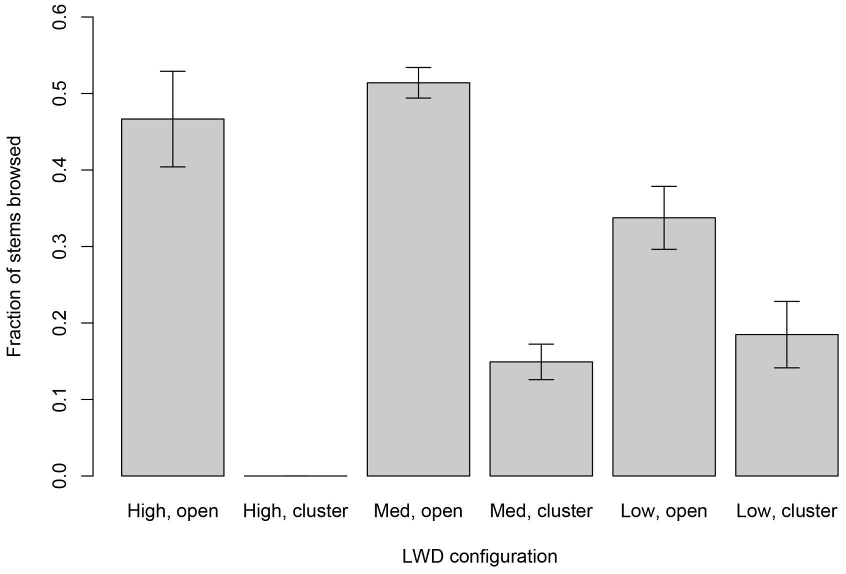

FIGURE 4
Browse intensity on Mills reservoir bed sorted by wood plot type and ungulates' plant selection intensity. Labels on the horizontal axis refer to combinations of large wood characteristics and plant selection intensity. "Open" plots were at least 10 meters from any LWD. "Cluster" plots were fully surrounded by LWD. "High" intensity plants were species reported in McCaffery et al. (2020) as exceeding 66% of previous year's stems browsed. "Med" were species reported in McCaffery et al. (2020) with browse values between 34% and 66%. "Low" were species reported in McCaffery et al. (2020) with less than 34% annual browse intensity. Values on the vertical axis are browse rates, expressed as fraction of stems browsed relative to all stems produced within the previous year. Bar heights are mean per-plant browse rates, and error bars are +/− one standard error.

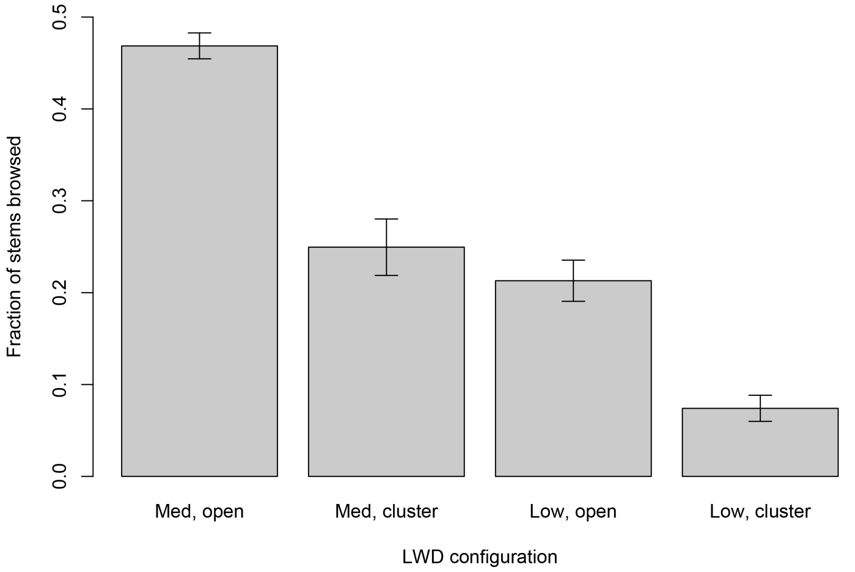

FIGURE 5
Browse intensity on the Geyser Valley floodplain, sorted by wood plot type and ungulates' plant selection intensity. Labels on the horizontal axis refer to combinations of large wood characteristics and plant selection intensity. "Open" plots were at least 10 meters from any LWD. "Cluster" plots were fully surrounded by LWD. "High" intensity plants were species reported in McCaffery et al. (2020) as exceeding 66% of previous year's stems browsed. "Med" were species reported in McCaffery et al. (2020) with browse values between 34% and 66%. "Low" were species reported in McCaffery et al. (2020) with less than 34% annual browse intensity. Values on the vertical axis are browse rates, expressed as fraction of stems browsed relative to all stems produced within the previous year. Bar heights are mean per-plant browse rates, and error bars are +/− one standard error.

magnitude of browse reduction within wood clusters increased disproportionately with strength of ungulate plant selection. In Geyser Valley, this protection-preference interaction was not significant, but preferred species were almost entirely absent from our Geyser Valley samples. Low abundances of ungulate-preferred species in Geyser Valley were unlikely due to effects of elevation, climate, or plant species pools, which are similar to those in the Mills valley (Table 3). Future work could evaluate more plausible factors of Geyser Valley successional history, recent flooding (Acker et al., 2008; Brown et al., 2022), and heavy browse pressure during the century following wolf extirpation (Beschta and Ripple, 2008). Such work should consider that species preferred by ungulates were planted in Mills, but no seeding or planting occurred in Geyser Valley (Chenoweth et al., 2011; Chenoweth et al., 2021).

Our results are consistent with patterns reported from old-growth forests in Olympic National Park (Schreiner et al., 1996). They found large wood clusters provided refugia from ungulate browsing, enabling growth of trees and shrubs that influenced structural and functional characteristics of the forest. Our results demonstrate that large wood refugia also function during early seral stages and in the new context of large dam removal.

Browse reduction within large wood clusters in Elwha valleys supported riparian forest restoration comparable to mechanisms reported from other regions. These included logs in a montane conifer forest in Patagonia (Relva et al., 2009) and a subalpine forest in Poland (Milne-Rostkowska et al., 2020), windthrow following fire in a Swedish national park (de Chantal and Granstrom, 2007), fenced ungulate exclosures in northern California (Opperman and Merenlender, 2000) and northeast Oregon (Brookshire et al., 2002), felled trees in southeastern Oregon (Matney et al., 2005), and wolf reintroduction in Greater Yellowstone (Beschta and Ripple, 2008; Beschta and Ripple, 2019). In Biaowiea National Park, Poland, large wood magnified wolf-mediated browse reduction by impeding wolf detection and ungulate escape routes (Kuijper et al., 2013; van Ginkel et al., 2019). With each mechanism, browse reduction allowed trees and shrubs to increase in density, cover, and survival to maturity. Large wood clusters can support forest restoration where fencing would not be appropriate or where wolves and other apex predators are rare or absent.

5.2 Caveats

Our work was restricted to areas where plants grow at low to intermediate density, at heights within reach of ungulates. These areas occurred in both study areas on coarse sediments where moisture limitation reduced plant density and growth rates. On substrates where moisture was less limiting, including fine sediment deposits and stream edges, woody plants established dense stands that grew rapidly above the reach of ungulates. Our results do not apply to such stands, where herbivory was minor and where active revegetation was not needed (Prach et al., 2019; Chenoweth et al., 2021). Similarly, our results may not be as relevant to areas where apex predators limit ungulate browse intensity (Beschta and Ripple, 2010). Our study areas were within a national park with abundant large riparian wood. In regions with smaller or younger trees, wood clusters formed by simple log polygons may not provide adequate browse reduction. In those regions, stacking logs or root balls could provide functional ungulate barriers. Extensive wood in continuous alignments could be counterproductive, by providing cover and

FIGURE 6
Growth forms of plants within large wood clusters vs. open sites. For each of the three species shown, plants within wood clusters grew rapidly to heights exceeding the reach of ungulate browsers. All apical meristems of plants in open sites were browsed, which impeded increases in plant height. **(A)** Douglas fir (*Pseudotsuga menziesii*): trees behind the log in the foreground are surrounded by large logs. The tree in the lower foreground is exposed to browsing on all sides except the log behind it. All trees in the photo had the same number of branch whorls, and likely germinated in the same year. Photo taken in Geyser Valley. **(B)** Black cottonwood (*Populus balsamifera*) saplings growing within a large wood cluster in Geyser Valley. The white ruler in the middle of the photo is 16 cm long. **(C)** Black cottonwood (*Populus balsamifera*) growing in sediment distant from large wood, in Geyser Valley, within 100 m of **(B)**. The white ruler in the middle of the photo is 16 cm long. The arrested growth form indicates chronic browsing (Keigley, 1997). **(D)** Willows (*Salix* spp.) growing within a large wood cluster on the former Mills reservoir. The white ruler in the lower center of the photo is 16 cm long. **(E)** Sitka willow (*Salix sitchensis*) growing in open coarse sediments on the former Mills reservoir. The white ruler at the bottom of the photo is 16 cm long.

connectivity for small mammals (McCaffery et al., 2020) that girdle saplings (Keeton, 2008). Finally, we collected our data within five years of dam removal. A more comprehensive assessment of wood roles in revegetation will require monitoring over time scales comparable to forest maturation (e.g., Reed et al., 2021; Woodward et al., 2021).

5.3 Cross-disciplinary Insights

(1) Cross-disciplinary approaches can enhance forest restoration. Riparian forest restoration is influenced by geomorphic drivers, including reservoir drawdown schedules, river channel distributions and dynamics, and resultant sediment composition and distribution. Revegetation progress is constrained by climatic factors and plant physiology. Plant distributions and growth also are affected by wildlife (McLaughlin, 2013; McCaffery et al., 2020). These considerations led Elwha revegetation staff to adopt an adaptive approach to respond to uncertainties (Chenoweth et al., 2011). Although climatic uncertainty necessitates flexibility, restoration would be more effective if dam removal planning and associated restoration put greater emphasis on inclusive cross-disciplinary coordination. Reservoir drawdown could be scheduled to coincide with seed dispersal and germination requirements of riparian plants (Chenoweth et al., 2021). Log translocations to enhance plant survival could be configured to mitigate browse impacts and facilitate greater wildlife connectivity. Woody plant installation could give priority to locations within

wood clusters. Revegetation and other restoration projects in future dam removals would benefit from cross-disciplinary approaches, which can leverage restoration resources to improve outcomes.

(2) Cross-disciplinary perspectives are required to understand large wood distributions, dynamics, and restoration roles. Ecological processes create large wood. Geomorphological processes determine large wood distribution and dynamics, wood influences on river structure and function, and wood-mediated distribution of water and sediment (Wohl, 2017). Fisheries science describes large wood as habitat structures providing eddies, cover, thermal refugia, and food essential to fish populations (Maser and Sedell, 1994; Roni et al., 2015). Integrating geomorphology and plant ecology is required to understand wood-mediated riparian vegetation establishment on LWD aggregations and sediment deposits (Fetherston et al., 1995; Pettit and Naiman, 2005; Montgomery and Abbe, 2006; Pettit and Naiman, 2006; Collins et al., 2012; Nakamura et al., 2012). Results in this paper and McCaffery et al. (2018) imply that restoration efficacy requires adding wildlife knowledge to geomorphology and plant ecology.

Effects of large wood often are underappreciated due to missing wood baselines. Anthropogenic removal of riparian wood and wood sources has reduced river wood quantities on most rivers by orders of magnitude (Wohl, 2014; Wohl, 2017). Nevertheless, large wood exerts strong influences on many rivers (Gurnell, 2013; Wohl, 2017) and can play important roles in restoration following dam removal. Large wood creates enduring structures (Hyatt and Naiman, 2001), which may pre-date dam construction on some rivers. These pre-dam structural legacies can catalyze restoration after dam removal by shaping local sediment distributions, providing fish habitat structures, and facilitating revegetation.

(3) Many non-human restoration partners function across disciplines. Rivers dredge sediment (Randle et al., 2015) in ways relevant to all restoration disciplines. Large wood affects and is affected by factors relevant to multiple disciplines, summarized above. Wildlife, including ungulate browsers and avian seed dispersers, respond to structures of concern to plant ecologists, attract study by wildlife ecologists, and ultimately influence vegetation with relevance to sediment stability and geomorphology. Restoration will be more effective when human efforts and resources consider and support non-human restoration partners.

5.4 Lessons learned and restoration applications

(1) Clusters of large downed wood can provide browse refugia that support woody plant growth to maturity. Wood clusters can reduce browse pressure where fencing or tree shelters would not be appropriate. Wood clusters can hasten woody plant growth by decades. Trees that escaped browsing by growing in dense stands in fine sediments on the Elwha's former reservoirs exceeded ungulate browse height within five years. Trees exposed to chronic browsing in Geyser Valley remain suppressed in arrested growth forms after several decades. Browse protection is particularly important in coarse sediment deposits on drained reservoirs, where slower growth rates prolong exposure to ungulate browsers. By facilitating growth of forest islands (Figure 7), wood clusters can play a restoration role similar to nucleation sites used to catalyze tropical forest restoration (Corbin and Holl, 2012).

(2) Results reported here may apply to forest restoration contexts beyond dam removal. Limiting browse can support riparian forest growth to enhance habitat in fish restoration programs (Averett et al., 2017). Similarly, using LWD clusters to mitigate browse can hasten riparian forest restoration associated with Floodplains by Design projects (WDOE (Washington Department of Ecology), Bonneville Environmental Foundation, and American Rivers, 2023), levee setback initiatives (Gergel et al., 2002; Knox et al., 2022), and other riparian restoration programs (Horner et al., 2016; NWIFC (Northwest Indian Fisheries Commission), 2020). Large wood clusters also could facilitate forest restoration following wildfire, timber harvest, or conversion to cattle pasture (Holl et al., 2000; Vanha-Majamaa et al., 2007; Puerta-Piñero et al., 2010; Rost et al., 2010; but see Forester et al., 2007). Large wood and other perch structures can attract seed dispersers to restoration sites (Robinson and Handel, 2000; Corbin and Holl, 2012; McLaughlin, 2013; Guidetti et al., 2016). If that wood is clustered to reduce browse exposure, it can facilitate plant growth following seed germination. Although installation of wood clusters may be resource-intensive, they are likely to persist longer and require less maintenance than alternative interventions such as fencing (Brookshire et al., 2002; Wassie et al., 2009; Kota and Bartos, 2010; Woodward et al., 2021; Monks et al., 2023) or tree shelters (Stange and Shea, 1998; Keeton, 2008). These applications share a common theme: restoring LWD structures and functions can catalyze forest restoration in diverse systems.

(3) Revegetation planning should span entire plant lifecycles. The Elwha revegetation program accurately anticipated sediment moisture as a factor limiting plant establishment on the former reservoirs, and it implemented measures to mitigate seasonal drought (Chenoweth et al., 2021). Nevertheless, early revegetation success may not translate to long term objectives without interventions to support later life stages. Results from several riparian systems demonstrate that establishment success can stall or reverse without measures to mitigate herbivory (Opperman and Merenlender, 2000; Brookshire et al., 2002; Osei et al., 2015; Averett et al., 2017). If revegetation programs address plant needs throughout the life cycle (Table 1), they can produce mature stands that achieve long term outcomes. In systems with intense ungulate browse pressure, strategic placement of large wood clusters or planting within natural clusters would complement measures directed at earlier stages. Different approaches may be appropriate in other systems, but they should mitigate factors that limit plant growth in stages ranging from dispersal to maturation.

(4) Restoration monitoring should continue until objectives are met (Woodward et al., 2008). For revegetation, monitoring timeframes should extend to stand maturity. This timeframe should be reflected in allocation of funding and other resources, which may necessitate strategies to continue monitoring under budget restrictions after dam removal success is declared and interest shifts to other projects. Monitoring also should give priority to LWD abundances and distributions, including LWD

FIGURE 7
Young forest islands growing within clusters of large downed wood in Geyser Valley. **(A)** Forest island consisting of black cottonwood (*Populus balsamifera*), red alder (*Alnus rubra*), and willows (*Salix* spp.), surrounded by large logs in an expanse of sparsely vegetated coarse sediments. **(B)** Black cottonwood (*Populus balsamifera*) saplings growing within a log jam on the Elwha River active channel bank.

clusters which rarely are given explicit attention (Gregory et al., 2017).

(5) For large dam removal and associated restoration, some important drivers are episodic and uncertain, such as federal funding or flood stage river flows. Other processes are regular and predictable, such as seed rain of wind-dispersed riparian trees or chronic ungulate browse pressure. Episodic processes determine the context, distribution, and time course for chronic predictable processes such as plant growth and browsing. Restoration programs should be poised for the former and plan for the latter.

(6) Strategic position or placement of multiple wood clusters can restore connections between rivers and terrestrial systems after dam removal. Just as individual wood clusters can facilitate growth of forest islands, series of clusters could generate forest archipelagos. If archipelagos are aligned to extend from the pre-dam forest to the active river channel, they can function as forest-to-river travel corridors for terrestrial wildlife. Many wildlife species perform important ecosystem functions, including dispersal of seeds and nutrients (Hobbs, 1996; McCaffery et al., 2018). At sites where girdling by small mammals causes high sapling mortality, LWD clusters should be discontinuous. Small mammal habitat connectivity would develop later as LWD-facilitated forest islands establish. For rivers with anadromous fishes, wood-catalyzed forest corridors can expedite restoration of positive feedback loops associated with marine-derived nutrient dispersal and rapid forest growth (Helfield and Naiman, 2001; McCaffery et al., 2018; Quinn et al., 2018). Individual wood clusters can reduce tree maturation time by decades. Similarly, strategic location of wood clusters in sequences potentially could advance restoration considerably in some contexts. More rapid achievement of restoration objectives may provide valuable mitigation of elevated extinction risks for aquatic species and accelerating impacts of climate change.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

CJ, CD, TM, and JM conceptualized the study. All authors coordinated the field planning. All authors participated in data collection and conducted the data analysis. CJ created Figure 1. JM wrote the manuscript. CJ, CD, TM, and JM edited and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Coastal vegetation responses to large dam removal on the Elwha River

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Introduction: Large dam removals provide a restoration opportunity for shrinking coastal wetland habitats. Dam removal can increase sediment delivery to sediment-starved river deltas and estuaries by restoring natural sediment transport and mobilizing reservoir-impounded sediment. However, rapid mobilization of massive quantities of sediment stored behind large dams also constitutes a major ecological perturbation. Information is lacking on coastal habitat responses to sediment pulses of this magnitude.

Methods: Removal of two large dams along the Elwha River (Washington, USA) in 2011–2014 released ~20.5 Mt of impounded sediment, ~5.4 Mt of which were deposited in the delta and estuary (hereafter, delta). We used time series of aerial imagery, digital elevation models, and vegetation field sampling to examine plant community responses to this sediment pulse across seven years during and after dam removal.

Results: Between 2011 and 2018, the Elwha River delta increased by ~26.8 ha. Vegetation colonized ~16.4 ha of new surfaces, with mixed pioneer vegetation on supratidal beach, river bars, and river mouth bars and emergent marsh vegetation in intertidal aquatic habitats. Colonization occurred on surfaces that were higher and more stable in elevation and farther from the shoreline. Compared to established delta plant communities, vegetation on new surfaces had lower cover of dominant species and functional groups, with very low woody cover, and lower graminoid cover than dunegrass and emergent marsh communities. Over time following surface stabilization, however, vegetation on new surfaces increased in species richness, cover, and similarity to established communities. By 2018, ~1.0 ha of vegetation on new surfaces had developed into dunegrass or willow–alder communities and ~5.9 ha had developed into emergent marsh. At the same time, dam removal had few discernible effects on established delta plant communities.

Discussion: Together, these results suggest that rapid sediment mobilization during large dam removal has potential to expand coastal wetland habitat without negatively affecting established plant communities. However, as sediment loads declined in 2016–2018, new delta surfaces decreased by ~4.5 ha, and ~1.6 ha of new vegetation reverted to no vegetation. Long-term persistence of the expanded coastal habitat will depend on ongoing erosional and depositional processes under the restored natural sediment regime.

KEYWORDS

coastal wetland restoration, dam removal, ecological succession, pioneer geomorphic surfaces, riparian, river delta, riverine estuary, sediment deposition

1 Introduction

Coastal wetland habitats have declined dramatically over recent centuries (Davidson, 2014). Along the United States West Coast, an estimated 85% of river delta, riverine estuary, and embayment wetlands have been lost since European settlement (Brophy et al., 2019). Coastal wetlands provide valuable ecosystem services, including nursery habitat for marine fisheries and invertebrates, shorebird breeding grounds and migratory stopovers, coastal storm protection, erosion control, and water purification (Barbier et al., 2011). Restoration efforts for coastal wetlands are widespread, but with mixed success (Elliot et al., 2016; Cadier et al., 2020).

Human-induced changes to river sediment transport are an important factor contributing to loss of river delta and riverine estuary habitats. Upstream dams and levees capture sediment, reducing downstream sediment loads by 50–100% on many regulated rivers and resulting in erosion and subsidence of coastal habitats (Tessler et al., 2018; Besset et al., 2019). Over longer time-scales (i.e., centuries or millennia), deforestation and cropping also have increased river sediment loads and transport to coastal habitats, but often not enough to offset recent and rapid effects of dams and channelization on coastal erosion and subsidence (Meade, 1996).

Dam removal is an increasingly common approach for restoring sediment transport to riparian and riverine ecosystems (O'Connor et al., 2015). Dam removal can have myriad positive ecological effects, improving connectivity (e.g., fish passage, hydrochory, transport of large woody debris), restoring natural hydrologic regimes, and increasing sediment delivery to sediment-starved downstream channels, floodplains, estuaries, and deltas (Bellmore et al., 2019). However, dam removal also constitutes a major ecological perturbation, as conditions maintained for decades by dam emplacement are changed over a period of weeks to years (depending on removal approach; Foley et al., 2017a). In particular, dam removal can lead to rapid mobilization and downstream transport of decades worth of sediment impounded upstream of the dam. While small to moderate sediment pulses from small dam removals mainly affect river geomorphology <5 km downstream, removal of large dams, which can store very large quantities of sediment, can generate large pulses of gravel, sand and mud that travel at least 30 km in the first few years, affecting the geomorphology of downstream coastal wetland habitats if the dam is within reach of the coast (Major et al., 2017; East et al., 2023).

Understanding and predicting both short-term and long-term effects of dam removal on downstream delta and estuary vegetation is important to inform coastal wetland habitat conservation and restoration as well as management practices in preparation for and following dam removal (Foley et al., 2017a). These communities may respond positively to large sediment pulses caused by large dam removal; like major sediment erosion and deposition events associated with large floods, large sediment pulses may create new geomorphic surfaces that can be colonized rapidly by riparian plants adapted to fluvial disturbance, thus maintaining or restoring the shifting habitat mosaic of different-aged stands along riparian corridors (Shafroth et al., 2002; Stanford et al., 2005). However, it is uncertain whether and how riparian vegetation responses might differ in the context of very high sediment loads persisting for months or years during and after large dam removal (Major et al., 2017), compared to much briefer high sediment loads caused by large floods. Such large disturbances could facilitate invasion by weedy, introduced species or otherwise result in novel successional trajectories (Shafroth et al., 2002). Large sediment pulses to watersheds, rivers, river deltas, and coasts also occur episodically as a result of landslides, volcanic eruptions, intensive mining, dam failures, and other major disturbances (Shafroth et al., 2002; Sutherland et al., 2002; Pierson and Major, 2014; Ferguson et al., 2015), but responses of river delta or riverine estuary vegetation to such large sediment-pulse events have rarely, if ever, been examined.

Recent removal of two large dams on the Elwha River, Washington, USA, in 2011–2014, provided an opportunity to examine coastal vegetation responses to a major sediment pulse event during large dam removal. Prior to removal, the Glines Canyon (64-m tall) and Elwha (32-m tall) dams reduced downstream sediment loads by >85% (Curran et al., 2009), capturing and storing ~30 Mt of sediment during the 84 and 98 years that they were in place (Randle et al., 2015). Among many effects on Elwha riverine and riparian ecosystems, reduced downstream sediment loads resulted in substantial and accelerating erosion at the Elwha River delta and adjacent coastline, with shoreline retreat of up to 160 m between 1939 and 2006 (Warrick et al., 2009). Effects of the dams on delta vegetation were not examined prior to dam removal, but shoreline retreat presumably resulted in loss of coastal vegetation. Plant community composition in the delta also may have been altered by the near century of reduced sediment deposition, large wood deposition and hydrochorous seed dispersal, as well as mildly altered streamflows (Shafroth et al., 2016).

Removal of the Glines Canyon and Elwha dams resulted in mobilization and release of 20.5 ± 3.2 Mt of sediment during the first five years (2012–2016), >5× more sediment than the next-largest dam removal in history and ~10× times more than the natural 5-yr sediment load for the Elwha River (Ritchie et al., 2018). This sediment release occurred as the dams were gradually removed in carefully timed phases designed to minimize negative effects of high sediment loads on fish populations (one year for Elwha Dam (2011–2012) and three years for Glines Canyon Dam (2011–2014)) (Randle et al., 2015; Warrick et al., 2015) and as reservoir sediments continued to erode after dam removal was complete (Ritchie et al., 2018). Of the released reservoir sediment, 5.4 ± 1.6Mt (~26%) were deposited in the Elwha River estuary and delta (Ritchie et al., 2018). These deposits were initially largely submarine, but sediment reworking by ocean swell and wind waves created extensive supratidal river mouth bars (Ritchie et al., 2018), increasing the surface area of the delta by ~15 ha by 2014 (Foley et al., 2017b). By 2016, ~1 Mt of sediment had been reworked to intertidal and subaerial positions in the delta (Warrick et al., 2019). These new surfaces were dynamic, with sediment reworking by waves and currents across and along-shore leading to local and seasonal erosion (Ritchie et al., 2018) and to down-shore sediment waves as new river mouth bars welded to the shoreline (Warrick et al., 2019).

Rapid, large-scale, and dynamic sediment deposition in the Elwha River estuary and delta (hereafter, the delta) has likely provided opportunities for extensive establishment of new coastal wetland habitats on the primary successional landforms of the expanded delta. Smaller sediment pulses and sediment trapping structures have led to rapid establishment and expansion of estuarine vegetation in other river deltas (Elsey-Quirk et al., 2019; Hu et al., 2019; Fivash et al., 2021). In the Elwha River delta, vegetation was already beginning to colonize some new landforms by the time dam removal was complete in 2014 (Foley et al., 2017b). However, information is lacking on the persistence, abundance, and composition of vegetation on these new surfaces, likely successional trajectories, whether these communities are at higher risk of invasion by introduced species, and how spatial variation in environmental conditions might influence these outcomes.

In addition, sediment deposition in the delta may have affected habitat structure and composition of plant communities that existed prior to dam removal. Prior to dam removal, the delta contained a patchy mosaic of riparian community types, including dunegrass communities at high topographic positions on beach berms, emergent marsh in narrow bands along tidally influenced margins of estuarine ponds, riparian shrub communities at intermediate positions along topographic gradients between emergent marsh and forest communities or interspersed within forest communities, young, dense willow–alder forest on gravel bars typically near the active river channel, extensive mixed riparian forest, including large trees, on older landforms, and less common mixed pioneer vegetation on frequently disturbed surfaces adjacent to the main channel and beach (Shafroth et al., 2011; Foley et al., 2017b). High sediment deposition and mobility may have influenced species composition of these established communities. Sediment deposition (e.g., during floods) can alter riparian community composition, particularly affecting herbaceous species and young woody plants (Lowe et al., 2010; Kui and Stella, 2016; Gonzalez et al., 2020). Upstream on the Elwha River, sediment deposition during and after dam removal altered species composition on bars, floodplains, and terraces between and below the former dams (Brown et al., 2022). In the delta, composition of established plant communities remained fairly stable during dam removal, with no significant change in species richness or community composition except for an increase in the invasive grass *Phalaris arundinacea* (reed canarygrass) and decrease in *Argentina egedii* (Pacific silverweed) in some emergent marsh plots (Foley et al., 2017b). However, longer-term responses to ongoing sediment deposition are possible, especially for species sensitive to burial or changes in tidal inundation and salinity (Shafroth et al., 2002).

In this study, we used time series of aerial imagery, digital elevation models (DEMs) derived from field topography surveys, and vegetation plot sampling to examine plant community development and change in the Elwha River delta in the first seven years during and after dam removal (2011–2018). Our overarching objective was to quantify and understand effects of large dam removal on abundance and composition of coastal wetland habitat. Specifically, for new delta surfaces that were created by sediment deposition during and after dam removal, we asked: (1) Which landscape positions and elevational histories supported vegetation establishment and persistence on new surfaces? (2) How did vegetation composition on new surfaces compare to delta plant communities that existed prior to dam removal? (3) How did vegetation on new surfaces change as surfaces aged? and (4) How did environmental conditions (i.e., elevation, soil depth and particle size) affect species and functional group composition? In addition, for delta plant communities that existed prior to dam removal, we asked: (5) Were there temporal changes in species and functional group composition that could be attributed to effects of dam removal? Finally, for both new and previously established vegetation, we asked (6) Did dam removal facilitate invasion by introduced species in the delta?

2 Materials and methods

2.1 Study area

The Elwha River flows northward 72 km from the Olympic Mountains to the Strait of Juan de Fuca on the Olympic Peninsula, Washington, USA (Figures 1, S1). Most (83%) of its 833 km^2 watershed is located within Olympic National Park, which is largely undeveloped. The Elwha River mouth is ~10 km west of the town of Port Angeles, which receives mean annual precipitation of 0.64 m and has mean maximum summer temperatures of 19.9°C (July–August) and mean minimum winter temperatures of 1.2–1.9°C (December–February) (Western Regional Climate Center, https://wrcc.dri.edu/, accessed October 6, 2022). Mean annual flow is 43 m^3 s^{-1} based on 104 years of discharge data at USGS streamflow gage 12045500, 13.8 km upstream from the river mouth (USGS, 2023). Peak flows occur during both winter rainfall and spring snowmelt. Annual exceedance probabilities of peak discharge prior to dam removal indicated 2-year floods of 400 m^3 s^{-1}, 25-year floods of 948 m^3 s^{-1}, and 100-year floods of 1,240 m^3 s^{-1} (Duda et al., 2011). The dams probably attenuated peak flows, so these values were predicted to increase by 10–15% after dam removal (Duda et al., 2011).

2.2 Aerial imagery

In previous work to assess changes to the Elwha River delta during dam removal, annual maps of geomorphic and vegetative cover types were developed for 2011–2014 using a combination of summer ortho-referenced, high-resolution aerial imagery and topographic data (Foley et al., 2017b). To evaluate ongoing change after dam removal, we developed maps for 2016 and 2018 following the same protocols, using aerial imagery (RGB) collected on 11 August 2016 and 19 July 2018 (imagery and metadata available in Perry et al., 2023) coupled with 1-m^2 resolution DEMs derived from topography and bathymetry field surveys conducted on 15–17 July 2016 and 23–26 July 2018 (Stevens et al., 2017). Habitat cover types included four geomorphic classes (beach, river bar, river mouth bar, aquatic), six vegetation cover types (mixed pioneer vegetation, dunegrass, emergent marsh,

FIGURE 1
Oblique aerial image of the Elwha River delta (U.S. state of Washington) taken May 30, 2016, ~20 months after removal of two dams on the Elwha River was completed. Image by John Gussman.

riparian shrub, willow–alder forest, mixed riparian forest), and a human-developed landscape class (roads and residential). The geomorphic classes were further subdivided by elevation into subtidal (below mean lower low water, MLLW), intertidal (between MLLW and mean higher high water, MHHW), and supratidal (above MHHW) subclasses, using the local coastal water datum from the NOAA tidal station at Port Angeles, Washington (NOAA Station ID 9444090). Starting from the 2014 map from Foley et al. (2017b), we used heads up digitizing to adjust polygon boundaries where existing patches changed in size and to delineate new polygons where new surfaces had formed. All work was done in ArcGIS (version 10.3), Esri, Redlands, California, USA with imagery zoomed to 1:1,500. Minimum polygon size was 100 m^2 for geomorphic and vegetation classes and 40 m^2 for elevational subdivisions of the geomorphic classes. We used field observations of estuary vegetation in summer 2016, 2017, 2018, and 2020 to verify and inform vegetation classifications, particularly in areas that appeared to have changed since 2014. This approach overlooked small patches and likely included location errors of up to a few meters in the boundaries between patches but provided a broad-scale view of the abundance of different habitat types over time.

To assess the timing and magnitude of habitat change, we summed polygon areas by habitat type within each image-year. Further, to characterize new habitat created by sediment deposition during and after dam removal, we summed 2018 polygon areas by habitat type for areas that were unvegetated prior to dam removal in 2011. In addition, we calculated mean annual elevation (m above MHHW) and mean annual change in elevation from 2011–2018 in vegetated versus unvegetated portions of the new habitat, using 1-m^2 resolution, annual DEMs derived from surveys of the delta in August 2011, August 2012, September 2013, September 2014, July 2015, July 2016, July 2017, and July 2018 (Stevens et al., 2017). Finally, to characterize predominant vegetation colonization and successional trajectories, we overlapped vegetation cover polygons from all years across the entire study area, and summed areas for each unique temporal sequence of vegetation cover types.

2.3 Vegetation plots

We sampled forty vegetation plots in the Elwha River delta for plant community composition, soil depth, and soil surface particle size distribution (Figure S2). Twenty-one of these plots were originally sampled in August 2007 as a stratified random sample of predominant vegetation types in the delta prior to dam removal, including dunegrass (3 plots), emergent marsh (5 plots), riparian shrub (5 plots), willow–alder forest (3 plots), and mixed riparian forest (5 plots) (Shafroth et al., 2011; Foley et al., 2017b). We resampled all 21 of these plots in August 2014, and 18 again in August–September 2018; two plots (emergent marsh, mixed riparian forest) were subsumed by the channel between 2014 and 2018, and data were lost for a third (mixed riparian forest). We added 12 new plots in 2014, mainly to sample vegetation on new surfaces that developed during dam removal (9 plots), but also to sample mixed pioneer vegetation that existed prior to dam removal (2 plots) and to add one new willow–alder forest sample (1 plot). We resampled 11 of these plots in 2018; one plot (new-surface vegetation) was subsumed by the channel. Finally, we added seven plots in 2018 to sample vegetation on new surfaces that developed after dam removal. Thus, sample size varied among years, but total N=16 new-surface vegetation, 2 mixed pioneer, 3 dunegrass, 5 emergent marsh, 5 riparian shrub, 4 willow–alder forest, and 5 mixed riparian forest plots.

All plots were 100 m^2. Two-thirds of plots were 10 × 10 m, while plots in narrow vegetation patches were 5 × 20 m or rarely 4 × 25 m. In each plot, we visually estimated cover by each vascular plant species within ten classes (trace, 0–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, >95%). We obtained information on species functional group (woody, forb, graminoid, perennial, annual/biennial, native, introduced) and wetland indicator value from the U.S. Department of Agriculture plants database (https://plants.usda.gov) (Table S1). For each plot in each year, we summed species richness and cover (midpoints of cover classes) by functional group and calculated a community-weighted mean wetland indicator value, weighted by the proportion of total plot cover occupied by each species (lower values indicate greater wetland adaptation).

We determined plot mean soil depth by measuring depth to refusal (rock or wood) at each plot corner using a 119-cm soil probe. We characterized the soil surface particle size distribution by calculating percent gravel/cobble (2–256 cm diameter) from Wolman pebble counts at 100 random points within each plot (Wolman, 1954). We surveyed elevations of dunegrass, emergent marsh, and riparian shrub plots in August 2007, 2014, and 2018 with a Magellan ProMark 3 Differential Global Positioning System in Real-Time Kinematic mode (RTK-DGPS) mounted on a survey pole, receiving corrections from a base station on a permanent survey monument (estimated systematic + random error = ± 10 cm). For new-surface vegetation plots, we calculated annual mean plot elevations from 1-m^2 resolution, annual DEMs derived from surveys of the delta in September 2010, August 2011, August 2012, September 2013, September 2014, July 2015, July 2016, July 2017, and July 2018 (Stevens et al., 2017). We adjusted all elevation data to units of m above MHHW using the local coastal water datum from the NOAA tidal station at Port Angeles, Washington (NOAA Station ID 9444090).

All data generated in this study are available in a U.S. Geological Survey data release (Perry et al., 2023).

2.4 Statistical analysis

We conducted all statistical analyses using R 4.1.0 (R-Core-Team, 2021). To evaluate effects of sediment dynamics and elevation on vegetation colonization of new delta surfaces created during dam removal, we took a stratified random sample of 326 points across polygons that had been unvegetated in 2011, with 88 points in polygons that were vegetated in 2018 and 238 points in polygons that remained unvegetated in 2018 (in proportion to 11.2 ha of vegetated polygons and 29.5 ha of unvegetated polygons). We restricted point selection to a 15-m minimum distance between points, resulting in a maximum of 326 points across polygons. Smaller minimum distances led to significant spatial autocorrelation, assessed using *testSpatialAutocorrelation* in the *DHARMa* package (Hartig, 2021). We developed logistic regression models of 2018 vegetation occurrence as a function of 2018 surface age (i.e., time since surface stabilization), 2018 elevation (m above MHHW), and distance to the nearest 2018 subtidal aquatic shoreline polygon (hereafter, distance to shoreline), using *glm* in the *lme4* package with a binomial distribution and logit link (Bates et al., 2015). We defined surface age as the number of years since net annual erosion or deposition slowed to a threshold rate that colonizing vegetation could potentially tolerate. To select the most informative threshold for this purpose, we used Akaike information-theoretic criteria adjusted for small sample size (AICc) to compare models with surface age defined by thresholds of 10, 15, 20, 25, 30, 35, 40, 45, or 50 cm of net annual erosion or deposition (i.e., 9 models).

For vegetation plots, we evaluated variation in species composition using non-metric multi-dimensional scaling (NMDS) ordinations of species cover (sqrt-transformed midpoints of cover classes) across all plots in all sampling years (N=90), computed using *metaMDS* in the *vegan* package (Oksanen et al., 2020) with Bray-Curtis distances, *try*=250, and *trymax*=500. We grouped species by genus for species that were rare or could not be distinguished with certainty, and excluded genera that were present in <5% of samples (i.e., <5 plot-years) (Table S1). We used *envfit* to compute vectors for correlations between the ordination and functional group composition.

To examine temporal trends and differences among community types in species and functional group composition in vegetation plots, we performed three sets of analyses using generalized linear models (GLMs), PERMANOVA, and SIMPER. For most GLMs, we used *lmer* in the *lme4* package with a Gaussian distribution (Bates et al., 2015), but for response variables with zero-inflation and/or significant heteroscedasticity, we used the *glmmTMB* package with a nbinom1 or nbinom2 distribution and log link (Brooks et al., 2017). For PERMANOVA and SIMPER analyses, we used *adonis* and *simper* with Bray-Curtis distances in the *vegan* package (Oksanen et al., 2020).

In the first set of analyses, we examined differences between community composition in new-surface vegetation plots versus other delta community types that existed prior to dam removal (mixed pioneer, dunegrass, emergent march, riparian shrub, willow–alder forest, mixed riparian forest). We used PERMANOVA to compare species composition between new-surface vegetation versus other delta community types (effects: community type, year), and used pairwise SIMPER analyses to characterize significant differences between community types. Further, we used GLMs to compare functional group species richness and cover and NMDS ordination scores among community types, with community type included as a fixed effect and year and plot nested within community type as random effects. We performed *post-hoc*, pairwise comparisons between new-surface vegetation and other community types using "trt.vs.ctrl" in the *emmeans* package (Lenth, 2021).

In the second set of analyses, we examined plant community development on new surfaces created during dam removal. We used PERMANOVA to analyze change in species composition between 2014 and 2018 in new-surface vegetation plots (effects: year, plot), and used SIMPER analyses to characterize significant differences in species composition between years. Further, we examined relationships between new-surface vegetation development and new-surface edaphic conditions using Akaike information-theoretic model selection. We developed GLMs of functional group species richness and cover and NMDS ordination scores in new-surface vegetation plots in 2014 and 2018 as functions of surface age (i.e., years since surface stabilization), mean annual elevation since surface stabilization (m above MHHW), soil depth (cm), and soil surface gravel/cobble (log-transformed %), with plot included in all models as a random effect. We defined the timing of surface stabilization *a priori* as the year when net annual erosion or deposition slowed to <25 cm yr^{-1}, a rate that we expected colonizing vegetation could potentially survive. This choice was subsequently supported by the logistic regression results for vegetation occurrence on new surfaces on aerial imagery (see statistical analysis methods above and aerial imagery results). Annual elevation data were unavailable for two new-surface vegetation plots located inland of the pre-dam-removal beach, so these plots were excluded from this analysis, resulting in N=22. To avoid overfitting, we evaluated support only for univariate and bivariate models, resulting in 11 models including the null model. To avoid discussing poorly supported models, we did not consider results for vegetation metrics with ΔAICc<4.0 for the null model relative to the best model.

In the third set of analyses, we examined temporal change in community composition during and after dam removal within established plant communities that were sampled both before and after dam removal (dunegrass, emergent march, riparian shrub, willow–alder forest, mixed riparian forest). For each community type, we used PERMANOVA to compare species composition among sampling years (2007, 2014, 2018) (effects: year, plot), and used pairwise SIMPER analyses to characterize significant differences between years. Further, we used GLMs to compare functional group species richness and cover and NMDS ordination scores among years, with year, community type and year × type included as fixed effects and plot nested within type as a random effect. To avoid confounding temporal change in community composition with change in sample size and plot identity, we included only plots that were sampled in all three years in these analyses (N=18).

3 Results

3.1 Aerial imagery

3.1.1 Expansion of the delta following dam removal

During dam removal, supratidal river bars, supratidal river mouth bars, supratidal beach, and intertidal aquatic habitats in the Elwha River delta increased dramatically, with a net increase of 24.6 ha of delta habitat between 2011 and 2014 (Figures 2, 3A; Foley et al., 2017b). Supratidal river bar, river mouth bar, and beach habitats continued to grow between 2014 and 2016, adding another 6.8 ha (Figures 2, 3B). In addition, ~5 ha of intertidal beach and aquatic habitats increased in elevation to supratidal positions during those years. However, between 2016 and 2018, these trends slowed or reversed; total delta habitat declined by 4.5 ha (14% of the new habitat created since 2011; Figure 3A), mainly reflecting losses of supratidal river mouth bars, intertidal beach, and intertidal aquatic habitat (Figure 3B) as coastal erosion and sediment reworking pushed the outermost new river mouth bars inland towards the pre-dam-removal shoreline (Figure 2).

3.1.2 Vegetation colonization of new surfaces created by dam removal

Between 2011 and 2018, a total of 16.4 ha of the delta that had been unvegetated prior to dam removal were colonized by vegetation (Figure 4). Of these 16.4 ha of new-surface vegetation, 58% (9.5 ha) were initially colonized by new-surface mixed pioneer vegetation, i.e., areas identified as early-successional communities too young and undeveloped to be defined as a particular established

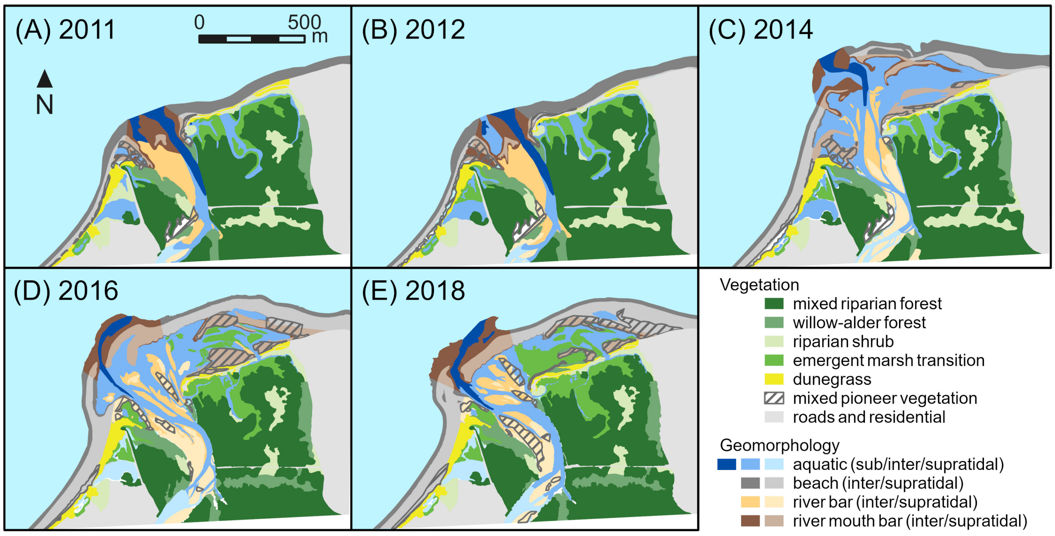

FIGURE 2
Changes in geomorphic and vegetation habitat types classified using aerial imagery from **(A)** 2011, **(B)** 2012, **(C)** 2014, **(D)** 2016, and **(E)** 2018 for the Elwha River delta (U.S. state of Washington). Removal of two dams on the Elwha River began in 2011 and was completed in 2014.

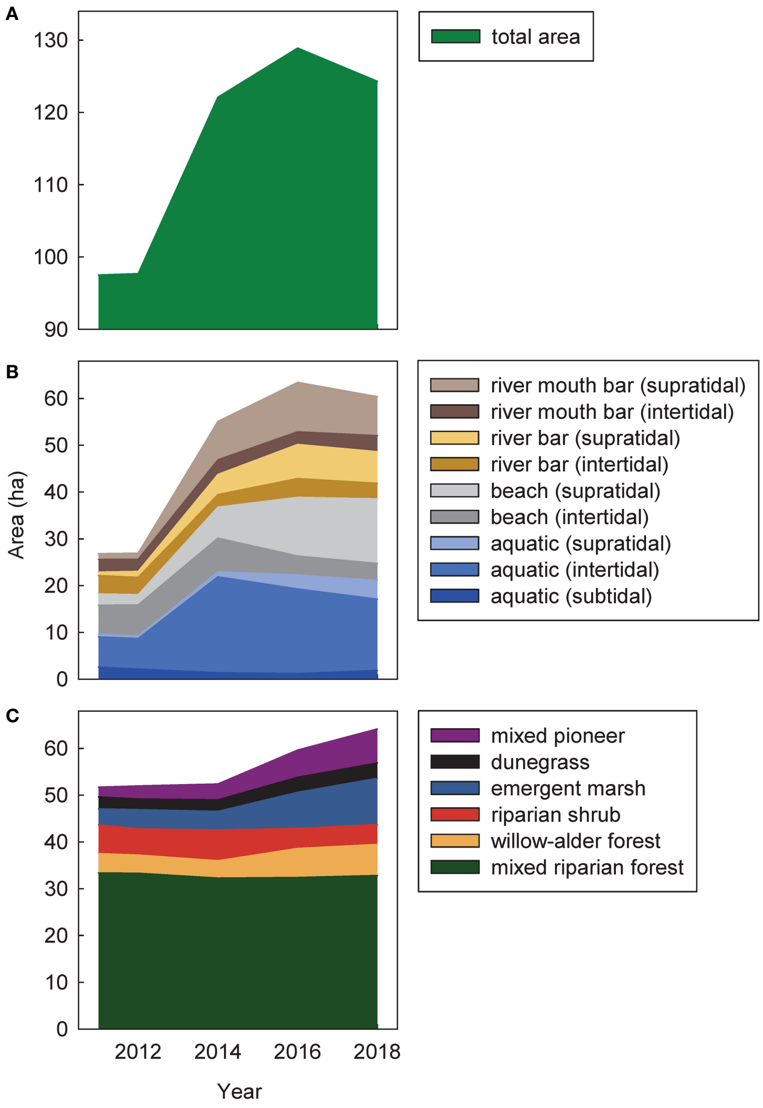

FIGURE 3
Temporal changes during (2011–2014) and after (2014–2018) dam removal in total cover of **(A)** all intertidal and supratidal surfaces, **(B)** geomorphic habitat types, and **(C)** vegetation habitat types in the Elwha River delta (U.S. state of Washington). Cover was estimated from polygons derived from aerial imagery. Areas in **(B, C)** overlapped where mapped geomorphic habitat types were vegetated. The total area in **(A)** accounted for those overlapping areas, but still was higher than the sum of the areas in **(B, C)** because it included areas with the human-developed landscape class, which changed minimally over time and were not depicted in **(B)** or **(C)**.

community type. Another 37% (6.1 ha) were initially colonized by new-surface early-successional emergent marsh vegetation. The remaining 5% (0.8 ha) were initially colonized by mixed riparian forest, willow–alder forest, riparian shrub or dunegrass communities. As these later-successional community types could not have developed within the 1–2 years between aerial images, recorded change in these 0.8 ha likely reflected either expansion of established plant canopies over adjacent bare ground or open water, or error due to small differences between years in aerial imagery analysis at the edges of established communities.

Most new vegetation established after 2014 (83% of new-surface mixed pioneer vegetation and 94% of new-surface emergent marsh; Figure 4). Also, much of the new vegetation persisted through 2018. Of new-surface mixed pioneer vegetation and emergent marsh that established in 2012–2016, 52% and 73%, respectively, remained mixed pioneer vegetation and emergent marsh in 2018. Another 28% of new-surface mixed pioneer vegetation matured into discernible, established community types by 2018, resulting in 0.3, 0.7, and 0.6 ha of new-surface dunegrass, emergent marsh, and willow–alder forest, respectively. However, not all new vegetation persisted; 20% of new-surface mixed pioneer vegetation and 24% of new-surface emergent marsh that established in 2012–2016 had reverted to no vegetation by 2018 (~1.9 ha in total, ~1.6 ha of which occurred after 2016).

Vegetation colonized new surfaces created by sediment deposition as well as existing surfaces that aggraded, stabilized, and/or became protected from wave action by adjacent new surfaces during dam removal (Figure 2). Where geomorphic surface types were also mapped (83% of newly vegetated areas), over half (52%) of newly vegetated areas occurred in intertidal aquatic and supratidal beach habitats,

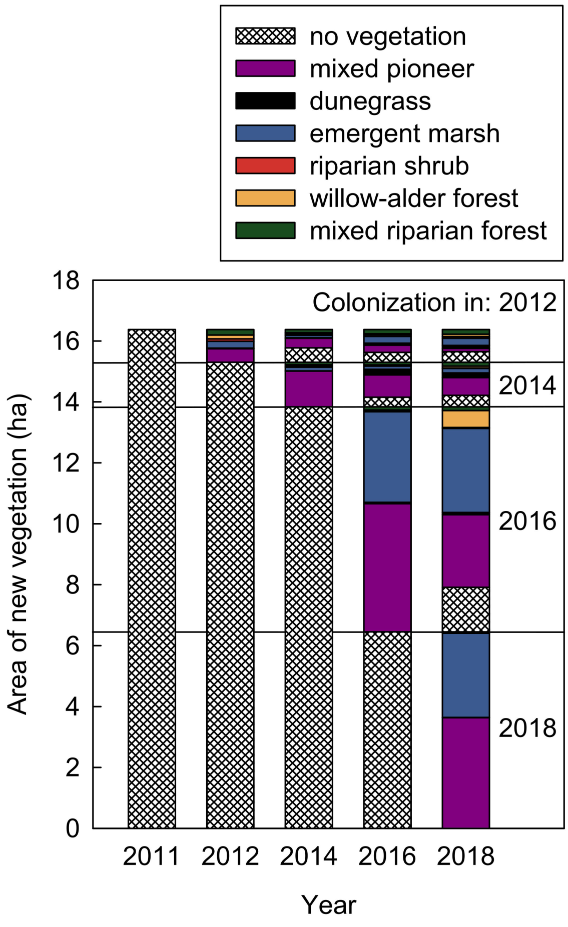

FIGURE 4
Colonization of new and previously unvegetated geomorphic surfaces during (2011–2014) and after (2014–2018) dam removal by different plant community types in the Elwha River delta (U.S. state of Washington). Vertical subsections of the stacked bars show community types for surfaces colonized in 2011–2012 (top), 2013–2014, 2015–2016, and 2017–2018 (bottom), including abundances of different community types in the first year of colonization and changes in those abundances in subsequent years. Cover was estimated by overlapping polygons derived from aerial imagery from different years.

which comprised 51% of 2018 geomorphic surfaces available for colonization (i.e., not already vegetated in 2011) (Figure 5). However, only slightly less colonization (41%) occurred on supratidal river bars and river mouth bars, even though these made up only 22% of available surfaces, suggesting that supratidal bars provided particularly suitable habitat for colonizing vegetation. Persistent new-surface mixed pioneer vegetation was evenly distributed among supratidal beach, river mouth bar, and river bar surfaces, whereas new-surface mixed pioneer vegetation developed into dunegrass and willow–alder forest predominately on supratidal river mouth bars, and new-surface emergent marsh predominately colonized aquatic intertidal habitat (Figure 5).

Surfaces that supported new vegetation in 2018 were, on average, ~0.4 m higher in elevation (Figure 6) and ~85 m farther from the shoreline than surfaces that remained unvegetated (158 ± 63 m compared to 72 ± 67 m). They were also less dynamic, with only 7–21 cm of mean net annual deposition and 6–12 cm of mean net annual erosion in 2015–2018, compared to 42–97 cm of deposition and 53–60 cm of erosion on unvegetated surfaces (Figure 6). Logistic regression of 2018 vegetation occurrence on surfaces that were unvegetated or did not exist in 2011 indicated that elevation, distance from shoreline, and surface age (i.e., time since surface stabilization) all influenced the likelihood of vegetation establishment and persistence (Figure 7). Response curves suggested that the likelihood of occurrence increased rapidly with increasing elevations >–0.5 m above MHHW and distances from shoreline >75 m (Figures 7A, B). The model with surface age defined as the number of years since there was >25 cm yr^{-1} of net annual erosion or deposition received considerably more AICc support than models with surface age defined by higher or lower thresholds of maximum net annual erosion or deposition (20-cm, ΔAICc=5; all others (10–50-cm), ΔAICc>14), suggesting that colonizing vegetation may frequently tolerate net annual erosion or deposition of <25 cm, but not larger perturbations. The likelihood of occurrence increased rapidly with increasing surface ages >2 years (Figure 7C), suggesting a 1–3-year lag between surface stabilization and discernible vegetation colonization on aerial imagery. The predicted likelihood of vegetation occurrence was 35% 3 years after surface stabilization, 60% after 4 years, 80% after 5 years and >90% after 6 years.

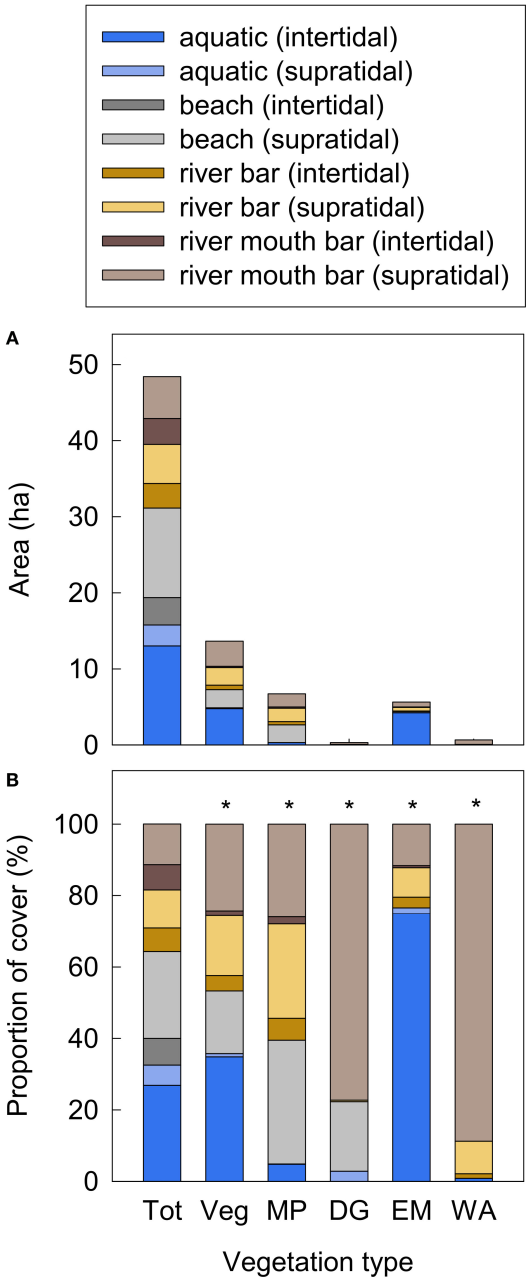

FIGURE 5
(A) Area (ha) and **(B)** proportional cover of mapped 2018 geomorphic surface classes in the Elwha River delta (U.S. state of Washington) that were unvegetated or did not exist in 2011 (i.e., prior to dam removal) and that were colonized by different vegetation types by 2018: total new area including surfaces that remained unvegetated (Tot), total new-surface vegetation (Veg), new-surface mixed pioneer vegetation (MP), new-surface dunegrass (DG), new-surface emergent marsh (EM) and new-surface willow–alder forest (WA). Colors indicate cover separately by geomorphic surface type. Asterisks (*) indicate p<0.0001 from Pearson's Chi-square frequency tests for each vegetation type comparing the frequency of different geomorphic surface types to expected frequencies based on the total area (Tot). Community types with total colonized area <0.2 ha are not shown.

3.1.3 Temporal trends in delta plant community abundance

Cover by mixed pioneer and emergent marsh communities in the delta tripled between 2011 and 2018 (Figures 2, 3C; Table S2), with a net increase of 5.2 and 6.5 ha, respectively. This increase mainly reflected colonization of new surfaces that had been unvegetated in 2011 (see above). However, emergent marsh vegetation also colonized 1.0 ha that had been mixed pioneer or riparian shrub vegetation in 2011, further increasing emergent marsh cover and offsetting the increase in mixed pioneer cover (Table S2). Also, some mixed pioneer and emergent marsh vegetation that was already established by 2011 developed into other, later-successional community types by 2018, or reverted to no vegetation, further offsetting the increases in cover.

During the same period, willow–alder forest cover in the delta increased by 2.6 ha (>50% increase), while riparian shrub cover

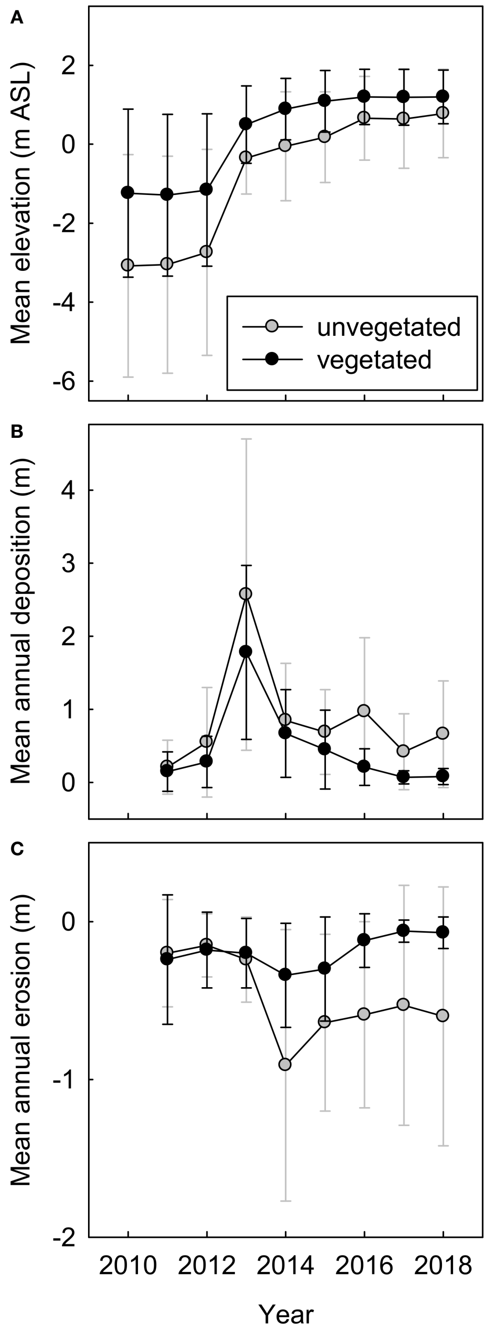

FIGURE 6
Temporal trends in elevation of new and previously unvegetated geomorphic surfaces in the Elwha River delta (U.S. state of Washington) during (2011–2014) and after (2014–2018) dam removal, comparing surfaces that were colonized by vegetation by 2018 versus surfaces that remained unvegetated: **(A)** mean surface elevation (m above mean higher high water), **(B)** mean annual net deposition (i.e., mean change in elevation for surfaces that increased in elevation that year), and **(C)** mean annual net erosion (i.e., mean change in elevation for surfaces that decreased in elevation that year). Error bars are one standard deviation of the mean.

decreased by 1.9 ha (>30% decrease) (Figures 2, 3C; Table S2). Although mixed pioneer vegetation development into willow–alder forest contributed to the increase in willow–alder forest cover, a larger portion of new willow–alder forest occurred in areas that had been riparian shrub in 2011 (1.4 ha; Table S2). Willow and especially alder were common in riparian shrub communities. As these willow and alder grew larger over time, they likely became more discernible on aerial imagery, changing the appearance of some communities from dominance by riparian shrubs to dominance by willow and alder, particularly in the southeastern corner of the study area farther from tidal and river influence. Development into willow–alder forest was the primary reason for declining riparian shrub community cover through 2018, although some 2011 riparian shrub cover also changed to emergent marsh or mixed riparian forest.

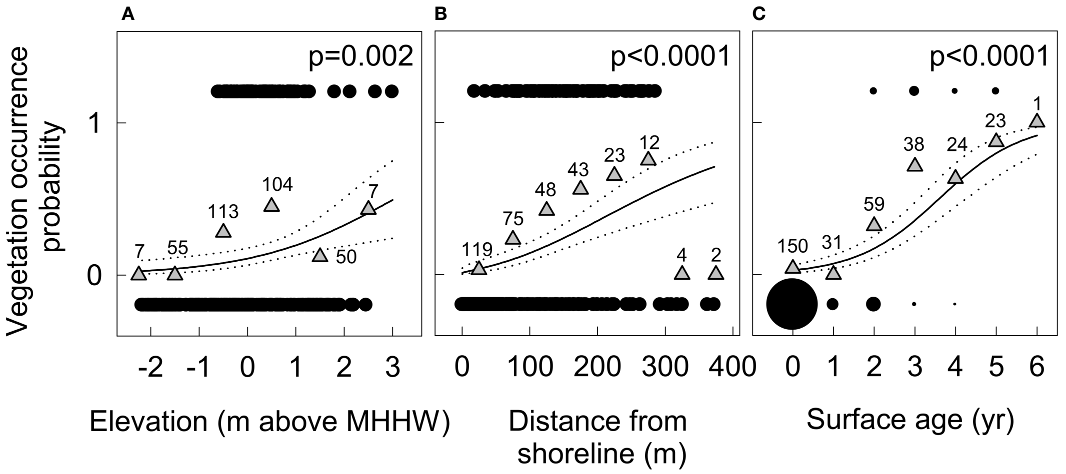

FIGURE 7
Response curves from logistic regression of 2018 vegetation occurrence on new and previously unvegetated geomorphic surfaces in the Elwha River delta (U.S. state of Washington) as a function of **(A)** surface elevation (m above mean higher high water) in 2018, **(B)** distance from shoreline in 2018, and **(C)** surface age, defined as years since >25 cm yr^{-1} of net annual erosion or deposition. Black circles in **(A, B)** show vegetation occurrence (presence/absence) for each random point in the dataset. The bubble plot in **(C)** shows the frequency of vegetation presence and absence for each year of surface age. Grey triangles show percent occurrence across points within evenly distributed bins (by meter in **(A)**, 50 m in **(B)** and year in **(C)**), labeled with the sample size within each bin. Distance from shoreline was square-root transformed for analysis; back-transformed values are shown in **(B)**.

3.2 Vegetation plots

3.2.1 Plant community ordination

Three-dimensional NMDS ordination of species cover in vegetation plots (final stress=0.1097) captured compositional differences between the seven riparian community types (Figures 8, S3). Dimension 1 distinguished woody from herbaceous communities, with high scores corresponding to higher tree and shrub species richness and cover and low scores corresponding to higher forb, graminoid, introduced, and annual/biennial species richness and cover. Dimension 2 captured variation in wetland adaptation, with high scores corresponding to lower community-weighted wetland indicator values and higher emergent macrophyte cover. Dimension 3 separated communities with higher graminoid cover and shrub richness and cover from communities with higher tree richness and cover. For both Dimensions 1 and 2, high scores were associated with lower annual/biennial species richness and cover. For both Dimensions 1 and 3, high scores were associated with higher total, native, and perennial cover.

3.2.2 Compositional differences between new-surface vegetation and established plant communities

Vegetation on new surfaces was dominated by sparse mixtures (66 ± 13% total cover) of native and introduced forbs and graminoids, with few woody plants. Not surprisingly, functional group composition of these pioneer communities differed strongly from other, well-established community types in the delta (Table S3).

Compared to mixed riparian forest, willow–alder forest, and riparian shrub plots, new-surface vegetation plots had lower woody, perennial, and native species cover, and lower woody species richness. New-surface vegetation also had lower total cover than mixed riparian forest and riparian shrub plots, lower forb cover than willow–alder forest and riparian shrub plots, higher introduced species cover, graminoid cover, and graminoid richness than mixed riparian forest plots, and higher annual/biennial richness and cover and lower native richness than riparian shrub plots.

New-surface vegetation was more similar to herbaceous-dominated, pre-dam-removal community types (mixed pioneer, emergent marsh, dunegrass), but still differed in several respects (Table S3). New-surface vegetation had lower graminoid cover than dunegrass and emergent marsh plots, lower woody species richness than dunegrass plots, lower perennial and native cover than emergent marsh plots, and higher annual/biennial richness and cover than emergent marsh plots. New-surface vegetation also had lower annual/biennial richness and higher woody cover than pre-dam-removal mixed pioneer plots.

Pairwise PERMANOVAs indicated that species composition in new-surface vegetation differed significantly from all other community types (Table S4). Generalized linear mixed models indicated that new-surface vegetation had lower NMDS Dimension 1 scores than mixed riparian forest, willow–alder forest, and riparian shrub plots (all $t_{32}>7.0$, $p<0.0001$; Figures 8A, B) and lower NMDS Dimension 3 scores than dunegrass and riparian shrub plots (both $t_{26}>5.0$, $p<0.0001$; Figures 8C, E). NMDS axis 2 scores were lower for most new-surface vegetation plots than emergent marsh plots ($t_{33}=2.9$, $p=0.03$; Figures 8A, E), but not for six plots (Figure 8A) that were on intertidal new surfaces in protected lagoons, classified as emergent marsh on aerial imagery. SIMPER analyses suggested that these differences were driven by substantially higher cover of dominant species in established community types than in new-

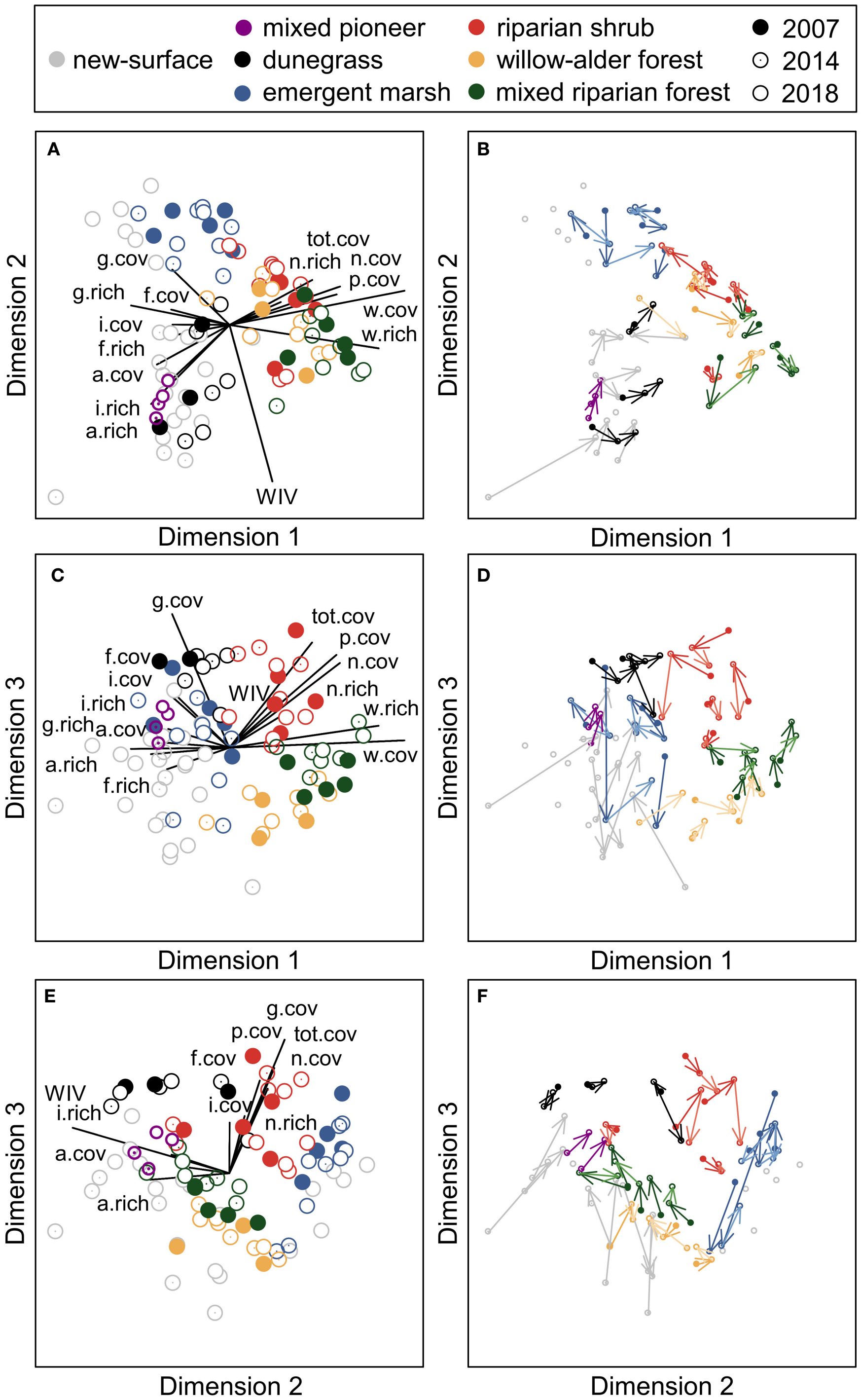

FIGURE 8
Non-metric multi-dimensional scaling (NMDS) ordination of plant species cover in vegetation plots in the Elwha River delta (U.S. state of Washington), showing each pairwise combination of three dimensions. **(A, C, E)** Overlay plots of community type (different colors) and year of measurement (filled circles=2007, dotted circles=2014, empty circles=2018). Joint plots illustrate the relative strength of correlations between ordination scores and functional group richness (".rich") and cover (".cov"); relationships with Pearson's $r \geq 0.2$ are shown. "tot"=all plants, "w"=woody, "f"=forb, "g"=graminoid, "p"=perennial, "a"=annual/biennial, "n"=native", "i"=introduced, and "WIV"=the community-weighted mean wetland indicator value. **(B, D, F)** Vector plots indicating the direction of temporal change for each plot from 2007 (before removal of two dams on the Elwha River) to 2014 (during dam-removal) to 2018 (after dam-removal).

surface vegetation (e.g., *Leymus mollis* in dunegrass communities, *Eleocharis palustris* and *Carex obnupta* in emergent marsh, *Rosa* sp. and *Malus fusca* in riparian shrub communities, *Alnus rubra* and *Salix sitchensis* in willow–alder forest, and *Oemleria cerasiformis*, *Alnus rubra*, and *Rubus spectabilis* in mixed riparian forest), as well as by higher cover of *Lathyrus japonicus*, a dune legume, in new-surface vegetation than in other community types (Table S4).

3.2.3 Vegetation development on new surfaces

In new-surface vegetation plots, rapid sediment accretion (up to 4.0 m yr^{-1}) began with initial dam removal in 2011–2012 in most plots (Figure 9). Sediment accretion slowed to <0.25 m yr^{-1} in different years in different plots (2012–2015), resulting in differences in surface age of up to six years among plots. In four plots, channel movement and sediment re-working during the 2014–2015 winter (following 2014 sampling) resulted in >1 m of erosion (Figures 9G–I, M). One of these plots was lost to the active channel (Figure 9I), but the other three received substantial re-deposition (0.4–0.9 m) in 2016, resulting in new, lower surfaces. Mean elevations following surface establishment varied among plots and sampling years from −0.6 m (intertidal) to 1.1 m (supratidal) relative to MHHW.

Model selection indicated that surface age, elevation, substrate gravel/cobble, and soil depth influenced different components of plant community composition on new surfaces (Table S5). We defined surface age (i.e., years since surface stabilization) *a priori* as the number of years since net annual erosion and deposition slowed to <25 cm yr^{-1}, a rate that we expected colonizing vegetation could potentially survive. This choice was subsequently supported by logistic regression model selection results for vegetation occurrence on new surfaces on aerial imagery (see *Vegetation colonization of new surfaces created by dam removal* results above). Models that included surface age received AICc support for both species richness and cover of nearly all functional groups, with substantially higher richness and cover on older surfaces for the total plant community, perennials, forbs, graminoids, native species, and introduced species (Figure 10). Lower-elevation new surfaces supported vegetation with lower community-weighted mean wetland indicator values, lower perennial cover, higher introduced species cover, and higher annual/biennial species richness and cover (Figure 11). Total, forb, and introduced species richness were higher on coarser substrates, while total, forb, and native species cover were higher on deeper soils (Figure 11). By contrast, woody species richness was lower on both deeper and coarser soils. Many of these relationships with elevation, soil depth, and soil particle size were largely driven by high species richness and low cover in two plots on an intertidal river bar adjacent to the active channel, on relatively young (0–2 yr), recently-reworked surfaces at low elevations with shallow, coarser soils (Figures 9G, H, 11A, D–G, I–K). Some of the relationships between cover and elevation or soil depth were driven in addition or instead by high cover in 1–3 plots on intermediate-aged (2–4 yr) intertidal aquatic surfaces at low elevations with deep soils within a newly formed lagoon (Figures 9J, L, M, 11B, C, E–G).

Model selection also indicated that lower-elevation plots with finer substrates had higher NMDS Dimension 2 scores, indicating similar species composition to emergent marsh plots (Figure 8A), while higher-elevation, older plots had higher NMDS Dimension 3 scores, indicating more similar composition to dunegrass plots (Figure 8E). For the six plots on surfaces that established before 2014 and were not reworked during the 2014–2015 winter, NMDS Dimension 3 scores increased notably between 2014 and 2018, resulting in closer proximity of these older plots to established community types in ordination space (Figures 8B, D, F). PERMANOVA indicated that species composition in these plots differed significantly between 2014 and 2018 ($F_{1,11}$=2.5, p=0.02). SIMPER analyses suggested that this temporal change was driven by higher cover of the most common species in 2018 (e.g., *Lathyrus japonicus*, *Leymus mollis*, and *Holcus lanatus*; Table S6).

3.2.4 Temporal change during and after dam removal in established plant communities

Plant communities that existed prior to dam removal changed in several ways between 2007 and 2018 that may have been related to dam removal but also could be related to successional processes. Across community types, woody cover increased from 75 ± 16% in 2007 to 83 ± 19% in 2014 and 89 ± 15% in 2018, while introduced species richness decreased from 6 ± 1 in 2007 to 5 ± 1 in 2014 and 4 ± 1 in 2018 (Table S7).

Significant year × community type interactions indicated additional temporal changes in dunegrass, emergent marsh, riparian shrub, and willow–alder forest plots but not in mixed riparian forest plots (Table S7). PERMANOVAs also indicated that species composition changed over time in dunegrass, emergent marsh, and riparian shrub plots (Table S8), but not in willow–alder and mixed riparian forest plots (p>0.05).

In dunegrass plots, SIMPER analyses suggested that temporal change was driven by substantial decreases in cover by dominant dunegrass community species (*Leymus mollis*, *Lathyrus japonicus*) and increases in cover by woody species (e.g., *Rosa* spp.), *Artemisia suksdorfii*, and introduced annual grasses (*Aira* spp.) (Table S8). Dunegrass plots also had higher NMDS Dimension 1 scores in 2018 than 2007 (year × type, $F_{8,26}$=2.3, p=0.048; Figures 8A, B), reflecting increased woody species cover. Further, forb cover in dunegrass plots decreased from 55 ± 25% in 2007 to 14 ± 2% in 2014 and 13 ± 4% in 2018 (Table S7). Plot topographic surveys indicated that the dunegrass plots received 11–57 cm of net sediment deposition between 2007 and 2014 (Figure S4). No net deposition was apparent between 2014 and 2018.

In emergent marsh plots, SIMPER analyses suggested that temporal change was driven by increases in obligate wetland species cover (*Carex obnupta*, *Typha latifolia*) and decreases in facultative wetland species cover (*Argentina egedii*, *Juncus arcticus*) (Table S8). Accordingly, community-weighted mean wetland indicator values in emergent marsh plots also decreased from 2.2 ± 0.3 in 2007 to 1.5 ± 0.2 in 2014 and 1.4 ± 0.2 in 2018 (Table S7). This increase in wetland adaptation occurred in conjunction with ongoing sediment deposition, with 23–55 cm of net deposition between 2007 and 2014 in three of the four plots and 12–23 cm of net deposition between 2014 and 2018 in all plots (Figure S4).

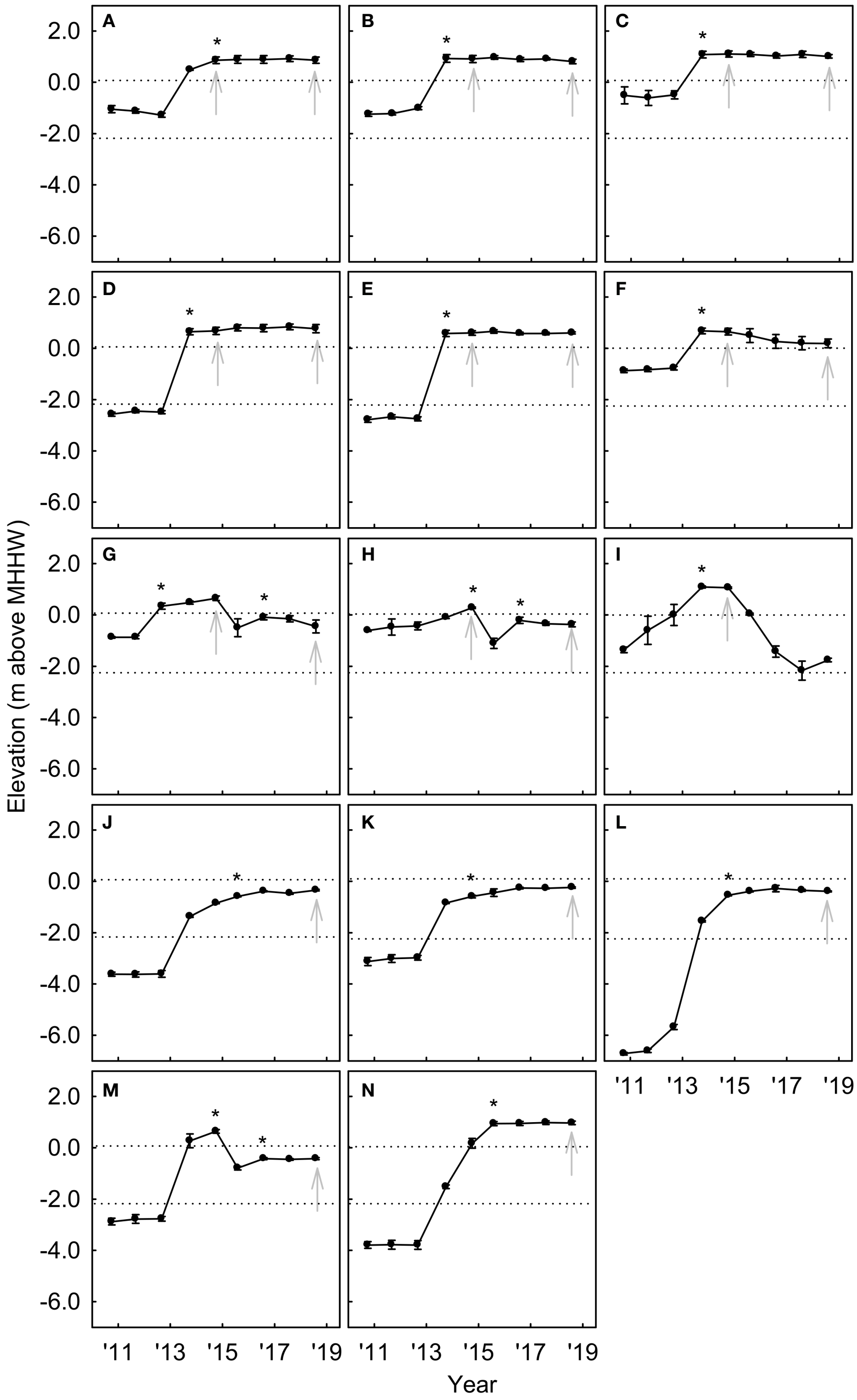

FIGURE 9
Annual surface elevation (m above mean higher high water) in new-surface vegetation plots from pre-dam-removal (2010) to four years post-dam-removal (2018) in the Elwha River delta (U.S. state of Washington). Each panel **(A–N)** depicts annual mean surface elevation over time within a single 100 m^2 vegetation plot. Dashed lines indicate elevations of mean higher high water (MHHW) and mean lower low water (MLLW) (USA NOAA Tidal Datums for Port Angeles, WA; https://tidesandcurrents.noaa.gov/). Gray arrows indicate years in which vegetation was sampled. Asterisks indicate timing of surface establishment, determined from cessation of substantial sediment accretion ($\geq$0.25 m yr^{-1}). In panels **(G, H, M)**, there are two asterisks, because channel movement and sediment re-working during the 2014–2015 winter removed initially established surfaces and sediment deposition in 2016 created new established surfaces. Error bars are one standard deviation of the mean.

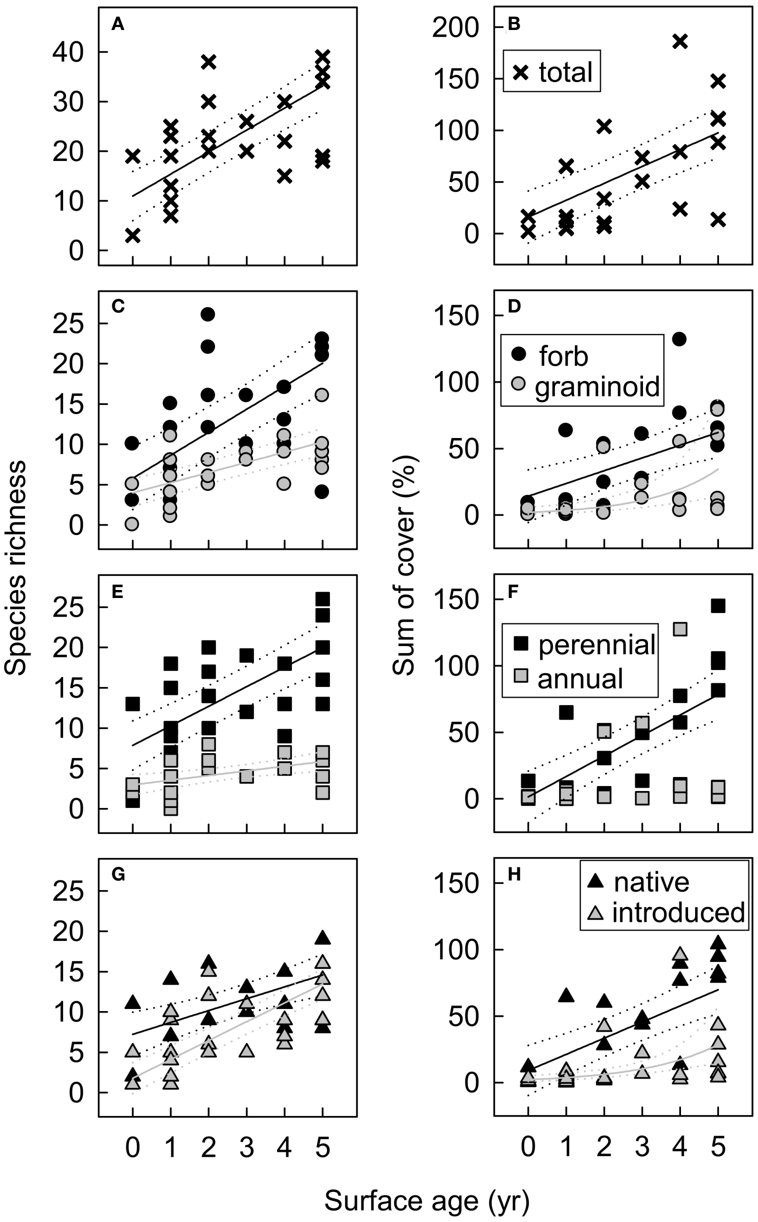

FIGURE 10
Functional group species richness and cover in new-surface vegetation plots in the Elwha River delta (U.S. state of Washington) as a function of plot surface age (years since >25 cm yr^{-1} of net annual erosion or deposition) for **(A, B)** the total plant community, **(C, D)** by growth form (forbs, graminoids), **(E, F)** by life history (perennials, annual/biennials), and **(G, H)** by origin (native, introduced). Model selection (delta Akaike information-theoretic criteria adjusted for small sample size (ΔAICc)) indicated support for surface age as a predictor for all functional groups shown (Table S5). Fitted lines and 95% confidence limits are from models that received the most AICc support, with a Gaussian distribution for most functional groups and a nbinom2 distribution for graminoid and introduced species cover **(D, H)**. Cover values are the sums of estimated cover across species within each functional group. Because species cover often overlapped, the sum of cover across species exceeded 100% in some plots.

In riparian shrub plots, SIMPER analyses suggested that temporal change was driven by decreases in shrub cover (*Rosa* spp.) and increases in riparian tree cover (*Salix sitchensis*, *Populus balsamifera*, *Alnus rubra*) (Table S8). Forb species richness in riparian shrub plots increased from 7 ± 1% to 11 ± 2% between 2007 and 2014, but then returned to 7 ± 2% in 2018 (Table S7). Riparian shrub plots received more gradual sediment deposition than dunegrass or emergent marsh plots, with 6–19 cm of net deposition in three of the four plots in 2007–2014 and 9–14 cm in 2014–2018 (Figure S4).

4 Discussion

Removal of two large dams on the Elwha River created substantial new coastal habitat at the river mouth. Sediment release and transport during and following dam removal increased the total area of intertidal and supratidal habitats in the delta and estuary by 26.8 ha between 2011 (prior to dam removal) and 2018 (four years after dam removal was complete) (Figures 1–3). Coastal wetland, riparian, and dune vegetation colonized 16.4 ha of new and previously unvegetated surfaces that aggraded with sediment from the former reservoirs.

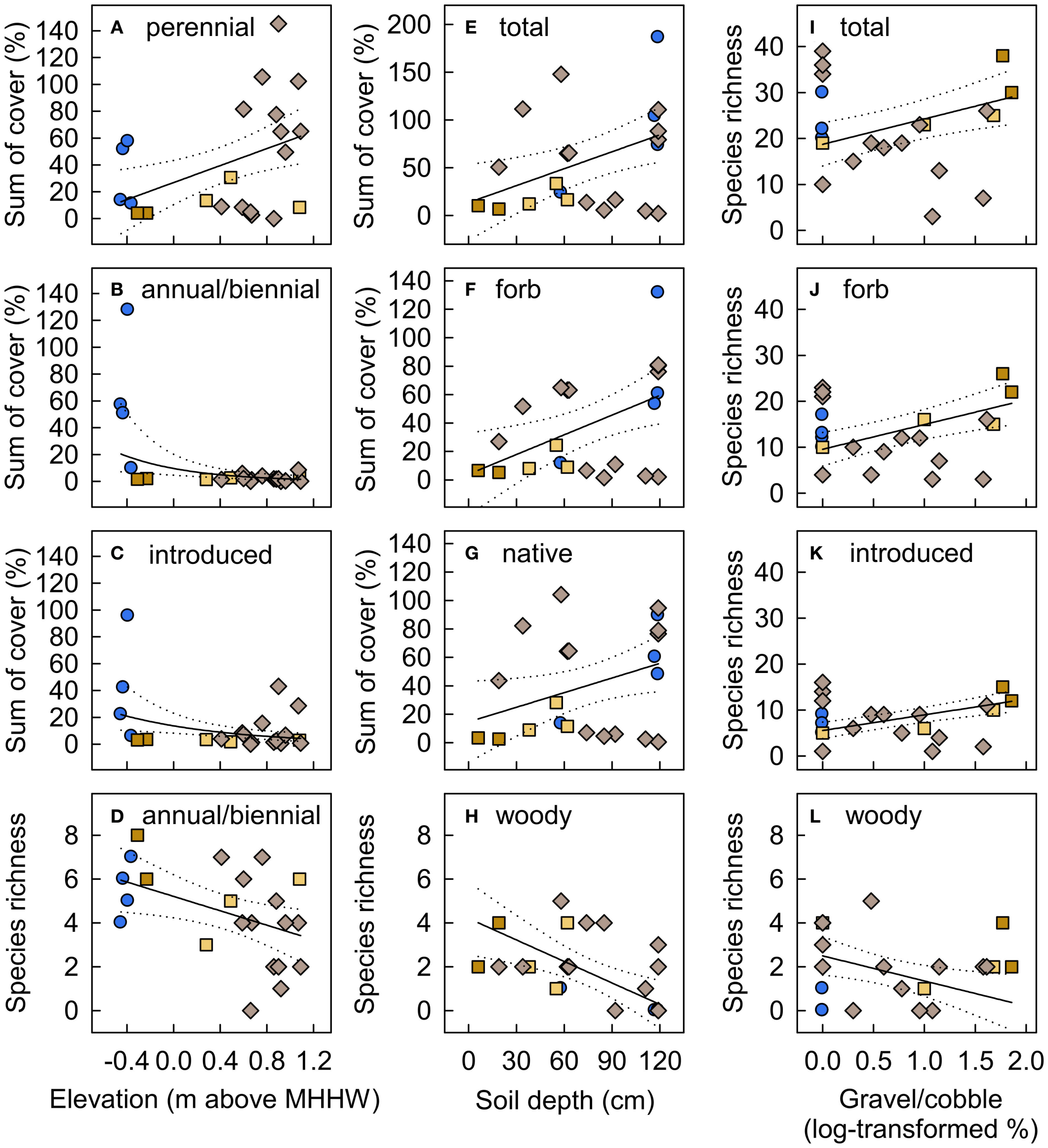

FIGURE 11
Functional group species richness and cover in new-surface vegetation plots in the Elwha River delta (U.S. state of Washington) as a function of plot **(A–D)** elevation (m above mean higher high water), **(E–H)** soil depth, and **(I–L)** substrate gravel/cobble. Model selection (delta Akaike information-theoretic criteria adjusted for small sample size (ΔAICc)) indicated support for these variables as predictors for the functional groups shown (Table S5). Fitted lines and 95% confidence limits are from models that received the most AICc support, with a Gaussian distribution for most functional groups and a nbinom2 distribution for annual/biennial and introduced species cover and woody species richness **(B, C, H, L)**. The best models also included plot surface age for all response variables except annual/biennial cover and woody species richness (Figure 10). Symbol shapes and colors are from Figure 3B, indicating plots on intertidal aquatic (blue circles), intertidal river bar (dark tan squares), supratidal river bar (light tan squares), and supratidal river mouth bar (light brown diamonds) surfaces. Cover values are the sums of estimated cover across species within each functional group. Because species cover often overlapped, the sum of cover across species exceeded 100% in some plots.

4.1 Which landscape positions and elevational histories supported vegetation establishment and persistence on new delta surfaces?

Among the new coastal geomorphic surfaces that were created following dam removal, vegetation colonized surfaces that remained relatively stable for at least 2–3 years (<25 cm net annual elevation change), were high enough in elevation to support wetland vegetation (>–0.5 m above MHHW), and were far enough from the sea to be protected from over-topping waves (>~75 m) (Figures 6, 7). Mixed pioneer vegetation colonized new supratidal beach, river bars, and river mouth bars, while emergent marsh vegetation colonized new intertidal aquatic habitats (Figure 5). In particular, supratidal river bars and river mouth bars supported >40% of new vegetation even though they made up <25% of new surfaces, suggesting that these surface types provided particularly suitable habitat for colonization. The importance of surface stabilization for vegetation establishment likely explains why most new-surface vegetation established after 2014

(Figure 4), as most new surfaces were highly dynamic during the first three years of dam removal (Ritchie et al., 2018; Warrick et al., 2019). Surface elevation and elevational dynamics have also been identified as key predictors in transitions between unvegetated tidal flats and vegetated saltmarsh in other coastal areas (Fagherazzi et al., 2006; Wang and Temmerman, 2013; Jia et al., 2023). Elevation in coastal habitats can serve as a proxy for more mechanistic predictors, such as inundation depth and duration. In the Elwha River delta, calculating these inundation metrics would require hydrologic models to integrate tidal and fluvial inflows and outflows, including within increasingly disconnected lagoons, which was beyond the scope of this study.

4.2 How did vegetation composition on new delta surfaces compare to other Elwha River plant communities?

Not surprisingly, vegetation on new surfaces retained early-successional characteristics into 2018 compared to the plant communities that existed in the delta prior to dam removal. New-surface vegetation had substantially lower cover of the dominant species typical of the established community types (Table S4). Low woody cover made new-surface vegetation resemble emergent marsh and dunegrass communities more closely than riparian shrub, willow–alder, and mixed riparian forest communities (Figure 8), but new-surface vegetation also differed meaningfully from emergent marsh and dunegrass communities, with lower graminoid cover than both emergent marsh and dunegrass communities, and lower native and perennial cover and higher annual/biennial cover than emergent marsh (Table S3).

The species present in new-surface vegetation, however, included a large proportion of the species present in established delta plant communities, as well as upstream on the Elwha River. Of the 88 species that occurred in >5% of established delta plant community plots in 2007–2018, 55% (49) occurred in new-surface vegetation plots, including 48% (29) of the 60 species that occurred in woody-dominated delta community types. Similarly, in vegetation establishing in the former Mills Lake reservoir upstream, 66% of indicator species identified on different surface types (Chenoweth et al., 2022) occurred frequently (>15% of plots) in new-surface vegetation in the delta, as did 42% of all species in the former reservoir with >1% mean cover (not including where planted) (Prach et al., 2019). On river reaches between and below the former dams, 90% of indicator species identified on gravel bars and 43% of indicator species identified on floodplains (Brown et al., 2022) also occurred frequently in new-surface vegetation in the delta, including common early-successional woody species (*Populus balsamifera*, *Salix sitchensis*) and native and introduced herbaceous perennials (e.g., *Agrostis stolonifera*, *Epilobium ciliatum*, *Equisetum arvense*, *Holcus lanatus*, *Artemisia suksdorfii*). However, none of the indicator species identified on upstream terraces (Brown et al., 2022) occurred in >5% of new-surface vegetation plots, suggesting that the new delta surfaces were not yet suitable for the latest-successional species along the Elwha River.

4.3 How did vegetation on new delta surfaces change as surfaces aged?

Although vegetation on new surfaces remained early-successional in 2018, differences with established delta plant communities diminished over time as new-surface vegetation developed, suggesting that new-surface vegetation may eventually mature into later-successional delta community types. On aerial imagery, ~1 ha of new-surface mixed pioneer vegetation developed into what appeared to be young dunegrass or willow–alder communities by 2018 (Figure 4). In vegetation plots, new-surface vegetation that established before 2014 (all supratidal) increased in compositional similarity to other delta plant communities by 2018 (Figure 8). Further, species richness and cover in new-surface vegetation plots increased with time since surface stabilization for all functional groups except woody species (Figure 10). Although woody cover remained low, early-successional woody riparian species (*Alnus rubra*, *Salix* spp., *Populus balsamifera*) occurred in 67% of new-surface vegetation plots, with potential to grow and spread. These trends of increasing species richness, cover, and presence of typical early-successional riparian woody and herbaceous species suggest similarities to typical early-successional riparian vegetation development following large floods (Gregory et al., 1991; Stromberg et al., 1993; Friedman et al., 1996; Van Pelt et al., 2006). In the future, vegetation at the tops of beach-facing new surfaces may develop into dunegrass communities, whereas vegetation on new surfaces more protected from salt spray and waves may develop into riparian shrub communities or willow–alder forest.

4.4 How did environmental conditions affect species and functional group composition on new delta surfaces?

Elevation strongly influenced community composition on new surfaces, with primarily obligate-wetland species in lower elevation (intertidal) plots versus facultative-wetland and upland species in higher elevation (supratidal) plots. Elevations of intertidal new-surface vegetation plots were similar to established emergent marsh plots, while elevations of most supratidal new-surface vegetation plots were intermediate between established riparian shrub plots and the higher dunegrass plots (Figures 9, S4). In particular, obligate-wetland vegetation established where sediment deposition formed shallow pools and lagoons that were largely cut off from the river and sea, creating new brackish and freshwater habitats (Figure 2). Species composition in the six new-surface vegetation plots in these protected intertidal areas resembled emergent marsh species composition (Figures 8A, E), although with lower cover of the dominant species (Table S4). A few of these plots also had relatively high cover of introduced and annual/biennial forbs (Figures 11B, C, E, F), driven by abundant obligate-wetland annuals, *Lythrum portula* (introduced) and *Limosella aquatica* (native), which did not occur in supratidal plots or established emergent marsh plots. These short-statured, short-lived species are likely to decline in abundance if longer-lived, more competitive species increase in these plots (Grime, 1977). Given the already close resemblance in species composition, vegetation on these protected intertidal new surfaces seems likely to continue to increase in similarity to established emergent marsh vegetation over time. However, it could develop into other community types if and where ongoing sediment deposition substantially increases surface elevation.

Community composition on new surfaces also varied with soil depth and particle size, with higher plant cover on deeper soils and higher species richness on coarser soils (Figure 11). These trends were driven largely by two new-surface vegetation plots that were on a recently reworked, intertidal river bar along the active channel (Figures 9G, H). These plots had higher gravel/cobble cover and shallower soils than most new-surface vegetation plots and supported unusually high plant species richness for such young surfaces, and low cover. Most delta deposits during dam removal were coarse (sand, gravel, cobble), and most fines (1/3 of released sediment; Warrick et al., 2019) were transported offshore (Ritchie et al., 2018), but surficial fines were deposited on protected surfaces in the developing delta (Miller et al., 2015). In particular, the former beach received large inputs of organic matter followed by sediment after removal of the upper dam, resulting in different soil from elsewhere in the delta. By 2018, the only new-surface vegetation plots with substantial gravel or cobble (>40%) and shallow soils (<20 cm) were on surfaces exposed to ongoing marine or fluvial disturbance, either on river bars along the channel or on the new beach. Spatial heterogeneity in inundation, erosion/deposition, soil particle size, and/or soil depth in these plots at the river margin may have created suitable niches for a greater variety of early-successional species than other new-surface vegetation plots (Naiman and Decamps, 1997; Lundholm, 2009), while recent fluvial reworking and/or low organic matter and nutrient availability maintained low cover. Similar patterns were observed in the former Vezins reservoir (France) during dam removal, with higher species richness on dynamic new surfaces closer to the channel, attributed to lower cover of competitive, later-successional species (Ravot et al., 2019). Regardless of the mechanism, high species richness and low cover on coarser, dynamic intertidal new surfaces along the active channel suggest that ongoing fluvial dynamics may result in different vegetation trajectories than on other new surfaces in the delta.

4.5 In established delta plant communities, were there temporal changes in species and functional group composition that could be attributed to effects of dam removal?

In contrast to new surfaces in the delta, dam removal had few discernible effects on delta plant communities that existed prior to dam removal. Many temporal trends in the composition of established delta plant communities seemed as or more likely to reflect natural successional processes than responses to sediment and organic matter deposition from dam removal, such as the increases in woody cover and decreases in introduced species richness across community types, the increase in wetland adaptation in emergent marsh communities, and the increase in riparian tree cover in riparian shrub communities and development of riparian shrub communities into willow–alder forest (Figures 2, 3; Table S7). Over time, these successional processes have potential to homogenize vegetation structure and composition on older, more protected surfaces in the delta, but on-going fluvial and marine disturbance are likely to continue to maintain a patchy mosaic of early-successional community types on less protected surfaces.

However, the decreases in dominant dunegrass community species (*Leymus mollis*, *Lathyrus japonicus*) and forb cover and increases in woody cover in some dunegrass plots were less typical of natural dunegrass succession. These changes may have resulted from increased protection from salt spray and storm waves by adjacent new river mouth bars, lagoons, and beach surfaces, particularly for dunegrass communities east of the main channel, where more of these new surfaces formed (Figure 2). Increased nutrients due to sediment and organic matter deposition (Figure S4) also may have contributed to vegetation change in dunegrass plots, particularly the increase in introduced, annual grasses (*Aira* spp.) (Table S8), which tend to be adapted to disturbed soils and high nutrient availability (Norton et al., 2007). *Aira* spp. cover increased only in the dunegrass plot west of the main channel, which received substantial deposition (~60-cm) and remained relatively exposed to marine forces. If these trends continue, much of the dunegrass communities along the former beach east of the main channel may develop into woody-dominated, riparian shrub communities, and perhaps eventually mixed riparian forest.

4.6 Did dam removal facilitate invasion by introduced species in the delta?

Dam removal appeared to increase overall introduced species richness but not local abundance in the delta. Prior to dam removal (in 2007), we identified 42 introduced species across vegetation plots (Shafroth et al., 2011), most of which were perennial grasses and forbs (62%) and most of which persisted in the plots in 2018 (74%). During and after dam removal (2014, 2018), we identified an additional 34 introduced species in the delta, most of which were annual/biennial grasses and forbs (59%; most frequently *Sonchus asper*, *Vulpia myuros*, *Medicago lupulina*, *Aira caryophyllea*, *Lythrum portula*, *Melilotus officinalis*, and *Poa annua*). Twelve of these new species were observed only in new-surface vegetation plots, but the other 22 species invaded established community types in addition or instead, most often dunegrass communities. Bare ground created by sediment deposition may have facilitated establishment by these short-lived, disturbance-adapted species, particularly on new surfaces and perhaps also in established communities.

However, the proportion of total species richness in the delta that was composed of introduced species remained unchanged from 2007 to 2018 at 35%, which was slightly elevated relative to typical riparian floras (Tullos et al., 2016). Further, dam removal did not increase plot-scale introduced species richness or abundance.

Introduced species richness per plot in established plant communities declined during and after dam removal (Table S7), indicating that introduced species that were present before dam removal became less frequent during this period, sufficient to more than counterbalance the influx of new introduced species. New-surface vegetation had similar introduced species richness to established communities, and higher introduced species cover only than late-successional, mixed riparian forest communities (Table S3), suggesting that the freshly disturbed new surfaces did not facilitate introduced species to a greater extent than established plant communities in the delta.

Results from a recent study of Elwha riparian vegetation upstream of the delta suggest that some of the introduced species in the delta may have reached the delta *via* hydrochory from upstream seed sources (Brown et al., 2022). Of the 76 introduced species we identified in the delta, ~70% (54) were also observed in upstream riparian areas, including >50% (18) of the introduced species that invaded the delta during and after dam removal. An additional 44 introduced species were observed upstream but not in the delta, including 21 annual/biennials, suggesting potential for additional invasion from upstream sources in the future.

Short-lived weedy plants that initially colonize disturbed areas are often displaced over time by later-successional perennials (Bazzaz, 1996). The future status of introduced species in the delta will depend on outcomes of ongoing colonization and competition by native and introduced annuals and perennials as these communities continue to develop.

4.7 Will restored coastal habitat in the delta persist?

Long-term persistence of new coastal habitat in the Elwha River delta is uncertain. As downstream transport of former reservoir sediment decreases and the river gradually returns to a quasi-equilibrium natural sediment regime, it is unclear whether ongoing sediment inputs will be sufficient to maintain the expanded delta. River sediment loads declined after dam removal was complete, but they were still elevated at 2.8× the estimated natural sediment load in 2016 (Ritchie et al., 2018). Accordingly, delta progradation continued after dam removal in 2014–2016, although more slowly than during dam removal (Figure 2A; Foley et al., 2017b). The net loss of 4.5 ha of new surfaces in the delta in 2016–2018 suggests that river sediment loads declined further during this period, such that shoreline erosion outweighed deposition of river-transported sediment, as sediments in the former reservoirs and downstream river corridor continued to stabilize and sediment transport gradually approached the natural sediment regime. As a result, ~10% (1.6 ha) of new coastal vegetation in the delta was lost in 2016–2018 (Figure 4), mainly to channel migration and landward migration of the beach east of the river mouth (Figures 2D, E). A series of "sedimentation waves" along the shoreline in 2015, 2017, and 2018 eroded surfaces east of the river mouth, re-depositing the sediment farther down the coast (Warrick et al., 2019).

Long-term persistence and/or expansion of the remaining 90% of new coastal vegetation in the delta will depend on the balance between ongoing erosional and depositional processes, as fluvial and marine forces continue to transport and rework former reservoir sediment in the context of the restored natural sediment regime (Ritchie et al., 2018). New vegetation is most likely to persist on higher new surfaces (e.g., the former beach), but also may persist on relatively protected, lower surfaces (e.g., new lagoons and their margins). In particular, vegetation on some lower surfaces may persist by generating positive feedbacks in which increasingly dense and structurally diverse plant communities facilitate sediment deposition, accumulate organic matter, develop complex root systems, and thereby create and maintain higher, more stable geomorphic surfaces (Miller et al., 2008; Nardin and Edmonds, 2014; Larsen, 2019; Weisscher et al., 2022).

4.8 Insights for coastal responses to future large dam removals

Rapid vegetation colonization and development on new surfaces in the Elwha River delta suggest that coastal surfaces created by dam removal can quickly support plant communities dominated by locally common, native species. The Elwha River dam removals were exceptional, however, in the magnitude of sediment released and their proximity to the coast (Foley et al., 2017b), resulting in larger, longer-lasting morphological changes in the delta than other large dam removals to date (Ritchie et al., 2018). Expansion of coastal habitat during and after dam removal depends on the ability of the river to mobilize and transport large quantities of former reservoir sediments to the coast, and then to retain those sediments within the delta and estuary. These processes will vary among dam removals depending on geographic and landscape context, reservoir sediment characteristics, dam removal strategies, downstream channel characteristics, and more (Foley et al., 2017a). In particular, dam removals that are designed to minimize mobilization of reservoir sediment in order to protect downstream infrastructure are unlikely to create substantial new coastal habitat (East et al., 2023). Coastal habitat also may respond differently to removal of dams that substantially alter streamflow, because the restored natural flow regime is likely to influence coastal geomorphic and vegetation dynamics, but to date few dams (and no large dams) that substantially alter streamflow have been removed and studied (Foley et al., 2017a).

5 Conclusion

Coastal responses to the Elwha River dam removals suggest that sediment pulses during large dam removal have potential to restore substantial coastal wetland habitat within a few years of dam removal, without negatively affecting established coastal plant communities. However, the long-term development and longevity of this restored habitat is not yet known. Vegetation establishment, persistence, and development on new coastal surfaces formed during dam removal depends on surface stability, elevation, exposure to fluvial and marine forces, and soil characteristics, all of which may change over time. Long-term monitoring of the Elwha River and future large dam-removals near coasts is needed to determine the long-term efficacy of large dam removal for restoring coastal wetland habitat under different conditions.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: LP, PS, SA, IM and Ritchie, A. C. (2023). Vegetation and geomorphic surfaces in the Elwha River delta, Washington, after dam removal, derived from 2016 and 2018 aerial imagery and 2007, 2014, and 2018 field surveys. US Geological Survey Data Release. doi: 10.5066/P9O6NML1.

Author contributions

LP wrote the original draft, performed the statistical analyses, and created the figures. PS conceived of and administered the project, designed the methodology, collected field data, and edited the manuscript. SA performed GIS analyses and interpretation and edited the manuscript. IM performed GIS analyses and interpretation and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1233903/full#supplementary-material

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Establishment of terrestrial mammals on former reservoir beds following large dam removal on the Elwha River, Washington, USA

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Terrestrial wildlife species are important yet often overlooked taxa in the recovery of ecosystems following dam removal. Their presence can shape ecosystem recovery, signal restoration of ecosystem function, and influence food web dynamics and nutrient transfer. We used camera traps to examine seasonal use of two former reservoir beds and an upstream reference reach by the mammalian community following the removal of two large dams on the Elwha River, Washington, USA. For certain taxa, we compared current species use to data collected prior to dam removal. Camera traps revealed use by at least fifteen mammal species, including but not limited to American black bear (*Ursus americanus*), Columbian black-tailed deer (*Odocoileus hemionus columbianus*), Roosevelt elk (*Cervus elaphus roosevelti*), puma (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and snowshoe hares (*Lepus americanus*). Coyotes were found mostly lower in the watershed outside the Olympic National Park boundary, while other species were distributed throughout the restoration area. We did not see major differences in species composition between the restoration areas and the upstream reference reach, though number of detections across study reaches differed for most species. Unlike previous findings, black bears were observed across all seasons in this study, suggesting a shift in seasonal use since dam removal. Full restoration of the terrestrial wildlife community could take decades to unfold, but early patterns demonstrate rapid establishment and use by wildlife on new riparian surfaces that are expected to continue to evolve with restoration of fish and vegetation communities.

KEYWORDS

camera-trapping, dam removal, Elwha, restoration, wildlife

1 Introduction

Opportunities to study large ecosystem restoration are rare and have been limited primarily to studies conducted after large-scale environmental perturbations like volcanic eruptions (Major et al., 2009), forest fires (Vallejo and Alloza, 2015; Alayan et al., 2022; Souza-Alonso et al., 2022), or long-term ecological degradation like occurred in the Florida Everglades (Doren et al., 2008). Dam removals are a relatively new but critical tool in ecological restoration efforts (Hart and Poff, 2002; O'Connor et al., 2015), and provide invaluable opportunities for monitoring ecosystem recovery over large spatial extents and long temporal scales. The increasing frequency of dam removals, particularly large dams, has amplified interest in comprehensive ecological monitoring and research programs to gauge the success of ecosystem restoration after these large-scale projects (Babbitt, 2002; Bellmore et al., 2016). While research and monitoring programs following dam removals are beginning to increase, research to date has been more focused on the physical or abiotic processes of dam removal than biotic restoration (Bellmore et al., 2016). Furthermore, ecological studies have focused primarily on aquatic biodiversity, with very little work on terrestrial vegetation and wildlife (Bellmore et al., 2016). To achieve restoration of ecosystem function following dam removal, restoration ecologists would benefit from understanding terrestrial and aquatic ecological processes as they relate to changes in the physical environment (Bellmore et al., 2016). Here, we focus on terrestrial wildlife as a facet of ecosystem restoration following large dam removal.

The removal of two large dams on the Elwha River, Washington, USA between 2011 and 2014 provided an unprecedented opportunity to understand how terrestrial wildlife both respond to and interact with the restoration process following dam removal (McCaffery et al., 2018). Removal of the Elwha dams reconnected anadromous fish to the upper reaches of this 72-km river after nearly 100 years of impoundment that restricted their movements to the lower 7.9 km of the river (Pess et al., 2008). Prior to deconstruction, the two dams inundated nearly 324 hectares of land (Department of the Interior, 1994) and trapped more than 19 million cubic meters of sediment (Bountry et al., 2010; Warrick et al., 2012). In the years since dam removal, eight species of anadromous fish have passed above the former dam sites (Duda et al., 2021) and nearly 324 hectares of land in two former reservoir beds have been restored through revegetation efforts (Chenoweth et al., 2022). Restoration has added habitat for terrestrial wildlife and reconnected nutrient linkages from the sea to the upper reaches of the watershed. For terrestrial wildlife, changes in fish availability and the creation and restoration of floodplain habitats may lead to changes in species distribution and seasonal use of the watershed, as well as increased wildlife use in the restored former reservoirs.

In addition to responding to new habitat, wildlife can play a large role in restoring ecosystem functions following dam removal (McCaffery et al., 2018, McCaffery et al., 2020). Wildlife species modify habitats, alter community structure, and shift ecosystem dynamics over short and long time scales (Naiman, 1988). For example, several species in terrestrial mammalian and avian communities may provide beneficial services in the form of seed dispersal (Willson, 1993; Wunderle, 1997; McLaughlin, 2013; Albert et al., 2015) and nutrient transport (Hobbs, 1996; Seagle, 2003; Helfield and Naiman, 2006; Quinn et al., 2009), while others could influence plant reestablishment, mostly through browsing planted seedlings (Ostfield et al., 1997; Gill and Beardall, 2001), seed predation (e.g., Bricker et al., 2010), or stripping woody stems of their bark (Ostfield et al., 1997). Herbivory by Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*) has the potential to be an important driver of plant successional development (Schreiner et al., 1996; Horsley et al., 2003; Woodward et al., 2021). In the Elwha restoration area, Roosevelt elk demonstrated a strong initial influence on woody plants in the restoration zone through browsing activity (McCaffery et al., 2020). Further, species as varied as American black bears (*Ursus americanus*), weasels (*Mustela* spp.), and raccoons (*Procyon lotor*) may distribute marine-derived nutrients in the form of salmon (*Oncorhynchus* spp.) carcasses throughout early successional forests, providing nutrients important for plant establishment (e.g., Cederholm et al., 1989; Helfield and Naiman, 2006; Quinn et al., 2009). Finally, beavers (*Castor canadensis*) may provide beneficial services by constructing small dams in tributary or side-channel habitats, impounding water and increasing habitat complexity for fish, mammals, and birds (Leidholt-Bruner et al., 1992; Pollock et al., 2004, Pollock et al., 2015).

A key step to understanding how wildlife could interact with the restoration process is to describe patterns and drivers of distribution and activity of these species over time. We used remote cameras to document mammalian wildlife use of the two former reservoir beds and a reference upstream river valley 10 years after dam removal on the Elwha River in Washington, USA. Here, we examine seasonal use of the restoration sites by a suite of mammalian species in comparison to the reference reach over a two-year period. We expected to see use by a diversity of mammalian species, with variation in activity among the seasons of the year as well as across the three different study reaches (i.e., the restoring floodplains above each former dam location and the reference upstream valley). Specifically, we predicted that Roosevelt elk and American black bear use would be higher in the reference valley than in the restoration areas and would show strong seasonal patterns. We expected bear use to be highest in the spring but consistent throughout the summer, with potential for seeing use in the fall and winter coincident with returning salmon. We expected that Columbian black-tailed deer would be commonly detected, but again with seasonal and study reach differences. For these and other taxa, our results provide a baseline with which to compare ongoing restoration of these dynamic landscapes while providing initial insights into how patterns of wildlife distribution and use have changed since dam removal.

2 Materials and methods

2.1 Study area

The Elwha River (Washington, USA) flows from its headwaters in Olympic National Park to where it empties into the Strait of Juan de Fuca (Figure 1). The region has a maritime climate characterized by cool, wet winters and dry summers. We examined wildlife presence in three distinct areas (hereafter 'study reaches') along the Elwha River (Figure 1): 1) within the floodplain of the former reservoir Lake Aldwell (60 m elevation; hereafter "Aldwell"); 2) within the floodplain of the former reservoir Lake Mills (181 m elevation; hereafter "Mills"); and 3) within Geyser Valley, a reference reach located approximately three km upstream of Mills (235 m elevation; hereafter "Geyser"). We selected Geyser as a reference reach to represent a mature riparian system that was not affected by dam removal activities yet is still relatively low in elevation in the watershed. The reference reach was defined by elevation contours that approximated the water level of the former Mills reservoir.

Vegetation and landform characteristics of the revegetating reservoir beds have been described previously (Chenoweth et al., 2022) and in this special issue (Shafroth et al., 2024). Vegetation in the reference reach was dominated by stands of pioneering willow, red alder (*Alnus rubra*), and black cottonwood (*Populus balsamifera* var. *trichocarpa*) communities on the active floodplain and mature mixed conifer/hardwood or conifer stands comprising Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and bigleaf maple (*Acer macrophyllum*) on the older alluvial terraces and sidehills (McCaffery et al., 2020).

2.2 Sampling design

From July 2021 to July 2023, we installed and monitored 10 remote game cameras (Browning ProDCL) in each study reach for a total of 30 cameras over a combined 17,037 trap-nights. To determine camera placement, we used ArcGIS to create a systematic grid of points spaced at 200-meter intervals across each of the three study reaches (Aldwell, Mills, and Geyser). Every second grid point was removed sequentially until ten points remained in each study reach. In the field, we traveled to each GPS coordinate and selected a suitable site within 25–50 meters of the randomly generated grid point, aiming for a site where the camera's view was unobstructed by vegetation. We limited site clearing where possible to leave native vegetation intact but removed light vegetation to reduce false triggers during wind events. We used webbing and cable locks to secure a metal lock box to a sturdy tree at an average height of 35 cm and no more than 0.6 m from the ground. When a sturdy tree was not available, such as on open gravel bars, we positioned rebar stakes into the substrate and attached cameras using heavy-gauge wire. We secured cameras within lock boxes to reduce thefts and limit damage caused by black bears. Each camera had a 42° wide angle of detection; within that range, we used a range finder to record six distance measurements (every 7°) to calculate the camera's viewshed, which varied based on the size of the clearing and proximity of surrounding vegetation. Because our aim was to document presence of all species passively rather than target or attract certain species, and because bait influences detection of some species positively and some negatively (Holinda et al., 2020; Dart et al., 2022; Barcelos et al., 2023), we used unbaited cameras at all sites.

We equipped each camera with six lithium batteries and either a 32, 64, or 128 GB SD card depending on how frequently we checked cameras, with larger SD cards being checked less frequently. At the Aldwell and Mills stations, we visited cameras every two to three months to switch out SD cards and check battery life. Because of the logistical constraints of accessing the more remote Geyser Valley study reach, we checked those cameras every two to nine months. We set cameras on a hybrid mode of motion trigger and time-lapse. Motion trigger images had a one second delay. Time-lapse images were taken to ensure camera functionality throughout each survey

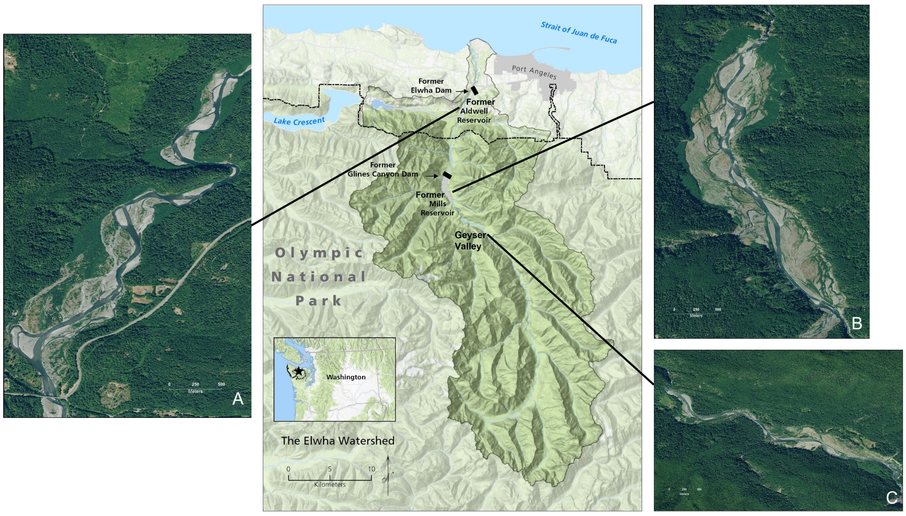

FIGURE 1
Map of the Elwha River watershed, Washington State, USA. The small inset map shows the location of the Elwha River on the Olympic Peninsula (dashed and dotted lines indicate the boundary of Olympic National Park). The central watershed map shows the locations of the three study reaches along the Elwha River, with zoomed-in imagery of the former **(A)** Aldwell and **(B)** Mills reservoirs, as well as **(C)** Geyser Valley, an upstream reference reach. Base map credit: R. Hoffman, Olympic National Park. Aerial photo credit: A. Ritchie, U.S. Geological Survey.

period and consisted of two images captured each day—one hour after local sunrise and one hour before sunset. Time-lapse images were not included in the analyses.

We recorded general habitat characteristics associated with each camera station in the field while setting up our camera stations. We characterized the dominant overstory tree species and the physiographic description of each sampling site; for example, gravel bar, remnant alluvial terrace, or sloped valley wall. We later used GIS to measure the distance of each sampling station from the shoreline of the former reservoir.

2.3 Image identification and data analysis

We used both manual and machine learning models for image classification. We performed manual classifications using Camera Trap File Manager (CTFM), a Panthera-derived software application (http://www.pantheracameratrap.org, Version 2.1.18, accessed 02/2023). Machine learning programs included both PantheraIDS (http://pantheraids.org, accessed 02/2023) and Wildlife Insights (https://wildlifeinsights.org, accessed 06/2023). We verified all images classified by machine learning programs for accuracy. We extracted metadata, including date and time stamps associated with each image, which we then used to build a database.

We calculated the difference in time stamps between each motion-triggered image and the image immediately preceding it of the same species at the same camera. To reduce temporal correlation between sequential images, we retained the first image in each series and removed all subsequent images that were captured within 30 minutes of the immediately preceding image. Thus, for an image to be retained it had to be at least 30 minutes apart from other images of the same species at the same camera. We refer to images retained by this process as independent detection events. We chose a cutoff of 30 minutes based on an examination of our data showing that the number of images excluded would change minimally (by 1% or less) if we increased the cutoff to values greater than 30 minutes. Further, 30 minutes is commonly used in camera studies for rating photos as independent events (O'Brien et al., 2003; Burton et al., 2015, Iannarilli et al., 2021, Ayars et al., 2023).

For each species, we calculated the total number of independent detection events in each study reach, as well as the number of detection events per season in each study reach. We then standardized independent detection events by the number of functional trap nights. This standardization allowed us to correct for occasional camera battery failures that occurred between checks and more accurately compare results across seasons and study reaches. When examining seasonal patterns, we followed typical season lengths for spring (March 21st–June 20st), summer (June 21st–September 20st), fall (September 21st–December 20th), and winter (December 21st–March 20th). Results are summarized as number of independent detections per 100 functional trap nights for ease of interpretation.

We used generalized linear mixed-effects models to examine the relationship between wildlife detection events and various temporal and site-specific covariates for 6 species: bobcat, snowshoe hare, coyote, Columbian black-tailed deer, Roosevelt elk, and American black bear. We fit Poisson models with the response variable defined as the daily count of independent detection events for a particular species. The covariates we assessed were sampling year, season (as defined above), study reach, distance from forest edge, and camera viewshed. We tested 10 candidate models related to our hypotheses for patterns of detections: a null model; single-variable models for each of the five covariates; additive models for season and year, study reach and season, and study reach and year; and an interactive model for study reach and season. We included random effects for camera station and date in all candidate models. We fit the set of models for each species using the *glmmTMB* package (Brooks et al., 2017) in R (Version 4.3.1, R Core Team, 2023). We ranked models according to the Akaike information criterion (AIC) using the *AICcmodavg* package (Mazerolle, 2023) and considered well-supported models to be those with a ΔAIC of less than or equal to 2 (Burnham and Anderson, 2002). We assessed the fit of top-ranked models using the diagnostic functions and workflow of the *DHARMa* package (Hartig, 2022).

3 Results

3.1 Habitat characteristics

We placed cameras in Aldwell primarily in deciduous stands; of 10 camera locations, 8 were in stands dominated by a cottonwood overstory, and one each had overstories dominated by alder and willow. Two locations were on the sloped walls of the former reservoir ("valley wall"), 4 were on the gravel bar, and 4 on remnant terraces. Similarly, camera locations on Mills were all located in deciduous (60%) or gravel bar (40%) habitats. Dominant overstory was split between cottonwood (3 of 10), alder (3 of 10), and willow (3 of 10), with one open site. Two locations were on valley walls, 3 were on the gravel bar, and 5 were on remnant terraces. In contrast, camera locations in Geyser (our established reference reach) were more mixed, with 4 locations in conifer habitats, 3 in mixed conifer/hardwood habitats, and 3 in gravel or deciduous habitats. Six of 10 locations had a conifer overstory (Douglas fir or western hemlock), one was dominated by bigleaf maple, and 3 were alder dominated. Four were located in upland forest, one was on the valley wall, 3 were on remnant terraces, and 2 were on the gravel bar.

3.2 Species composition and seasonal use

After removing blank and unknown images as well those of humans, domestic dogs, birds, and small rodents, we documented a total of 107,658 images, consisting of 5,473 individual detection events (McCaffery et al., 2024). We identified 15 species of mammals over the two years of the study (Table 1) including American black bear, bobcat, chipmunk (*Tamias* spp.), Columbian black-tailed deer, coyote, Douglas squirrel (*Tamiasciurus douglasii*), fisher (*Pekania pennanti*), unspecified mustelid, northern flying squirrel (*Glaucomys sabrinus*), puma, raccoon, Roosevelt elk, snowshoe hare, spotted skunk (*Spilogale gracilis*), and opossum (*Didelphis virginiana*). Most species exhibited variations in detections across both study reach and season (Table 1, Supplementary Table S1).

We fit all 10 candidate models for bobcat, snowshoe hare, coyote, and Columbian black-tailed deer. For all four species, the best supported model contained an interactive effect of study reach and season, with no support for any other models (Table 2, Supplementary Table S2). Model diagnostics did not indicate any problems with model misspecification. We detected snowshoe hares most frequently during the summer, and much more often in Mills (15 detections per 100 trap nights), than in Aldwell (6 detections per 100 trap nights), or Geyser (1 detection per 100 trap nights; Tables 1, 2, Supplementary Table S1). We observed coyotes, a species not native to the Olympic Peninsula, almost exclusively in Aldwell, which is located outside of Olympic National Park. We saw 8 coyote detections per 100 trap nights in Aldwell, compared to less than 1 in Mills and Geyser (Table 1). Coyotes were observed most frequently in the fall (Table 2, Supplementary Table S1). For deer, Mills and Geyser had much higher detection rates (20 and 17 detections per 100 trap nights, respectively) than Aldwell (5 detections per 100 trap nights; Table 1, Figure 2A). Columbian black-tailed deer were most common in the spring and fall seasons, and least common in winter (Table 2, Supplementary Table S1). In contrast to other species, bobcat detections occurred more evenly among seasons and among study reaches, at a rate of approximately 1 detection per 100 trap nights (Tables 1, 2, Supplementary Table S1).

TABLE 1 Summary of mammalian detections per 100 trap nights by study reach in the Elwha River watershed, Washington, USA from July 2021-June 2023.

Species	Aldwell	Mills	Geyser
American black bear	0.36	2.05	3.84
Bobcat	1.10	1.22	0.72
Chipmunk	0.02	0.00	0.05
Columbian black-tailed deer	4.68	20.38	17.17
Coyote	7.56	0.53	0.02
Douglas squirrel	0.09	0.17	1.56
Mustelid spp.	0.00	0.03	0.33
Northern flying squirrel	0.00	0.00	1.01
Pacific fisher	0.00	0.02	0.00
Puma	0.23	0.34	0.92
Raccoon	0.16	0.29	0.05
Roosevelt elk	0.64	1.95	6.15
Snowshoe hare	5.96	15.09	1.12
Spotted skunk	0.00	0.00	0.04
Virginia opossum	0.00	0.03	0.00

Study reaches include the dewatered reservoir beds Aldwell and Mills above the two former dams, as well as the upstream Geyser Valley reference reach.

For Roosevelt elk and black bear, the candidate model with an interactive effect of study reach and season produced a singular convergence warning due to the lack of detections at certain combinations of study reach and season. We therefore excluded it from further consideration. Among the other 9 models, the best supported model for both species contained an additive effect of study reach and season (Table 3, Supplementary Table S2), with no support for any other models. Model diagnostics did not indicate any problems with model misspecification. For Roosevelt elk, Geyser had the highest frequency of detections at 6 detections per 100 trap nights (Figure 2B; Table 1). Mills and Aldwell had less than 2 elk detections per 100 trap nights. We observed elk more often in spring and fall than in summer and winter (Figure 2B; Supplementary Table S1). Black bear detections were highest in Geyser (4 detections per 100 trap nights) and Mills (2 detections per 100 trap nights; Figure 3; Table 1). Bear detections were more frequent in the spring than in any other season (Figure 3; Supplementary Table S1).

We were unable to model factors associated with puma detections due to the small number of photos of this species. We detected pumas more frequently in Geyser (about 1 detection per 100 trap nights) than in Aldwell and Mills (less than 0.4 detections per 100 trap nights; Table 1). Puma detections were lowest in the spring (Supplementary Table S1). Detections of other species were variable and mostly infrequent (Table 1, Supplementary Table S1). We detected one Pacific fisher (*Pekania penannti*) on Mills in February 2023, a rare species that was reintroduced to the Olympic Peninsula between 2008 and 2010 after decades of absence. We detected raccoons on only three occasions in the Geyser study reach, but more frequently in Mills and Aldwell. We had two detections of the non-native Virginia opossum (*Didelphis virginiana*) at Mills in summer 2022 and two detections of the spotted skunk (*Spilogale gracilis*) at Geyser in fall 2021. Weasel (*Mustela* spp) detections were infrequent and occurred almost entirely in Geyser.

4 Discussion

Over two years of camera trapping, we revealed early patterns of use by a diverse suite of mammalian species on revegetating former reservoirs behind the two former dams, as well as in an upstream reference reach on the Elwha River. These data provide an initial snapshot of mammalian use of the two novel, revegetating habitats in comparison to an upstream river valley 10 years following dam removal, showing different patterns of use in newly forming riparian zones (Aldwell and Mills) relative to an established, mature riparian zone (Geyser). We were able to broadly compare distributions of American black bear (Sager-Fradkin et al., 2008) and small carnivores (Jenkins et al., 2013) in this study to studies conducted prior to dam removal. Further, we compared current patterns of use by Columbian black-tailed deer and Roosevelt elk to a study conducted in the three years immediately following dam removal (McCaffery et al., 2020). For other species, the data presented here provide a baseline to which we can compare future work on species distribution and use of the Elwha watershed as restoration and successional processes continue

TABLE 2 Parameter estimates (log scale) and standard errors for the four species with a top-ranked model of Study Reach * Season.

	Bobcat		Columbian black-tailed deer		Coyote		Snowshoe hare	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	***-5.504***	0.402	***-4.985***	0.346	***-3.184***	0.352	***-5.184***	0.729
Geyser	0.371	0.523	***2.632***	0.445	-20.796	2783.674	-1.140	1.045
Mills	*1.047*	0.488	***2.801***	0.443	***-3.265***	0.672	1.657	0.982
Spring	0.261	0.399	***1.540***	0.227	***-0.623***	0.197	0.221	0.179
Summer	0.589	0.350	***1.581***	0.215	***-0.656***	0.164	0.340	0.174
Winter	-0.782	0.503	***-1.191***	0.405	*-0.429*	0.168	0.338	0.176
Geyser: Spring	-0.573	0.545	***-0.591***	0.219	16.644	2783.674	-1.002	0.533
Mills: Spring	*-1.055*	0.505	***-0.806***	0.216	1.147	0.598	0.141	0.199
Geyser: Summer	***-2.657***	0.837	***-2.535***	0.231	-4.397	34641.253	0.314	0.331
Mills: Summer	***-1.882***	0.490	***-2.288***	0.212	***1.661***	0.534	***0.714***	0.188
Geyser: Winter	0.321	0.632	-0.187	0.419	-4.587	35269.030	***-2.084***	0.763
Mills: Winter	0.110	0.577	*-0.842*	0.425	-0.118	0.743	-0.356	0.203

Statistically significant variables are indicated with italics for p-values < 0.05 and with bold italics for p-values < 0.01.

to unfold. Finally, our data can be used as a basis to understand how mammalian wildlife contribute to restored ecosystem function over time.

Our data showed preliminary patterns that suggest American black bear use of the watershed may be expanding seasonally to encompass a larger portion of the year than documented prior to dam removal. A study of black bears prior to dam removal in the Elwha watershed found that they exhibited predictable and synchronous patterns of elevation change throughout the year (Sager-Fradkin et al., 2008). Bears used low-elevation conifer and hardwood forests during spring, mid-elevation forests and meadows during summer, and mid-to-high-elevation forests and meadows during late summer and fall, with limited movement during the winter denning period (Sager-Fradkin et al., 2008). Researchers concluded that bears may change annual distribution patterns after dam removal and salmon restoration by increasing use along the floodplain during late summer and fall when coho and Chinook runs return upriver (Sager-Fradkin et al., 2008). Our detections indicated some evidence that bear presence is higher in the fall to winter than previously documented in Sager-Fradkin et al. (2008 [Figure 2]); moreover, we have recently documented bear use of the Mills reservoir during December, including fishing for coho salmon in a tributary stream (K. Sager-Fradkin, personal observation). However, we expect that fuller shifts in seasonal use could take longer to establish and be a function of both time and recovery of salmon populations. While anadromous fish have now moved upstream past both dams and into the upper watershed (Duda et al., 2021), the restoration process is early and ongoing and fish numbers are influenced by many factors beyond the restoration of the river. Future work should aim to quantify bear use more comprehensively and to understand the role of bears in moving fish and marine-derived nutrients into the surrounding ecosystem once salmon are more established.

Small and mesocarnivore detections were low and variable in this study, in contrast to a pre-dam removal study conducted along the entire river between 2006 and 2008 (Jenkins et al., 2013). The pre-dam removal research documented that populations of some small carnivore species were most common on the lower river reaches (i.e., below and between the dams), although the potential effects of salmon availability (i.e., no salmon present above the lower dam) were confounded with other human uses of the lower river (Jenkins et al., 2013). In this study, small carnivores were rarely detected and in small numbers. Notably, the previous study used bait to attract carnivores (Jenkins et al., 2013), while we used unbaited cameras. Use of baited stations would likely be necessary to better characterize use by this group of species and compare them to pre-dam removal distributions. We had one detection of the Pacific fisher in the second year of our study, a rare mesocarnivore that was reintroduced to the Olympic Peninsula between 2008-2010 after decades of absence presumably due to overtrapping and habitat loss (Hayes and Lewis, 2006), and which was not present when the pre-dam removal study was conducted. This detection adds to other camera detections of this rarely seen species in the area, contributing to our understanding of post-reintroduction use of Olympic National Park and surrounding areas (e.g., Happe et al., 2020). Primary prey for fisher in this area includes snowshoe hares, which we commonly detected in Aldwell and Mills (where the fisher was observed), and which thrive in disturbed or early-stage vegetation (Parsons et al., 2020; Table 1). The regenerating riparian area may provide beneficial hunting areas

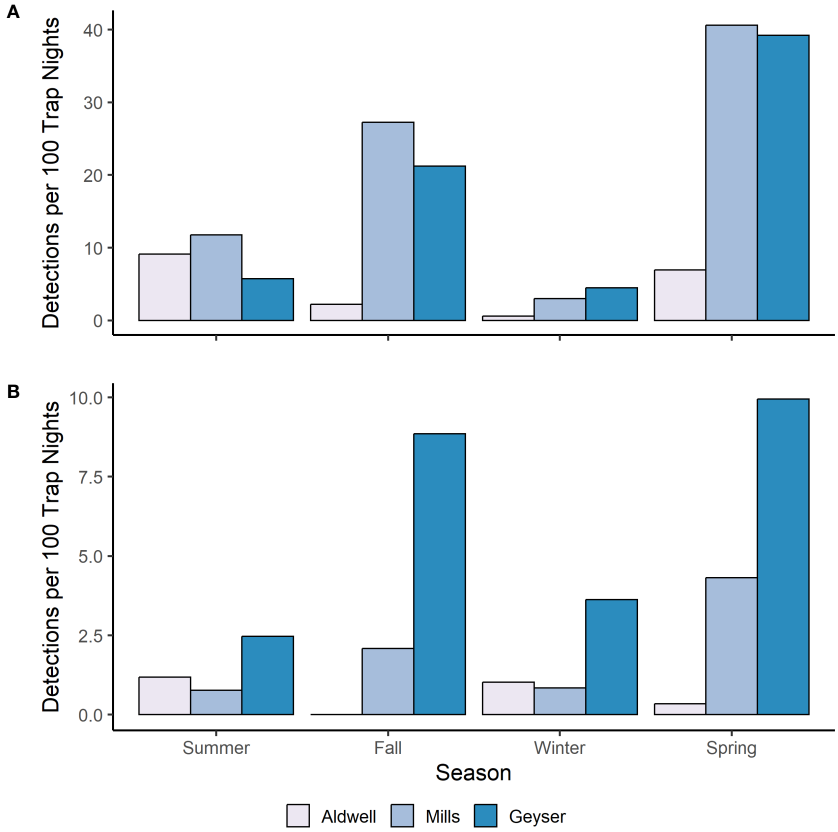

FIGURE 2
Number of independent photo events per 100 camera trap nights for **(A)** Columbian black-tail deer and **(B)** Roosevelt elk and in each study reach and season in the Elwha River from July 2021-June 2023.

for fishers adjacent to mature forests typically used for denning (Lewis et al., 2016). In fact, the fisher we photographed on Mills had a snowshoe hare in its mouth.

We found widespread use of the revegetating reservoir beds and Geyser Valley by Roosevelt elk and Columbian black-tailed deer but continue to see differences across the three study reaches and across seasons. Floodplain bottomlands and riparian zones are key habitats for Columbian black-tailed deer and Roosevelt elk on the Olympic Peninsula (Jenkins and Starkey, 1984; Schroer et al., 1993), and both species used the former Elwha reservoirs relatively quickly after dam removal (McCaffery et al., 2020). In previous work, we examined presence of deer and elk in the three study reaches over the winter and into spring by using pellet counts as indices of use (McCaffery et al., 2020). In that study, we found elk use to be highest in Geyser, low but increasing over time in Mills, and virtually absent from Aldwell (McCaffery et al., 2020). Overall, these general patterns have been maintained in this camera-based study: Geyser still has the highest elk use, but there is some suggestion that winter-to-spring elk use has increased in Aldwell and Mills compared to five years ago (Figure 2B). We found very little overwinter use by deer in study plots in Aldwell and Mills in our previous study (McCaffery et al., 2020). Patterns of use appeared similar in our

TABLE 3 Parameter estimates (log scale) and standard errors for the two species with a top-ranked model of Study Reach + Season.

Parameter	American black bear		Roosevelt elk	
	Estimate	SE	Estimate	SE
Intercept	***-7.529***	0.485	***-5.872***	0.395
Geyser	***2.702***	0.540	***2.658***	0.467
Mills	***1.782***	0.542	***1.506***	0.471
Spring	***2.136***	0.208	0.224	0.156
Summer	***0.866***	0.228	***-0.897***	0.188
Winter	***-2.292***	0.610	***-0.816***	0.185

Statistically significant variables are indicated with italics for p-values < 0.05 and with bold italics for p-values < 0.01.

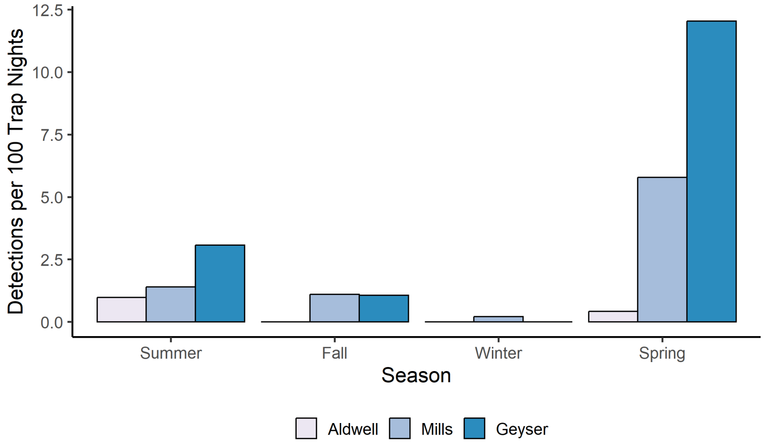

FIGURE 3
Number of independent photo events per 100 camera trap nights for American black bears in each study reach and season in the Elwha River from July 2021-June 2023.

current study, with deer detections being lowest in the winter season, and lowest in Aldwell compared to the other two study areas (Figure 2A). The area surrounding the Aldwell reservoir bed is more developed and more human-influenced than Mills and Geyser. The availability of safe deer habitat in residential yards and fields as well as the prevalence of hunting in Aldwell and on adjacent public lands may lead to diminished deer use of the Aldwell lakebed. Again, since methodologies differ and rely on indices of use in these two studies, these data provide a qualitative comparison that can serve as a basis for ongoing monitoring of use.

Our results showed differences in detections by species in the regenerating lakebeds compared to the upstream Geyser reference reach, which is dominated by conifer overstory and represents an older, mature riparian system that was relatively unaffected by dam removal activities. Moreover, Geyser is the furthest upriver reach that we studied, is located in wilderness within Olympic National Park, and is much harder to access and thus has a much smaller human footprint than both Aldwell and Mills. We documented bear, elk, and puma more frequently in this upper part of the river (Figures 2B, 3; Table 1), and documented more forest-associated species like squirrels and chipmunks in Geyser compared to Mills and Aldwell (Table 1). Differences between Geyser and the two regenerating lakebeds were less striking for deer (Figure 2A), which, despite their lower detection numbers in Aldwell, were ubiquitous across study areas. Further, we detected coyotes – a nonnative species that has become relatively widespread on the Olympic Peninsula – predominantly in Aldwell, with some detections in Mills but only one coyote detection in Geyser in the second year (Table 1). Coyotes are found at higher elevations in other parts of the park (Witczuk et al., 2013), and it is unknown what led to the strong differences between detections in Aldwell versus the two other areas. Over time, we will be able to monitor if use by this species shifts further upstream in this system. Finally, snowshoe hare detections were much higher in Mills and Aldwell where forests are still in early stages of regenerating compared to Geyser. These differences in use and composition likely reflect both habitat differences (early seral stage riparian-dominated habitats in the regenerating lakebeds above the former dams v. mature riparian zone in Geyser) as well as elevational position in the watershed.

While cameras provide a useful tool for remotely monitoring a suite of rare or elusive species alongside more common ones, they have some limitations. We aimed to control for obvious repeat detections of the same individuals by removing adjacent pictures of the same species, but we had no way to identify individuals, so our data only represented an index of current use. Camera location likely affected the diversity and numbers of species captured in our images. For example, more targeted studies for individual species may have led to different approaches in the study design such as camera baiting or targeting specific habitat characteristics (i.e. closer to river channels or beaver dams). However, as this is the first attempt to capture the suite of mammalian species using the dewatered lakebeds following dam removal, this work should have increasing value going forward as successional processes in these habitats continue and a longitudinal record of species composition in relation to habitat changes develops.

As changes in the Elwha ecosystem continues to unfold, terrestrial mammals are expected to both respond to and interact with the changing landscape. In addition to becoming established as permanent or seasonal residents in novel and changing habitats, species may interact with new vegetation in the former reservoirs (e.g., McCaffery et al., 2020), disperse seeds across the restoration area and beyond (e.g., McLaughlin, 2013), or consume and transport marine-derived nutrients brought to the system by anadromous fish (e.g., Tonra et al., 2015). Comprehensive restoration of the Elwha ecosystem could take decades but should ultimately include reestablishment of important terrestrial-aquatic linkages. Ultimately, wildlife should continue to play a pivotal role in ongoing revegetation and succession following dam removal and should not be overlooked as players in and beneficiaries of restoration of large watersheds following dam removal. This study provides a baseline of data from which to develop hypotheses for studies of wildlife roles in restored ecosystem function; establishes patterns of use that can be monitored over time as the system changes; and provides a template for understanding the role of wildlife within recovery processes in other large dam removal systems around the world.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://doi.org/10.5066/P1BJD7OH.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because the research was non-invasive and did not involve any handling of any animal. Remote cameras were used to monitor animal presence without any manipulation or contact.

Author contributions

RM: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. SC: Investigation, Writing – original draft, Writing – review & editing, Data curation, Formal analysis. KG: Formal analysis, Writing – review & editing, Methodology, Writing – original draft. KJ: Conceptualization, Methodology, Writing – review & editing. PH: Writing – review & editing, Conceptualization, Methodology. KS: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research 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.2024.1266474/full#supplementary-material

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Why does geography matter in big dam removal projects? Lessons from a comparison between the Sélune and Elwha River cases

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The dam removal movement is resulting in numerous projects worldwide, especially in Western countries. Whether completed or in progress, these undertakings often trigger conflict. Nearly 30 years after the initiation of the first major projects, this article examines the conditions for the local appropriation of dam removal projects. From the perspective of two pioneering and emblematic projects in France (Sélune River) and the United States (Elwha River), this article highlights the geographic specificities of dam removal projects carried out in European rural areas. The aim is to discuss how to implement ambitious ecological projects without running the risk of local people losing their sensitive relationship (history, experience, landscape) with the areas once they have been restored. In other words, ecological restoration should not result in a loss of meaning and quality in the relationship between local people and newly restored spaces; it should instead enrich it. In fact, the removal of a dam is not just a technical project; it profoundly affects landscapes, disrupting uses and creating new places. We identify the modalities by which a new space is produced and appropriated by local populations based on a comparison of the relevant spaces (national park vs. rural agricultural space), the populations involved (river users, Native American tribes, residents, and NGOs), and, finally, the governance processes and interactions between expertise and politics, all to highlight the need to take geographical context into account. Based on a detailed knowledge of the formation of the Sélune dam removal project, which has been the subject of continuous participant observation since 2011, we examine these projects' singularities and commonalities to identify the factors that contribute to their success. This study highlights the importance of the spatial scale at which the dam removal project should be framed, the role of government, and the importance of considering people's attachment to local places. Finally, this comparison makes recommendations for improving the socio-territorial quality of ecological projects, especially in Europe, with the aim of ensuring their sustainability and success.

KEYWORDS

dam removal, river restoration, governance, geography, scale, place attachment

1 Introduction

Among the various projects regarding the ecological restoration of rivers, the dismantling of dams has been one of the most extensively studied, both from a biophysical (Foley et al., 2017a) and social (Sneddon C. et al., 2017; Habel et al., 2020) perspective. The removal of small dams and weirs are by far the most common in both Europe and America (Bellmore et al., 2016; Belletti et al., 2020). However, in the last twenty years, a few large dams have been removed that are over 30 m high with reservoirs extending over several hundred hectares. Work on these projects has been concentrated in the Western world, where the dam removal movement is active, and predominantly in the US, where it first gained momentum in the 1990s (Doyle et al., 2003; Barraud, 2017; Grabowski et al., 2017). The social sciences have mainly addressed governance processes, as dam removal is an emblematic process, but also one of the most conflictual (Lejon et al., 2009; Germaine and Barraud, 2013a; Fox et al., 2016). The literature describes the obstacles and difficulties that developers face when implementing these projects. In particular, the often long and chaotic phase leading up to the decision is studied by analyzing the various actors' arguments and the negotiation processes, as Brewitt (2019) has done for three cases in the US (Hilbert-Wolf and Gerlak, 2022) have also shown how the role of science, economic analysis, and stakeholder interactions have kept the debate ongoing over the removal of four dams on the Snake River. The debates that accompanied the relicensing and subsequent decommissioning of four dams in the Klamath Basin have also been well documented (Allen, 2010; Gosnell and Kelly, 2010; Chaffin and Gosnell, 2017; Albertson, 2019; Yigit, 2021). Several works have demonstrated the role of the representations of nature (Jørgensen, 2017), heritage (Germaine and Barraud, 2013b; Fox et al., 2016), and attachment to place (Drenthen, 2009; Germaine et al., 2016; Howard et al., 2017). In fact, these works deal with the reasons for opposition (Diessner et al., 2020; Hommes, 2022), and several have examined the arguments for adherence. On the other hand, research on the material dimensions, i.e., landscape configuration and transformation, and the process of space appropriation[1] and place attachment[2] remains rare (Drapier et al., 2023; Gonin et al., 2023).

Nearly 30 years after the initiation of the two pioneering programs in the United States and in France, this article compares dam removal projects on the Elwha (Washington, USA) and the Sélune (Normandy, France) rivers (Duda et al., 2008; Germaine and Lespez, 2014). In particular, it highlights the specificity of geographical dimensions in the formation of dam removal projects implemented in European rural areas, even though the majority of feedback comes from the United States. In ecological river restoration projects, geography is still too often approached as a context that is analyzed mostly as a "study area." We believe that the geographical dimensions should be better taken into account, as already shown by a comparison of landscape transformations caused by the removal of dams in France, North America, and England (Lespez and Germaine, 2016). Not only does the landscape context weigh on the biophysical responses of the system warranting such a consideration (Foley et al., 2017b), but these construction sites also profoundly affect the landscapes' configuration. Dam removal cannot be reduced to an engineering operation. It disrupts spatial configurations by removing reservoirs, transforming associated uses, and producing new places. Geography is invoked here not to describe the context of projects, rather to analyze environments and their transformations insofar as they generate relationships between socio-economic actors, human and non-human, through the affordances[3] created in this process (Ingold, 2002; Gonin et al., 2023). By shifting the focus from intrinsic to relational values, relational thinking (Chan et al., 2016; Eyster et al., 2023) invites us to consider more precisely the relationships between human and non-human entities. This approach also situates contemporary projects within the historical trajectory of these relationships (Drapier et al., 2023). In this perspective, the removal of large dams is seen as an opportunity to repair the relationship between people and their environment (Higgs, 2012).

After introducing the two study sites and the approach used, we will present the theoretical framework for our work. Then, we present the results of this comparison, proposed for the first time, which helps identify important insights into the carrying out of dam removals. Finally, we discuss the question of reference scales, the role of the state as a territorial actor, and the relational aspects of implementing ecological projects. Thus, while we concluded in 2017 (Germaine and Lespez, 2017) that the consultation process on the Sélune had failed, this comparison instead inspires us to suggest ways to help ensure the success of such projects.

2 Research framework and methods

2.1 Study area

Located on the Olympic Peninsula of Washington State in the western United States, the Elwha watershed is mountainous. It covers an area of 833 km^2 dominated by ridgelines rising to over 2,000 m where the river originates. The river flows north for 72 km to its mouth in the Strait of Juan de Fuca. This tectonically active area has very steep terrain. Located at 48° N, it is exposed to westerly winds from the Pacific Ocean, which explains the Elwha's high discharge and velocities during flood periods. It is a gravel-bed river that runs through the middle of an often narrow alluvial plain

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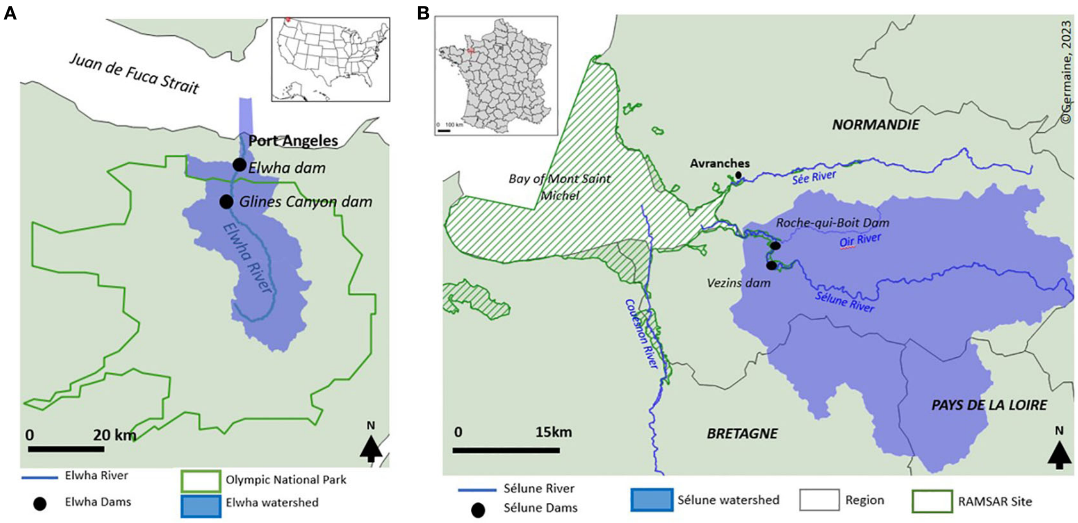
[1] Appropriation has been studied as a mechanism by which space is transformed into place (Benages-Albert et al., 2015) through uses as well as representations.

[2] Place attachment has been defined as "the bonding that occurs between individuals and their meaningful environments" (Scannell and Gifford, 2010).

[3] Affordance refers to the fact that we perceive an environment as an optical arrangement structured in a meaningful way that addresses our vital behaviors by "inviting" us to engage in this or that type of interaction (walking, lying down, grabbing, climbing, etc.).

which alternates with several gorges that provide habitat for juvenile fish and other aquatic organisms (East et al., 2018). The Sélune watershed in northwestern France has comparable dimensions. This coastal river drains a catchment area of 1,014 km² and flows for 68 km before entering the Bay of Mont Saint-Michel. It is located on a passive continental margin, and its relief is generally modest (elevation of the headwaters <200 m). The Sélune is generally a sinuous to meandering river of low energy. On the same latitude as the Elwha, it is fed by precipitation from the westerly winds that circulate over the North Atlantic Ocean. In this context, the area formerly occupied by the reservoirs stands out, with gorge landscapes over 80 m deep and a river characterized by more energetic flows.

Along with the Edwards Dam removal on the Kennebec River (Crane, 2009), the demolition of the Elwha dams between 2011 and 2014 represents the one of the more iconic dam removals in North America. The removal of the Sélune dams from 2018 to 2022 is considered unprecedented in the European context (Germaine and Lespez, 2017; Basilico et al., 2021) (Figure 1). These pairs of dams were similar in height and in the size of the water impoundments affected (Figure 1; Table 1). Both were hydroelectric dams built by private companies at the beginning of the twentieth century in the downstream section of rivers frequented by migratory fish, especially salmon. These two projects took a very long time to be completed. Roughly 20 years passed between the first discussions and the removals of the structures: from 1992 to 2014 for the Elwha,



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	Length	Watershed area	Discharge	Source elevation	Mouth
Elwha	72 km	824 km²	43 m³/s	1 114 m	Strait of Juan de Fuca
Sélune	68 km	1 038 km²	11 m³/s	180 m	Mont Saint-Michel Bay

FIGURE 1
Localization and characteristics of the Elwha and Sélune Rivers: **(A)** Elwha watershed; **(B)** Sélune watershed; **(C)** main characteristics of each watershed.

TABLE 1 Characteristics of the Elwha and Sélune dams.

Dams	Building	Removal	Height	Impoundment length and surface	Water volume	Distance to the mouth	Installed capacity	Owner	Dam removal total cost	Scientific monitoring
Elwha	1910–13	2015	33 m	7,9 km 110 ha (Lake Aldwell)	10 million m^3	8 km	14.8 MW	Successive owners from logging industry	$324.7 million	2000–now Fish ecology Vegetation Fluvial dynamics Community science
Glines Canyon	1927	2012	64 m	4 km 168 ha (Lake Mills)	28 million m^3	21 km	13.3 MW			
La Roche-qui-Boit	1916–19	2022–23	16 m	5 km 72 ha	4 million m^3	14 km	1.6 MW	Private energy company + State (Vezins) and EDF (Roche qui Boit) since 1945	€60 million	2012–2023 (may be continued) Fish ecology Vegetation Fluvial dynamics Social sciences
Vezins	1929–32	2019–22	36 m	19 km 200 ha	19 million m^3	22 km	12.8 MW			

and from 2005 to 2022 for the Sélune. In both cases, the decision to remove the dams was made at the highest level of government (US federal government, French state), but the Sélune case was more controversial (Germaine and Lespez, 2017).

2.2 Material, methods, and previous work

The approach used lies within the conceptual framework of hydrosocial territories, defined as "socially, naturally and politically constituted spaces that are (re)created through the interactions amongst human practices, water flows, hydraulic technologies, biophysical elements, socio-economic structures and cultural-political institutions" (Boelens et al., 2016). Even though geographical context clearly matters, few works demonstrate this, focusing instead on discourses, representations, and governance processes. The aim here is to pay more attention to the links with the materiality of places, distinguishing between what falls under the heading of spatial configuration or history on the one hand, and political organization on the other. To do so, we describe how a new space is produced and appropriated by local populations by comparing the different dimensions of the hydrosocial territories: hydraulic technologies (the dams removed), water flows (modified by the removal of the dams as much as by their construction), biophysical environments (consisting of the river's material heritage and ecological potential, and its constituting an object of attachment), people involved (the various local or external actors who participate in, or react to the project), and institutions (that promote, finance and direct the project). More specifically, we examine the governance processes, scales, and the relations between people and their environment throughout the project. Mobilizing the field of hydrosocial territories helps identify how a new space is produced and then appropriated by inhabitants and users.

On the Sélune, this analysis is based on several survey methods (Table 2). We addressed the positions of institutional actors and elected representatives through continuous participant observation beginning in 2011 (Germaine and Lespez, 2014; Germaine and Lespez, 2017). We used participant observation to follow up on the two studies that proposed new pathways for the valley's landscape and economic transformation. We also participated in the thematic workshops conducted at the prefecture's request to build a socio-economic conversion project, as well as in the infrequent informational meetings. We analyzed the interim documents and final reports delivered by consultants, as well as the rare communication documents produced by the entities promoting the dams' removal (Germaine et al., 2019). At the same time, we conducted more than 150 semi-structured interviews with local stakeholders (Drapier et al., 2023) to explore the forces driving the conflict and people's attachment to the valley. We also organized two focus groups with local residents, one dedicated to the history of the valley (2018) and the other to its future (2022). Finally, a photographic landscape observatory was set up to monitor the transformation of the valley's landscapes[4].

TABLE 2 List of academic publications resulting from the socio-geographical work on the removal of the Sélune dams.

Topics	Sources	Language
Relations to salmon (history, fishing)	Thomas and Germaine, 2018a, 2019a	French
Place attachment and relation to nature / landscape (inhabitants, users, lake sheds users)	Germaine et al., 2016, 2019; Le Lay and Germaine, 2017; Germaine and Thomas, 2023	French
	Germaine and Thomas, 2019 (movie)	Movie in French (subtitles in English)
Governance processes and conflicts	Germaine and Lespez, 2014, 2017	French + English
History of social hydro-territories	Lespez et al., 2023	French
	Drapier et al., 2023	English
Materiality, affordances: space appropriation processes after dam removal	Gonin et al., 2023	English
Relational thinkings: emergence of a multifunctional valley	Germaine and Gonin, submitted	English

All this work has documented the social failure of the project to date. A conversion project has yet to see the light of day due to a lack of ownership by local stakeholders. Today, the dams have been removed and no trace of them has been preserved, while spontaneous vegetation is growing in the former lake areas (Figure 2B) and jeopardizing access to the valley (Germaine and Gonin, submitted).

The Elwha case study is based on an extensive review of scientific publications and grey literature (e.g. Duda et al, 2008; Pess et al., 2008; Crane, 2011; Sadin et al., 2011; Brenkman et al., 2012; Johnson, 2013; East et al., 2015; East et al., 2015; Warrick et al., 2015; Foley et al., 2017a; East et al., 2018; Brewitt, 2019; Morley et al., 2020; Hess et al., 2021; Quinn et al., 2021; Brown et al., 2022; Chenoweth et al., 2022), supplemented by a field visit to the restored sites and lengthy specific interviews with the project's managers (NOAA, NPS) conducted in April 2022. We did not meet with Lower Elwha Klallam Tribe representatives who were central players in the removal; we instead used various available peer-reviewed papers (e.g. Duda et al., 2011; Guarino, 2013; Bauman and Kardouni, 2018; Duda et al., 2018; Mauer, 2020).

3 A comparative study: from ecological projects to geographical differences

The comparison is based on the role of non-humans, specifically salmon, the socio-political situation around the dams, the involvement of local communities, and different understandings of nature.

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[4] http://www.bassin-selune.fr/content/suivi-photographique-de-la-vidange-des-barrages-de-la-s%C3%A9lune

FIGURE 2
Photographs of landscapes along the Sélune River (after the dam removals): **(A)** Former Vezins dam (summer 2021); **(B)** Former Vezins Lake (summer 2021); **(C)** Former La Roche qui Boit Lake (summer 2022); **(D)** Former Vezins Lake (fall 2022).

3.1 The decisive role of salmon, a charismatic umbrella species

Salmon restoration is the primary goal of both projects (Pess et al., 2008; Forget et al., 2018). Removal of the dams should restore access to most of the river's length and spawning grounds, which have been inaccessible for nearly a century, to allow fish populations to recover.

3.1.1 Salmon, the iconic migratory fish

The Elwha is one of the rivers with the greatest salmon recovery potential in the Northwest, which justified its restoration (Duda et al., 2008; Pess et al., 2008). Salmon numbers declined from 500,000 in the early twentieth century to 5,500 prior to the dams' removal (Duda et al., 2021). Of the ten migratory fish runs still present, five are salmon: Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*). While steelhead (*O. mykiss*) are politically and ecologically important, the return of the chinook has captured the spotlight; the size and weight of these legendary "kings," which can exceed 100 pounds, have become the focus of restoration rhetoric. Other anadromous species include Pacific lamprey (*Entosphenus tridantus*) (Hess et al., 2021). On the Sélune, Atlantic salmon (*Salmo salar*) is the main species targeted for restoration, although other migratory species such as Pacific lamprey (*E. tridentatus*) and eel (*Anguilla anguilla*) also frequent the river. Although the dams prevented reproduction upstream, salmon continue to spawn downstream and in the nearby Sée and Couesnon Rivers, thus maintaining the species' presence in the Bay of Mont Saint-Michel. According to France's Biodiversity Office, if ecological continuity were restored, more than 1,300 additional adult salmon (over 7% of the national stock) would swell the spawning contingent of the Bay of Mont Saint-Michel complex, bringing the total average number of salmon returning to these three coastal rivers each year to 3,150 (18% of the national stock). While the goals and potential in terms of numbers are different in each case, their importance at the regional level legitimizes the ecological project in both instances.

3.1.2 The fishermen's interest

Keeping salmon in the river is a powerful lever for dam removal projects because it raises the prospect of a more active fishery. Salmon are central to the economy and culture of the Lower Elwha Klallam Tribe (LEKT), a federally recognized indigenous nation living in the Lower Elwha River valley and adjacent bluffs on the north coast of the Olympic Peninsula. They are known as the "salmon people" (Sadin et al., 2011; Guarino, 2013). Fish are an important economic resource: tribes depend on them for subsistence and economic well-being. Salmon have always been an important food source and year-round activity; they have long been fished, preserved, and traded (Warrick et al, 2015; Johnson, 2013). While indigenous people can continue to fish along the coast, the restoration of fishing in the river is at the heart of their demands. The tribes have fishing rights derived from nineteenth century treaties. After much litigation, these were reaffirmed in 1974 by the Boldt Decision, which granted all Washington tribes half of the total catch. Despite the replenishment of fish stocks by hatcheries, these rights have not been respected because the dams have deprived the indigenous population of access to the resource, which entitles them to demand compensation from the government. Furthermore, commercial and recreational fisheries are multi-billion-dollar industries in the Pacific Northwest of the United States (National Park Service, 2005).[5] Economics play a crucial role in controversies regarding salmon, and NGOs that promote the conservation of fish are often closely tied to recreational pursuits (e.g. Trout Unlimited).

Salmon net fishing has become part of the heritage of the Bay of Mont Saint-Michel. Salmon remain an important symbol of the local fishing history in the Sélune, as embodied by the Auberge de la Sélune (Thomas and Germaine, 2018a). Salmon are embraced by

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[5] According to the NPS, the benefits to the region from sportfishing from the Elwha River stood at roughly $9.5 million in 2001.

anglers, who continue to frequent downstream areas,[6] even though after a century of lake and dam construction, a decline in catches has been accompanied by a decline in the importance of salmon to the general population. Initial discussions on the future of the dams, organized within the local water commission (CLE), a local governance body that brings together elected officials, user representatives, and state services, led to the highlighting of a very significant fishing potential. The benefits of recreational fishing were estimated at around 20 jobs over 30 years and 150,000 to 470,000 euros per year (Salanié et al., 2004). The French national fishermen's federation, the regional one, as well as several local fishermen's associations outside the Sélune Valley took up these arguments when, in 2011, they formed the group "Les Amis de la Sélune" together with other environmental associations. This group is also supported by several specialized NGOs.[7] It advocates for a return to "the salmon-filled river of yesteryear," placing a salmon at the center of its logo (Figure 3C).

3.1.3 The alliance of environmental NGOs and scientists

Migratory fish, particularly salmon, are charismatic species (Lorimer, 2007) and salmon are an integral part of the American conservation movement (Garibaldi and Turner, 2004). The long distances that they travel between the headwaters of rivers and the oceans has granted them a strong cultural and symbolic value among many people. The salmon's strong swimming and jumping abilities are used to promote ecological restoration. Salmon is also described in scientific literature as an umbrella species because many species depend on its presence. Thus, the Pacific salmon has become the object of a symbolic battle over the dams installed on the Columbia River (Kareiva and Carranza, 2017). On the Elwha, the LEKT became the first major advocate for complete dam removal in the 1980s (Blumm and Erickson, 2012). They received support from environmental NGOs (Seattle Audubon Society, Friends of the Earth, Sierra Club, and Olympic Park Associates). Government agencies,[8] mediated by the National Park Service, or NPS, would later endorse and technically defend the removal scenario as the best alternative (Crane, 2011). The LEKT received federal funding to conduct studies on the impacts of the dams. This marked the birth of a coalition between the tribe, government agencies, environmental groups, and fishermen that proved instrumental for the passage of the Elwha River Ecosystem and Fisheries Restoration Act in 1992 (a federal law). In France, scientists identified threats to salmon and highlighted the potential of small coastal rivers along the English Channel and Atlantic coast to support salmon populations (Baglinière and Porcher, 1980; Ombredane et al., 1998; Perrier et al., 2013). The Atlantic salmon is a threatened species in France, where it has been on the IUCN Red List since 1996. The first salmon plan was adopted in 1976 with the aim of improving fish passage. In 1994, the Diadroumous Decree marked the organization of migratory fish management at the level of large river basins (Thomas and Germaine, 2018b). Fishermen and scientists have joined forces to protect migratory populations by influencing regulatory changes (Barthélémy, 2013; Bouleau and Gramaglia, 2015).

An alliance was thus formed between the scientific world, a section of the fishing world, environmental NGOs, and indigenous people on the Elwha that uses salmon as a lever in a political struggle to restore the ecological continuity of the two coastal rivers. As a result, salmon were featured prominently in numerous brochures and posters promoting the dams' removal (Figure 3). Even if the effects of dam removal on salmon populations take a long time to materialize, and the focus temporarily shifts to other anadromous species such as lamprey in both basins (Morley et al., 2020; Hess et al., 2021), it is clear that the ecological success of the two decommissioning efforts will be judged first and foremost on the return of this emblematic fish to these coastal rivers.

3.2 Two government projects

3.2.1 From the start: the questionable legality of dams

In both watersheds, the dams, which were not *per se* illegal, nevertheless flouted the spirit of the rules. Once built, they posed environmental problems that had been identified from the start. The lower Elwha dam was not licensed by the Federal Energy Regulatory Commission (FERC)[9] because it was built before the federal law establishing its authority was passed. Nevertheless, in response to an 1881 Washington state law that prohibited obstructing salmon passage, the dam's owner had to build a hatchery, which was considered a way to circumvent the spirit of the law (Chasan, 2000). No effective fish passage device was ever built, and the hatchery closed in 1922. When the Glines Canyon Dam's license came up for renewal in the 1980s, the owners argued that the old dam should be included in the Glines Canyon Dam license. This is when people began advocating for the dam's removal (Brewitt, 2019). The Sélune is classified as a migratory river by a 1924 decree prohibiting any obstacle to fish migration; therefore, the Vezins dam, built in 1932, was illegal from the start. Here too, compensatory measures were taken. These included the release into the river of thousands of juvenile salmon from Brittany and southwest France to compensate for the loss caused by the dams, estimated at 20,000 smolts/year, which was respected for the first few years. The obligation to allow the free movement of migratory species was reactivated in 1986 by a ministerial decree that gave the

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[6] Only 25 fishing permits were issued in 2013, compared to over 300 in the 1960s.

[7] For instance, the Association Bretonne pour la Pêche à la Mouche, Atlantic Salmon Federation, North Atlantic Salmon Fund, ANPER Truite Ombre Saumon, and the Association Nationale de Défense du Saumon Atlantique.

[8] The US Fish and Wildlife Service and the National Marine Fisheries Service.

[9] FERC is responsible for issuing licenses for hydropower and determine licensing conditions for a term of 30–50 years. When a hydroelectric dam license expires, the dam owner must renew it through a complex, administrative process known as re-licensing.

FIGURE 3
Images of migratory fish: **(A)** Interpretative display at the former Glines Canyon Dam; **(B)** Touristic board along the highway near Ducey; **(C)** Friends of the Sélune flyer.

dam owner, EDF (*Electricité de France*[10]), five years to bring the structures into compliance, which proved to be technically impossible. The Fishermen's Federation has repeatedly denounced this non-compliance in legal actions. In 2010, the administrative court of appeal ruled in their favor and ordered EDF to restore river continuity by the end of 2013; however, work to remove the dams would not begin for several years.

3.2.2 Local situations favorable to environmental projects

In both cases, the decision to remove the dams was the result of a long process in which the state played a major role, first by failing to ensure strict compliance with regulations, and then by initiating and directing the removal process. This is one of the arguments widely mobilized on the Sélune by the Fishermen's Federation when the Water Framework Directive (WFD) of 2000 and French legislation stimulate projects to restore river continuity (Drapier et al, 2018). The government announced the removal of the Sélune dams in 2009 (Germaine and Lespez, 2017). The Agence de l'Eau Seine Normandie, a public water management agency funded by water utility bills, was the main financier of this project, with EDF taking over part of the La Roche-qui-Boit Dam site. The proximity of the Bay of Mont Saint-Michel has been an additional argument for improving the Sélune River's water quality. The bay, known for its tidal range, one of the highest in the world (over 10 m), has been a UNESCO World Heritage Site since 1979 and is protected for the quality of its natural heritage (RAMSAR Convention, Natura 2000) (Lefeuvre and Bouchard, 2002). The Amis de la Sélune Association uses the famous monument in its logo and highlights images of the bay in its brochures, while scientists communicate the importance of exemplary environmental management to improving the quality of this highly significant wetland.

The Elwha dams were instead privately owned. The controversy has grown with the relicensing process for the Glines Canyon Dam in 1986. Negotiations began due to the complexities of licensing in a national park, and because the stakes in hatcheries had become higher for FERC. The LEKT and its allies established a strong partnership with the NPS which brought together all the stakeholders (Guarino, 2013; Johnson, 2013). This led to the 1992 Elwha River Ecosystem and Fisheries Restoration Act, which provided federal support and funding for the project. The Department of the Interior was authorized to purchase the dams and the Secretary of the Interior, to conduct the studies and the dam removal project (Crane, 2011). The US Congress appropriated funding for the Elwha dam removal project in over 20 appropriation bills over several years after their acquisition by the federal government in 2000 (Blumm and Erickson, 2012). Commissioned by the Department of the Interior, the National Park Service held a leadership role in planning, permitting, and conducting the restoration project.

3.3 Local communities with opposite positions

3.3.1 The settlement of the Elwha: between dispossession and urban development

Over 80% of the Elwha basin is forested and has no visible material heritage. On the other hand, it is rich in a long human

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[10] A multinational electric utility company owned by the French state.

history, which is also the starting point for a sense of attachment. This absence is not due to an absence of people in the valley, but to their eviction (Guarino, 2013). For at least three millennia, the LEKT living along the Juan de Fuca Strait had settled along the banks of the Elwha. The advance of the US frontier led to the displacement of these peoples, who were not granted any legal claim to the land, unlike the settlers who benefited from the Donation Land Claim Act (1850) and the Homestead Act (1862). The LEKT members were forced to cede their lands under the Treaty of Point-No-Point in 1855, which ceded 438,000 acres to the United States. The land allotment was not made available to them until 1875, after the land had already been distributed. The indigenous peoples then found themselves deprived of access to the river, as their fishing and hunting rights, recognized in 1855, were reserved only for the unclaimed lands. The Indian Reorganization Act of 1934 allowed the tribe to purchase 324 acres in 1937, but the reservation wasn't officially established until 1968. Today, the tribe owns 1,014 acres, forming a discontinuous territory that is situated primarily on the Elwha Delta. The tribe has 882 members.[11]

Within the National Park, development is limited to the network of old logging roads and the National Park Service's administrative and lodging infrastructure. In addition, there are the preserved and developed remains of the Glines Canyon Dam. Nevertheless, given the central location of the Elwha in relation to the rest of the National Park, it is a heavily visited[12] site for recreation purposes, mostly hiking and fishing. In addition, the city of Port Angeles, founded in 1890 and with a population of 20,000, also stimulates the use of this area, in an initial phase, for forestry and timber production and then for recreational activities, as the city is located only 10 km east of the river. Furthermore, suburban sprawl is now arriving at the park's doorstep, and there are dozens of homes and properties between the Elwha and Glines Canyon Dam outside the tribal reservation. Very few homes have a direct view of the river due to the thickness of the riparian forest.

3.3.2 The rural world of the Sélune

The main difference between the two basins is the existence of an age-old farming landscapes in the Sélune Valley, which, like almost all stretches of the European countryside, were established between the Iron Age and the Middle Ages at the latest (Lespez et al., 2015). Today, there are almost 200 dwellings within 500 meters of the former reservoirs (Drapier et al., 2023). These include main residences overlooking the lake, as well as numerous temporary fishing huts, called *cabanons*, with direct access to the water and, in most cases, a mooring pontoon (Germaine et al., 2016). The lakes were renowned fishing grounds for whitefish enthusiasts. From the 1990s on, the shores of the lakes were largely monopolized by the owners of these *cabanons*, but they were also developed with hiking trails. At the time of the decision to remove the lakes, there was a leisure center (la Mazure), a recreational park (le bois d'Isigny) and a café-restaurant (l'Autre Café) which are still in business (Figure 4). With 10,300 inhabitants, the nearest town to the dam is Avranches, 15 km away.

Local European populations, as well as Native Americans and newcomers to the United States, tell the stories of places based on their own experiences and those of their ancestors. In the case of the Sélune, this leads to the transmission of knowledge predating the dams, as in the case of Amerindian populations (Lespez et al., 2023). Although the old hydraulic structures of the Sélune disappeared almost a century ago with the valley's flooding, they have remained present in the local memory and are known to a number of inhabitants. These memories are particularly vivid for farming families, where memories of land expropriation from energy company by grandparents or great-grandparents were passed down through the generations and then revived with talk of removing the dams. The valley floor below the lakes is therefore not seen as a natural space without a social history, instead as a space linked to individual and collective histories, as evidenced by postcards and old pictures of the meadows and mills that used to line the rivers before the dams were constructed.

3.3.3 The role of local populations

On the banks of the Sélune, Avranches has become the main political decision-making center. It is the capital of the Mont Saint-Michel–Normandie agglomeration of municipalities, which brings together 95 townships, including the entire Sélune valley. It is also the seat of one of the sub-prefectures in the La Manche administrative department. It centralizes administrative functions and has been identified as the preferred contact point by the government services managing the dam removal project. Most elected representatives at the town and higher levels (Department, Region) have refrained from intervening in the project. Although the hydroelectric potential of the dams was often presented as able to supply a city like Avranches, the inhabitants of the city have generally remained indifferent to, and unaware of the project. In fact, the local scene has been dominated by the Association des Amis Du Barrage (ADB), created in 1993 to celebrate the statutory, ten-yearly emptying of the lakes. Since the first rumors of their removal, it has become a defense and advocacy association. Bringing together fishermen, *cabanon* owners, and residents, especially from hamlets and villages in the flood zone, the association, with the support of local elected officials, campaigned to keep the dams in place. It organized demonstrations and numerous public meetings, and it occupied public spaces with protest banners. The removal of the Elwha dams was opposed by some residents of Port Angeles. Gathered in 1994 in the REAL (Rescue Elwha Area Lakes) collective, they feared an increase in energy prices, especially for industrial activities, and they were committed to the scenic and recreational role of reservoirs. They also denounced the federal government's interference.

In this way, the geographical conditions played a role in creating an inverted front between the two case studies. The urban centers defined different positions. Port Angeles was home to the only opposition movement to the ecological project, while Avranches cultivated its indifference to the Sélune project. But the most important factor lay elsewhere. The people of the Elwha Valley,

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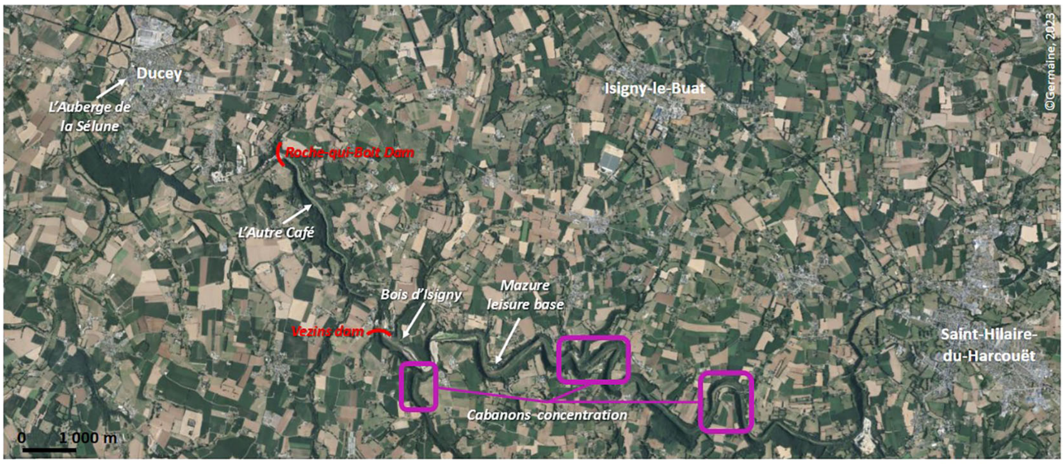
[11] https://www.ncai.org/tribal-vawa/sdvcj-today/the-lower-elwha-klallam-tribe-in-washington

[12] The park receives ~2,000,000 visitors per year.



Source : Géoportail, IGN France

FIGURE 4
Landscape structures in the Sélune watershed.

mainly the Lower Elwha Klallam Tribe, were committed to dismantling the dams. In fact, they were the driving force behind the project, which they saw as a way to mitigate the effects of their despoliation and to reconnect with the river, the life it supports, and the fishing practices at the heart of their culture (Mauer, 2020). On the other hand, the people living in smaller communities along the Sélune, who are attached to a way of life that has existed for a century and around which they have developed a social life, practices, and a sense of attachment to the lake environment, were for the most part strongly opposed to the dismantling of the structures (Drapier et al., 2023). The demolition of the dams was perceived as a process alien to the territory, driven from the outside by the state and its local representatives. While the tribes were victims of the dispossession associated with colonization and were fighting to recover their rights to the river, members of the ADB experienced the opposite; it was the dismantling that deprived them of their resource and stimulated their active and persistent opposition.

3.4 Unmatched environments but nature everywhere?

At first glance, the two rivers may seem incomparable, given their different fluvial styles and watershed landscapes (Figure 2, 5). The Elwha is representative of American nature, which ecological restoration projects aim to keep as wild as possible, regardless of direct or indirect human pressures on the environment. The Sélune is instead an example of European nature, which can be described as hybrid (Latour, 1991; Lespez and Dufour, 2021), and in this context, the restoration project aims to help restore spontaneity and even wildness. Despite these obvious differences, it is worth noting that both discourses are characterized by abundant references to nature and the desire to recover a natural river.

3.4.1 Very different environments...

The landscape of the Sélune watershed is representative of the rural landscape of northwestern France. Land consolidation has led to the opening up of the landscape and a sharp degradation of the bocage,[13] with many hedgerows being torn out, while cornfield plots and above-ground livestock buildings have multiplied. At the same time, towns and small cities have expanded, while the number of single family homes on the outskirts of towns has increased. This situation reinforces the role of the Sélune valley as a green corridor, especially in the gorges. The forests on the slopes are dominated by oak, beech and chestnut, with occasional stands of conifers; they have been little studied. Along the lakeshore, a few stands of trees and shrubs have survived, characterized by a dozen riparian species. Initial vegetation studies have shown that the many woody species reclaimed since the disappearance of the lakes are locally available species, suggesting the possibility of a passive restoration of the 200 ha of Vezins Lake (Ravot et al., 2020). This structuring of the landscape distances agricultural activities and creates a situation where the valley floor appears to be protected from the effects of intensive agriculture, although nitrate concentrations remain high, thus demonstrating the link between the aquatic environment and the rural landscapes of the watershed.

The Elwha watershed is mainly occupied by forest landscapes organized by a stratification of biophysical conditions. The low-elevation forests (below 400 to 500 m) are mixed, temperate rainforests with dense, mossy undergrowth, abundant epiphytes, and dead trees (Figure 5). They can support very old trees (100 to 300 years), in particular Douglas fir, grand fir, and western hemlock,

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[13] Bocage is a characteristic landscape of parts of northern France, southern England or Ireland resulting from the enclosure of open fields with hedgerows, stone walls, and fences. This landscape is composed of mixed woodland and pasture used mainly for pastoral farming.

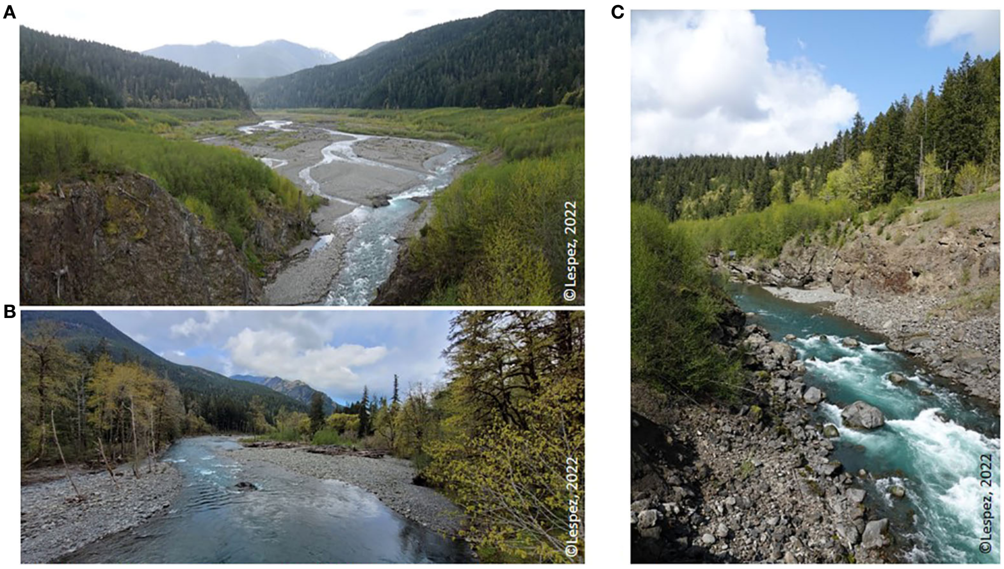

FIGURE 5
Photographs of landscapes along the Elwha River (after dam removals): **(A)** The former Glines Canyon Dam; **(B)** Elwha River; **(C)** Elwha River (former Elwha dam), April 2022.

which can reach very large heights (50 to 60 m), as well as the Sitka spruce (Chenoweth et al, 2022). A narrow band of deciduous trees can be observed along the river and wetlands, including red alder, willow, big leaf maple, black cottonwood, and balsam poplar. Between 400–500 m and 1,200 m, this forest gives way to a mixed forest, where the most common species are western hemlock, western red cedar and Douglas fir. Although indigenous peoples have long used these areas and modified their ecology, these forests were primarily exploited with the development of European settlements. The forests were first exploited for timber, with cut logs floated to sawmills for processing. Later, the wood was used to fuel the pulp mills in Port Angeles. Old forest industry practices prior to 1938 were often destructive, with clearcutting leading to soil erosion and the degradation of the forest ecosystem. The creation of reservoirs also led to the destruction of riparian forests. At the same time, agriculture developed downstream of the watershed, with a few small farms devoted to livestock and fodder crops.

3.4.2 … that are both valued in relation to their geographical context

Beyond the differences between the watersheds, the assessment of the restoration potential of the two valleys is based on an identical observation. The Elwha and Sélune dams are not as economically significant as those on the Columbia or Snake Rivers, or even Poutès Dam, located on a tributary of the Loire River[14]. For this reason, these dams were identified as realistic projects by the environmental activists who saw them as ideal restoration sites. But more importantly, they contain landscapes that are valued in relation to their surrounding regional environments. As such, they offer original, even exceptional potential.

The Elwha watershed is characterized by spectacular forest landscapes, home to a rich biodiversity that led to the creation of Olympic National Park in 1938, and covering 83% of the watershed. Olympic National Park is a World Heritage Site and Biosphere Reserve. The nature of the basin enabled a return to pristine nature, as the restoration project has sought to do. Scientists insisted on the unique opportunity to restore a wild river that this project represented (e.g. Duda et al., 2008; Warrick et al., 2015), as the dams were located downstream from a protected natural area; the physical restoration took place in a context where the physical and chemical quality of the water was very good. This situation was considered ideal to obtain the necessary funding for conducting comprehensive research and monitoring studies.

The mouth of the Sélune, the Bay of Mont Saint-Michel, is recognized for its natural heritage of major interest. The downstream section (from Ducey to the river mouth) is listed in the national inventory of natural areas of ecological, flora, and fauna interest. In contrast, the former dammed section is not a protected area. Nevertheless, the gorges of the Sélune, which are hard to access due to their steepness, offer a unique setting away from the surrounding agricultural plateaus. The presence of rocky outcrops reinforces their originality in the context of Northwest France, where the relief is generally not very marked. This intimate landscape is enhanced by the absence of roads along the river and a low number of crossings. The gorge section is identified as a space that stands out from ordinary valleys, not only because of the

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[14] This dam was slated for removal but was finally reconfigured to maintain hydroelectric power production while meeting ecological connectivity requirements. See more: https://www.nouveau-poutes.fr/vers-le-nouveau-poutes/le-barrage-actuel/

presence of lakes, but also because of its relief, its hidden character, and the perception of its scenery as "natural" (Germaine et al., 2019).

3.4.3 The weight of representation: nature everywhere

References to nature are ubiquitous in the planning documents or public dialogue around the projects. This is obvious in the Elwha project, since the entity promoting of the operation is the NPS. Its objectives were clear from the very start and were reiterated in the Elwha River Ecosystem and Fisheries Restoration Act (Public Law 102-495): there was a stated need to return the Elwha River and the ecosystem to its "natural, self-regulating state" to fully restore the Elwha River ecosystem and native anadromous fisheries through the decommissioning of Elwha Dam and Glines Canyon Dam. And it was fully supported by the LEKT, which sought to restore its cultural relationship with nature by dismantling the dams. People in Port Angeles were incredulous about the removal project, claiming they wanted to preserve the opportunities the lakes offered to experience nature. Stakeholder groups "saw fundamentally different things" looking at the dams, the lakes and the river (Brewitt, 2019). Crane (2011) describes how the project to re-imagine the river was supported by preservationist attitudes inspired by John Muir. Indeed, the Sierra Club and Friends of the Earth, along with fishing group such as Trout Unlimited, played an important role portraying the dams as symbols as destruction. This vision of nature has been largely reappropriated by the people of Port Angeles, who have continued to use the area for outdoor activities after the dams' remval. Due to a very different history and environment, the relationship with nature is more complex in the Sélune Valley. The announcement of the removal revealed a strong place attachment (Germaine et al., 2019). Surveys showed that the attachment to the lakes was especially strong among residents. Their experiences were commonplace. As a part of people's daily lives, these landscapes were also seen as a restful environment, ideal for relaxation and contemplation. The owners[15] of the 150 or so *cabanons* built on the banks of the river had a special relationship with nature. This is evident in the construction and maintenance of shelters and pontoons using local materials, and the skill with which they harnessed a spring, built a path on a steep slope, and ensured views of the water while remaining hidden by the surrounding trees, as well as in the broader practice of outdoor activities, in which fishing often took a back seat to gathering (mushrooms, berries), observation, or boating (Lespez and Germaine, 2016; Germaine et al., 2019). For example, the vice-president of the ADB association organized several outings to discover *Lathraeas clandestinas*, of the orobanchaceae family, located in the wetland at the end of the Vezins Lake. He participated in nature photography exhibitions with pictures of animals taken on the lakeshore, which testifies to his attachment to living things. The reservoir was seen as a living ecosystem in its own right, perceived and known simply as "nature".

This relationship with nature has been reconfigured by the removal of the lakes, but it remains a fundamental element in the appreciation of the area. The transitional period following the removal of the dams shows that the interest in these landscapes was not just in the water, but also in the environment, considered as a preserve. While there were strong fears that the valley would become overgrown, the spontaneous growth of vegetation (Figure 2) now seems to be welcomed as a means of maintaining the spirit of the place (Germaine and Gonin, submit). While maintaining their desire to keep open landscapes for physical and visual access to the water, several stakeholders have expressed an interest in wooded landscapes that contribute to the intimate character of the area. These inaccessible gorges have encouraged the emerging perception of an island of nature within an agricultural area that inspires a sense of tranquility (Figure 2D). The afforestation contributes to the difficult access to the valley floor and the longitudinal division of the space, reinforcing this hidden, intimate character.

Both valleys have been considered exceptional from an ecological point of view, although scientists, institutions, and NGOs have insisted on their degraded nature as a way to justify their restoration. Despite the different sense of materiality in each case, once the structures were dismantled, the sense of place in both instances is strongly influenced by the natural character attributed to the places and the relationship to nature that they provide.

4 Discussion

By placing the relationships between material forms (biophysical elements and infrastructures), local populations and their practices, and cultural and political institutions at the center of the analysis, the hydro-social territory approach highlights the importance of taking into account the local scale and all populations connected to the river or lakes to ensure the success of a dam removal project. If these precautions are not taken, there is a risk that the project will be carried out in an overly restrictive approach which deals with ecological issues by developing appropriate operational techniques, but ignores the dimensions of the living environment of the people and users to which they are attached and which they value. This may restore the river, but it does not guarantee that the relationship of the inhabitants with it will be restored. The comparative approach highlights the convergence of the two projects. The role of state authorities clearly raises the question of their responsibility for the successful completion of the process and their relationship with the local population. It also raises the question of the spatial scale at which the ecological project should be designed. At the same time, the attachment to nature shared by local populations in different ways and on specific cultural bases raises the question of how relational dimensions can be taken into account in ecological restoration projects. These are the questions we would like to discuss to highlight several useful lessons for a better understanding of dam removal projects.

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[15] A part of them live in the valley and another part live in cities near the valley like Avranches, Rennes or Fougères (Germaine et al., 2016).

4.1 At which spatial scale should large dam removal projects be framed?

Long and conflict-ridden (Crane, 2011; Germaine and Lespez, 2017; Brewitt, 2019), the two projects demonstrate the multiplicity of spatial and temporal frames of reference of the actors involved. This raises the question of the relevant scale at which to build a common project.

4.1.1 A lack of consideration of inhabitants and outside NGOs on the Sélune River

On the Sélune, the people most affected were those closest to the river: those who inhabited the gorges overlooking the lakes or who had the opportunity to visit it every day, as well as those downstream who feared a worsening of the risk of flooding. *Cabanon* owners used the valley seasonally for fishing and vacation. Recreational users (fishing, hiking, kayaking) encountered the valley on a more intermittent basis. Scientists and environmental NGO activists lived outside the region and visited the valley only occasionally. Their relationship to the river was therefore distinct over time. The proximity of the participants' residence to the river influenced their opinion of the removal works; people living near the old lakes found it more difficult to imagine themselves in a new valley without the lakes. Conversely, occasional users found it easier to project themselves onto the new landscape and to recognize its new potential. This dichotomy observed in the post-removal surveys echoes the results of the public survey organized in 2014. Participation was high, with 4,565 opinions submitted. Most of the favorable opinions were expressed electronically, reflecting outside support. Opening the survey to the Internet raises the question of who has standing to express an opinion on the future of a territory. This has reinforced the sense of dispossession of inhabitants. Furthermore, successive territorial reforms contemporaneous with the project have further distanced local elected representatives from the power process. Until 2017, a dialogue was organized at the level of the cantons (Ducey, Saint-Hilaire-du-Harcouët, Isigny-le-Buat, and Saint-James), all of which are affected by the river. The merging of these townships into an agglomeration has shifted the decision-making center to the bay-oriented town of Avranches, which has little interest in the future of the Sélune. This reorganization has stressed that decision-making spaces are different from use spaces, since power is located outside the valley. More generally, the merger has marginalized the elected representatives of the riverside communities, making it difficult for them to force the agglomeration of municipalities to take charge of the Sélune's rehabilitation. Although the local community has not been the only reference scale for political decision-making, it should have been taken into account as such, since it has its own specific issues.

On the Sélune, the fishermen's federation is the only environmental NGO who advocated for the removal from the beginning, and which attended some public meetings organized by the ADB locally. The other advocates of the dam removal arrived later without any local contacts. The "Amis de la Sélune" collective is a dormant network of associations that share the same vision of the river and which are capable of organizing themselves to express their position when necessary. The collective is active on the Internet with a website, which has been replaced by a page dedicated to the project on the European River Network (ERN) website. Rather than inform the valley's inhabitants, the aim is instead to use the project as a showcase in Europe, as evidenced by the mobilization of media networks. Taking advantage of this project, considered "the largest dam removal operation in Europe," the ERN organized the international symposium "Renaissance of the Sélune Valley" in September 2019. This event could have been an opportunity to present the results of the scientific program carried out on the Sélune, but this part took place in Rennes (over one hour away), while the second day, held in Avranches, instead presented the international feedback. While NGOs and local tribes managed to work together on the Elwha, the support for the dismantling of the Sélune dams was exclusively external to the area.

4.1.2 The building of a coalition at the local level on the Elwha River

For the Elwha, the question of local actors and their political power was equally complex. The dams initially benefited the industry and energy sector of Port Angeles, while at the same time depriving LEKT members of their land and key resources. Thus, while the Lower Elwha has regained power and legitimacy through the ecological project (though not completely, as the area is managed by the NPS), Port Angeles inhabitants have largely remained outside the project, despite numerous community information meetings. Building the political basis for the decision was not easy either.

Because most of the Elwha River is in a national park, its situation is unique. A coalition of NGOs was formed locally with the tribes and have been engaged in defending the removal project. They were formed before the relicensing process and were well organized to challenge FERC's authority. They were based in Washington State (Audubon Society and Sierra Club chapters), while Olympic Park Associates was locally based. They became involved in 1986, when they intervened in the Lower Elwha FERC proceeding, and they participated in the preparation of several motions and petitions over three decades to win approval and funding for the river restoration project. By the early 1990s, the coalition had grown stronger as government agencies also began pushing for removal. But the finalization of the Elwha River Ecosystem and Fisheries Restoration Act (1992) consolidated the opposition to the project, as many local residents resented what they saw as outside interference. LEKT members and environmental groups (Olympic Park Associates and Trout Unlimited) occupied the local stage to collectively debate the future of the dams, while this local opposition fueled federal debates and slowed the negotiations for purchasing and remove the dams (Brewitt, 2019). The Elwha Citizens Advisory Committee was an informal body that formed just as opposition began to grow in Port Angeles. The locally formed group brought together 16 citizens with opposing views on the removal, who spent six months developing a report that presented a shared vision. In the end, this informal group concluded that the energy produced by the dams was modest

(Lydiard, 1996). In addition, after the removal, scientific symposia were organized, each of which was open to the public and included presentations by scientists on the monitoring of the dams' removal.

4.1.3 The need to expand the range of actors considered

This situation also testifies to the limits of global environmental movements, which come up against the specificities of a given area and whose demands can be perceived as ecological interference by local residents. It is also interesting to compare the ERN's involvement on the Sélune with the history of this environmental association, which was created on the Loire in the 1980s from local roots to fight against the construction of dams on that river. The association, then known as SOS Loire Vivante, stood out for its combination of local mobilization and national and international connections, which enabled it to influence the debate. Transformed into a Europe-wide association since its victory on the Loire, the ERN struggled to cultivate local partners and thus appeared as an outsider (Hayes, 2002; Barraud, 2011). Dam removal advocates often appear as outsiders who underestimate the potential for opposition to the removal of the structure and who may even exacerbate this resistance (Fox et al., 2016).

All these observations reveal the need of organizing consultations at various levels, not because they make it possible to find a solution outside the legal and democratic bases on which states operate, but because this is the only way to ensure that the people concerned are heard and taken into account in the legal and democratic process. There is no easy solution to propose, but broadening the range of actors involved is a *sine qua non* for the long-term acceptance of the project (Germaine et al., 2021). This is essential to limiting resentment, both towards the project itself, and the legal and democratic process by which it was promoted (procedural justice), and thus to avoid permanently discrediting the institutions that took charge of this process.

4.2 The state as a territorial actor?

In both cases, the state played a key role, firstly in the decision-making process, because of the regulatory dimension, and secondly in the implementation process. But beyond these similarities, crucial differences emerge in the in the way government action is organized and implemented at the local level.

4.2.1 A state with powerful local leverage that supports the political project at the local level

In the case of the Elwha, the environmental rationale permeated the entire process. The federal government was both the primary funder and operator of the removal process, as well as the environmental champion, since the dewatered areas and most of the river lie within the national park. The NPS has been on the ground since the Olympic National Park was established and places environmental issues at the core of its mission. There is a large staff (100 employees and as many seasonal workers) which is local; they know the watershed and all the local actors. One of the various departments is specifically dedicated to education. The information challenge was not anticipated, however, and the NPS was overwhelmed by requests from local and international media. Important but routine processes that are used on a nationwide basis led to the organization of a stakeholder dialogue. The first was FERC process, which since the late 1980s has included topical commissions, public meetings, and workshops to produce a report to Congress. Then there was the Environmental Impact Statement (EIS) process, which took place in the early 1990s. The Department of the Interior and the NPS prepared this process, which consisted of a public comment period (600 comments) and a series of public meetings in Port Angeles and on the Peninsula that were attended by up to 200 people. The goal of this phase was to reach a decision among several options. The entire process was publicized in the local press and communicated to the various communities. In particular, one of the NPS representatives, Brian Winter, led this project for about twenty years and was able to rally a large community around common goals. The Elwha Citizens Advisory Committee was one of the tools used to build the project and create the "glue." The trajectory of the Elwha dams is specific due to their partial location within the boundaries of a national park. FERC was initially set to rule on the renewal of the Glines Canyon Dam license, but LEKT members and NGOs demanded that FERC be recognized as lacking jurisdiction over this issue due to the presence of the national park. This dispute was the subject of several legal rulings and contributed to the rise of the controversy at a national level (Busch, 2008). Ultimately, the potential for a lengthy legal quagmire over the question of federal jurisdiction led to the decision to opt for a compromise involving the removal of the works from federal funds.

A community and citizen science initiative was launched in 2004, which has involved members of the LEKT (Diver et al., 2022; Eitzel et al., 2023). The national park brought scientists and local people together in the Elwha Research Consortium. In this way, local people have been encouraged to participate in field data collection. There was a moratorium on fishing, which was prohibited until 2022 for both commercial and tribal purposes. LEKT members participate in the decision-making group that renews the diagnosis every year to determine whether the state of the populations allows for the authorization of fishing. Thus, the National Park Service operates within its boundaries as the exclusive decision maker, working with partners cooperatively wherever possible, including the long-standing Fisheries Technical Committee (members including the LEKT, Washington State Department of Fish and Wildlife, NOAA, US Fish and Wildlife Service, and the US Geological Survey). This situation is quite unique as most US dam removals do not take place on federal land.

4.2.2 A state that decides and steers, but has no desire to engage in local politics

The situation at the Sélune has been very different, since the ecological restoration is taking place in an unprotected environment. It is not, therefore, a controlled area whose functioning and evolution are controlled by a major environmental protection agency such as the NPS, instead by a multitude of actors with divergent interests. The decision to dismantle the dams was announced more than 150 km away, and then the local offices of central government departments and EDF were entrusted with its implementation. The department in charge of managing the project was located in Saint-Lô, in the La Manche prefecture, which is one hour away by car. The unit dedicated to the dams consisted of a single full-time project manager and a secretary to support the administrative aspects. The project manager was an engineer by training, responsible for managing the project and coordinating the various engineering firms involved in the project. Lacking naturalist skills, and with the expectations of successive prefects limited to regulatory aspects, the unit has adopted a technical approach and has few resources to lead a consultation process. Instead of relying on the local water commission (CLE), which promotes a watershed scale management, the government set up three interlocking working groups. A project group composed of government departments, EDF, AESN and three local councils oversaw the studies. A steering committee, open to other elected representatives, validated the studies and directed the work as necessary. A local information commission met infrequently and by invitation only. This configuration has evolved over time, but governance remains characterized by a lack of dialogue with local elected representatives, with most exchanges taking the form of letters that are mailed months apart. At the same time, the French government communicates very little, at a late stage, and on purely technical aspects (the work), making no significant educational effort to explain the reasons for the dismantling and to support the ecological process. Except for the distribution of a few leaflets (four during the project's construction, and three during the works), the public authorities did not organize any public meetings and never went to meet the residents. This stimulated the emergence of opposition and its organizing among people whose daily lives or practices were directly affected by the project. Although entities that promote smaller projects make an effort to conduct door-to-door consultations and/or organize community meetings ahead of their project (Germaine et al., 2021), the Sélune restoration project has been characterized by an absence of consultation.

In practice, the project was divided into a technical project, which is handled by the state, and a local conversion project, which the state has sought to entrust to elected representatives. The State itself did not want to take on a territorial project, proposing the allocation of the drained areas to an overall environmental project led by the Ministry of Ecology (a National Nature Reserve or a “Natura 2000” contract), which would have legitimized its role. Nor was it willing or able to rely on local authorities such as the Normandy Region or the Department of La Manche, which would have anchored the environmental project in the territory by creating a Regional Nature Reserve or a Departmental Sensitive Natural Area. As a result of old regulations that have not been complied with as well as several new laws, the project has therefore mainly been technical, with regulatory (WFD, ecological continuity) and safety objectives (preventing polluted sediments from flowing downstream, controlling flood risks). All other aspects have been considered to be the responsibility of the local authorities, to whom the French government has sought to entrust the released land. These local authorities have therefore been invited to draw up a program for the landscape and economic conversion of the valley. However, in their opposition or indifference to the dam's removal, they have struggled to take ownership of the project, especially since the dismantling was temporarily questioned by the Minister of the Environment in 2014 (Germaine and Lespez, 2017). In the past five years, the dismantling operation has mainly been a vast site for the deconstruction and management of sediments from the erosion of the agricultural watershed that have accumulated since the last emptying in 1993, and the stabilization of polluted sediments in one of the Sélune's tributaries, caused by decades of industrial activity. Ultimately, the two projects were built in parallel, but the two aspects never came together, leaving a number of unforeseen dimensions. This process is responsible for the current uncertainties over the future of the dewatered areas and, more generally, the relationship between the ecological project and the local territory.

4.2.3 Considering the role of the state and its territorial dimension from a project's outset

In the case of these two large-scale projects, central governments play a key role in initiating and steering an environmental project through their departments, even more so when the projects can rely on regulatory aspects. However, as the example of the Sélune shows, state commitment is not everything; it's also a question of knowing how, with whom, and through which local institutions it can support the environmental project. The way in which the state acts does depend to a large extent on the regulatory and financial framework on which it can rely. Our previous research has shown that the regulatory framework influences the emergence of bonds between an environmental policy and community development projects (Drapier et al., 2018). A clear divergence appears between France and the US when it comes to environmental policy and its link to the territory into which it is embedded (Drapier et al., 2023). Projects in the US involve non-profit associations that allow for the creation of stronger links across a longer timeframe between the dam's removal and which contribute to local development, whereas in France, regulations impose a timetable and a standardized approach that is more often focused on the ecological project and its acceptance by riparian owners. This greatly limits the potential for projects to be used as tools for local development. The formation of dam dismantling projects in the United States is part of a project-based approach (building a collective, seeking funding) that forces players to collaborate, whereas the top-down approach imposed by French regulations is not conducive to ownership and collaboration. Thus, the Sélune project is rooted in a very different culture of restoration project management. Our study of the Sélune process shows that in cases where the state is responsible for restoration projects, territorial cooperation is crucial to the project's success, over and above the initially targeted biophysical aspects. In fact, the territorial dimension of the initiative must be identified from the outset, and the governance issues at stake must be considered before the project is implemented (Ohno, 2019; Fostvedt et al., 2020). From there, the question arises of whether and how the state should play an active role in producing restored areas and their geographic consequences, undertaking initiatives and accepting responsibilities itself, or whether and how it should play a supportive role by encouraging co-construction dynamics in conjunction with local authorities.

4.3 Attachment: an impossible environmental reset

A decommissioning project cannot be based solely on redefining a biophysical trajectory (Dufour and Piégay, 2009; Lespez et al., 2015); it is essential to work with local communities, their specific relationships to the environment, and their histories (Eden et al., 2000; Germaine et al., 2019). It cannot involve wiping the slate clean or returning to an illusory past. It must pay attention to people's relationships to the river, and it must create the conditions for restoring relationships when they seem to have disappeared, rather than impose new ones.

4.3.1 The pivotal role of indigenous peoples in North America

The removal of the Elwha dams is part of the Native American movement to regain their rights and their land. These two movements cannot be separated (Linton and Pahl-Wostl, 2023). Though displaced by colonization, the tribes have been the NPS' most important partner. This alliance is strategic because they have the ability to take legal action under nineteenth century treaties, which the NPS does not have the authority or political will to do (Sweetser, 2019). They participated in FERC negotiations that led to the 1992 Elwha Act, and today, as co-managers with the Washington Department of Fish and Wildlife for commercial and recreational salmonids and the NPS, they participate in defining the yearly fishing moratorium.[16] Mauer (2020), however, explains that what is at stake is not just dispossession, but rather the mechanisms that led colonial and capitalist occupiers to transform the physical world into an instrument of colonialism itself. Hatcheries, as adopted by the LEKT, serve as an eloquent example of the imposition of technological devices aimed at dominating nature and legitimizing infrastructure (Crane, 2009). Since their removal, the tribes still do not have the right to fish in the Elwha. Symbolically, ceremonies celebrating the return of salmon can be held again, but the number of returning fish remains insufficient to authorize their harvest. Until 2022, the Klallam will only be allowed to fish at sea and will continue to farm salmon to meet their economic needs. The LEKT has retreated to peripheral struggles and focused all of its attention on restoring the river, leaving a number of injustices in place (Crane, 2011) and discussions with the NPS are ongoing.

The role of indigenous peoples is often crucial in dam removal projects in North America. Tribes have been involved in at least thirty projects, most often through direct participation in the demand for removal (Fox et al., 2022). This is the case, for example, with the Penobscot Indian Nation on the Penobscot River (Opperman et al., 2011), the Hoopa Valley Tribe, Yurok Tribe, and Karuk Tribe on the Klamath River (Gosnell and Kelly, 2010; Diver et al., 2022), and the Yakima Nation on the White Salmon River (Gimblett et al, 2017). As described by Linton and Pahl-Wostl (2023), Indigenous peoples have traditionally held a different kind of relationship with what Westerners call “nature.” This relationship sees the environment as a living being to be cared for, not as a resource or a fixed state. The dismantling of dams is undoubtedly a crucial stage in the redefinition of the relationship between indigenous peoples and the environment. However, restoration is underpinned by an ecocentric approach that values the intrinsic value of living things rather than the relationship between humans and non-humans. Thus, the dismantling of the dams alone cannot complete the process of decolonization, i.e., restoring indigenous peoples' relationship with their environment, and the durability of the alliance between the advocates of ecological restoration and the tribes remains questionable.

4.3.2 What place is there for local people and local knowledge in Europe?

The lack of consideration for the relationship between the people of the Sélune and their environment on the part of the public authorities has been demonstrated by several events. For example, the presence of *cabanons* along the shores of Vezins Lake was overlooked by elected officials and government departments. Initially they underestimated their number, and then, they considered them a minor problem, given that most of the structures were abandoned (Germaine et al., 2016). The public authorities limited their analysis to the public domain, which they must ultimately manage and develop, but this meant that they focused only on the pontoons, thus minimizing the scale of the buildings concerned. The *cabanons* were considered “black marks” on the landscape from an aesthetic point of view, and as infrastructures that posed safety problems (risk of collapse, liability issues). At no point was the presence of these sheds seen as evidence of a strong relationship with the environment. The salvage fishing organized during the lake drawdown is another example of the neglect of the relationship between the inhabitants and the river. The lakes were described by regulars as full of fish, and lake lovers were seen as spokespeople for a merely “ordinary” biodiversity. Guided by the need to restore salmon populations, the French government has also paid little attention to carnivorous fish and whitefish. These common species did not receive the attention of the public authorities when the Vezins reservoir was emptied. Anglers complained that they did not receive any response from the public authorities regarding the organization of a recovery fishery and the fate of the 15–20 tons of fish in the lakes (perch, pike, pikeperch and even catfish). The socio-environmental knowledge of the local population has therefore been neglected. Since the demolition of the structures, we have witnessed a tentative reappropriation of the valley by new actors, mainly hikers and kayakers who want to make this their new playground, and hunters who want to preserve the tranquility of the area and its hunting potential. It is the immersive and direct experience of the landscape that leads them, through landscape patterns, to appropriate and

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[16] The most recent plan is for in-river subsistence fishing to return to the Elwha in 2023.

project themselves onto this new space, independently of the plans of experts and decision-makers (Gonin et al., 2023). In the case of river ruins or small waterfalls created by former dams and fisheries, stakeholders and local residents have no official representative structure to turn to with their questions and interests regarding the fate of these heritage assets.

As we have demonstrated, the local population is therefore not indifferent to nature, but its relations, based on common or devalued species, common practices, or even debatable activities (hunting, agricultural seeding of the river,[17] introduction of fish), are poorly considered or even ignored by the public authorities (Gonin et al., 2023). They are also ignored by environmental NGOs, who find it difficult to approach them to support the decommissioning project. The situation is very different for Amerindian populations, whose cosmology has been adapted to the objectives of public policies. In Europe, the modern character of the WFD, which perpetuates the separation between nature and society, even while recognizing the need to integrate multiple stakeholders, does not value the relational nature of environmental projects. Local populations are still too often considered illegitimate and their relationship to their environment is underestimated. The Sélune restoration project is still part of a modern ecological restoration initiative that combines environmental expertise and democratic political power rooted in representative democracy; however, it does not really invest in the relationship between riparian societies and their environment, which would guarantee ownership of the ecological project by as many people as possible (Eden and Tunstall, 2006; Sneddon C. S. et al., 2017).

This discrepancy also applies to most elected officials, who view the valley's restoration in a relatively detached light, due to their physical distance from the environment, which they continue to view primarily as a resource to be developed, and the relative number of their directly affected voters. The proposals made by elected representatives in collaboration with the consulting firm reflect a tourism-oriented approach. This is far from the expectations of the local population, which is primarily concerned with the quality of the living environment and the ability to access it and develop activities there. Through its geographical proximity and daily use of the area, the local population's sensitivity for the river is undoubtedly strong. Local people's expectations are rooted in a phenomenological approach and an experience of a lived space that is not shared by elected officials and government services.

4.3.3 All is not lost: tribes as models?

Projects carried out in the United States can undoubtedly provide inspiration for taking this relational dimension into account. Indeed, without idealizing them, projects carried out in contexts where tribes have played a strong role can serve as lessons for a more general consideration of indigenous peoples and their relationships with the environment, as suggested by Linton and Pahl-Wostl (2023) and Gosselinge and Bartoli (2022) The relational ethics promoted by these peoples have the merit of reminding us that the environment is not just a living space, rather a set of relationships in which we are engaged. As Gosselinge and Bartoli (2022, p. 154) put it: "If the logic of interest is individual and rational, the relational logic is holistic and pathic: it brings into play bonds of attachment that cannot be translated into the order of calculation or compensation, because they involve the beings who inhabit and frequent the living environment in relationships of reciprocal obligations." The recognition of this dimension is not specific to indigenous populations, but it may characterize all local peoples who develop relationships with their living environment and its other inhabitants, human and non-human, and who can transmit this relational dimension from generation to generation. As the American Indian philosopher Burkhart (2019) points out, "the condition of being 'indigenous' refers less to belonging to an ethnic group than to belonging to a community whose practices and customs have taken shape in relation to an inhabited environment and the other-than-human inhabitants that make it up." Drawing inspiration from phenomenology and more-than-representational approaches, this involves paying attention to the everyday acts, habits, and affects in which the ordinary relationship to the environment is embedded (Thrift, 2007; Anderson and Harrison, 2010). This lesson, recalled by the Amerindians in their struggle for the environment, can be extended in the New World, as well as in Europe, to areas where indigenous populations have disappeared or where native populations do not have a specifically indigenous status.

However, the existence of this relationship is not automatic; it is not enough to reside somewhere to inhabit it. In this sense, it seems necessary to question the traditional categories of actors to recognize forms of legitimacy other than land ownership and take co-appropriation relations into account. It is not a question of highlighting the inhabitant, but rather the person who, through his or her practice, participates in a community and expresses an attachment to the living environment that he or she helps to produce. Recognizing these relationships requires us to move away from the binary nature/society approach rooted in Western modernity and spread by the colonial process. In our time, it is important to "stay with the trouble" (Haraway, 2016) and move beyond this binary vision of nature by developing relational approaches. We gladly follow in the footsteps of Milstein et al. (2023), p. 421), who promote a resolutely optimistic perspective according to which "the capacity of our species to collectively, even rapidly, adopt ecocentric systems of meaning that trigger massive change should be widely recognized and actively promoted." So as not to lose the thread of dwelling (Mathieu, 2016), including in Europe, and to make it one of the driving forces of people's attachment to a quality environment, we must include the history of the relationship between riparian populations and rivers within the environmental project. Ecological restoration must be carried out within a framework of cultural and socio-environmental continuity with regard to the local, indigenous community, which thereby slowly renews itself, its vocation being to stay and live in the area. For example, history

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[17] With selected forage species.

also underpins the legitimacy of local residents to express their views on the future of the valley in the name of a previously held property right. In all cases, the spaces are invested with tangible or intangible legacies, and the project revives ghosts, such as the meadows at the bottom of the valley and the old mills and fisheries on the Sélune, or the productive fisheries and sacred sites inundated by lakes on the Elwha. The ecological project cannot and must not erase the past.

At a time when Europe is witnessing a proliferation of demands for the recognition of the legal personality of rivers (Appel du Rhône, Parlement de Loire), it seems that other ways of promoting the recognition of multiple relationships with rivers might be more productive. Such projects could be inspired by bioregionalism, which promotes direct relationships with the land at the scale of a habitat, such as a valley or a watershed (Berg and Dasmann, 1977; Sale, 2000). By advocating for a community-based approach, bioregionalism pays close attention to local specificities to capture and integrate the interdependencies between biophysical environments and communities, while promoting an improvement in our relationship with other living beings.

5 Conclusion

The comparison of the dismantling of the Elwha and Sélune dams reveals, first and foremost, the importance of environmental projects on a global scale. In the context of an unprecedented biodiversity crisis, governments have taken up ecological issues; the removal of large dams is one of the most emblematic actions today, and undoubtedly one of the most successful from an ecological point of view. Nevertheless, a comparison of the two projects highlights the need to take geographical conditions into account in their implementation, whether these are biophysical conditions – which naturalists generally take care of – or socio-spatial dimensions, which have been identified as one of the main obstacles to the development of ecological restoration in Europe (Cortina-Segarra et al., 2021). The latter are still neglected or only partially addressed. Social dimensions often rely on indigenous populations in the Americas, with whom an alliance can be built around the return to better functioning rivers. However, the relationship with local native people has been neglected in the Sélune project. This international comparison is an opportunity to demonstrate that the long-term management of human/non-human relationships is a way to involve local populations in an ecological project. In this way, from the beginning of the project, advocates must take the territorial dimensions and the complexity of the spatial scales of reference into account as a prerequisite for the ecological project's complete success. The integration of relational dimensions is undoubtedly also crucial for sharing a river culture with all stakeholders and envisioning a more vital project that goes beyond the still dominant ecological and/or technical objectives. It seems to us that such an approach would enrich ecological projects and renew the relationship between the inhabitants of these ecologically degraded areas, the people in charge of the ecological project, and the environment itself (Higgs, 2003; Dicks, 2021). Under these conditions, the dismantling of large dams could then be an opportunity to outline more generally what a community could be, bringing together humans and non-humans around the river (Wantzen et al., 2016).

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

The authors contributed equally to this work and share first authorship. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research 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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Lessons learned from community and citizen science monitoring on the Elwha River restoration project

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Community and citizen science (CCS) projects – initiatives that involve public participation in scientific research – can both sustain and expand long-term monitoring of large dam removal projects. In this article, we discuss our perspectives on CCS associated with the Elwha River dam removals. We summarize how the public has been or could be involved in monitoring and distill lessons learned for other large dam removal projects. Much of the Elwha monitoring involved technical field work requiring training and incurring potential liability risks, guiding projects towards smaller-scale public involvement. Partnering with organizations that have capacity for volunteer management expanded CCS opportunities and provided logistical support to project managers committed to public engagement. We found that many projects engaged with students and/or with paid or unpaid interns; compensating participants in various ways can help to create reciprocal relationships that support long-term monitoring. In the future, other large dam removals could consider planning ahead for community involvement in dam removal monitoring to accommodate the technical and potentially hazardous nature of the work – broadening who may be able to participate. In addition, involving community members in setting research agendas could be an important first step in engaging them in long-term monitoring, in turn facilitating multi-generational research at the timescale of landscape-level changes. Finally, explicit relationship-building with Indigenous communities can enhance the benefits of community engagement in dam removal science for all involved.

KEYWORDS

citizen science, community science, dam removal, Elwha River, watershed restoration

1 Introduction

Large-scale dam removal can benefit from community and citizen science (CCS) that includes public engagement in directing research agendas, participation in long-term monitoring, and collaborative analysis, interpretation, and application of research results. The Elwha River dam removals are a prominent success story for watershed-scale restoration (Allan et al., 2023), and this success can be attributed in part to substantial CCS endeavors. As a group of Elwha scientists and scholars of public engagement, we characterized past, current, and potential CCS projects associated with the Elwha River restoration (Eitzel et al., 2023). In this Perspectives article, benefiting from our collective knowledge of CCS and experience working on the Elwha, we summarize the various projects described in Eitzel et al. (2023), distill lessons learned from the variety of CCS initiatives that emerged from Elwha ecosystem restoration, and provide guidance for future dam removals and similar large-scale restoration projects. As in Eitzel et al. (2023), we define CCS projects as those that involve local and/or non-local individuals without formal training in the research topic, including projects in which participants may be financially compensated or receive academic credit for their work.

1.1 Why community and citizen science in large-scale watershed restoration?

CCS projects can vary widely in how many people they engage in what stages of the research process, ranging from contributions to only one aspect (e.g., data collection) to community-driven projects where participants determine research questions and methods as well as implementing the work (Shirk et al., 2012). Use of CCS in environmental monitoring is attractive for multiple reasons (Conrad and Hilchey, 2011; McKinley et al., 2015; Jadallah and Wise, 2023). It has the potential to cost-effectively expand the scope and scale of data collection through the participation of volunteers, and the diverse perspectives and experiences of participants can encourage a more thoughtful research approach featuring a wider range of questions. CCS may also provide a variety of benefits to participants and their communities such as learning (National Academies of Sciences, and Medicine, 2018), enhanced connection to place (Newman et al., 2016), and a sense of agency with respect to environmental issues and policy and management processes (Jordan et al., 2012). Such benefits are even more significant when CCS projects center the contributions of marginalized and underrepresented communities (Soleri et al., 2016). Ideally, all of these benefits mutually reinforce one another, enhancing the sustainability of research and monitoring programs.

These co-benefits are particularly important for watershed-scale restoration projects such as large dam removal, where many individuals and communities are involved and the scope of data collection often outstrips typical monitoring budgets (Aceves-Bueno et al., 2015). Most published dam removal studies do not implement pre- and post-monitoring, and research projects are often short-term and/or focused on narrow parameters (Groves, 2019). In addition, because dam sites are highly varied, most dam removals will have different ecological response trajectories, even if they follow similar generalized forms (Bellmore et al., 2019). Because specific and detailed data are essential to inform decision-making during dam removal, local community members are ideal allies to expand monitoring. Finally, in situations that are contested or controversial (which dam removals often are), community-based approaches to monitoring can contribute to consensus-building (Fernandez-Gimenez et al., 2008).

2 Background: community and citizen science on the Elwha

2.1 The Elwha River restoration project

Among the nearly 4000 dams that have been removed globally in the last 50 years (Ding et al., 2019), the Elwha River in Washington State, USA (Figure 1) remains a prominent success story for advocates, scientists, resource managers and policy makers alike (O'Connor et al., 2015). Two dams were built on the River in 1913 and 1927 without fish passage, drastically curtailing habitat for multiple anadromous fish species, damaging the connections of the Lower Elwha Klallam Tribe (a member of the Lower Elwha Tribal Community) to culturally-significant practices and places, and reducing the delivery of sediment and wood to the lower river and nearshore (Winter and Crain, 2008). Following sustained advocacy by the Tribe and other groups, the dams were removed from 2011 to 2014 in one of the largest and best-studied large-scale dam removal efforts to date.[1]

As part of the dam removal effort, various formal and informal teams of scientists and resource managers came together to coordinate, facilitate, develop, and implement interdisciplinary research, education, and public outreach programs in the Elwha River watershed and nearshore coastal areas. These consortia of tribal, federal, state, educational, and community groups hosted the 2022 Elwha River "ScienceScape" symposium to mark the 10-year anniversary of dam removal, synthesize the first decade of system responses, and plan for the next ten years of Elwha monitoring – with CCS playing a central role in that future effort. As part of this focus on CCS, we (ScienceScape organizers, participants, and scholars from the University of California, Davis Center for Community and Citizen Science) documented examples of CCS on the Elwha (see Eitzel et al., 2023), which we summarize below.

2.2 Foundations of Elwha community and citizen science

Elwha CCS emerged, in part, from a long tradition of community engagement in, and care for, the Elwha River watershed. We first recognize the deep and traditional knowledge of the Elwha (ʔéʔɬx̣ʷaʔ) River ecosystem held by the Klallam (nəxʷsƛ̓áy’əm’) people as foundational to CCS on the Elwha. While Indigenous Knowledge Systems are a distinct way of experiencing and understanding the

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[1] More than 250 studies of the Elwha dam removals have been published as of August 2023: https://www.zotero.org/groups/4740476/elwha_bibliography.

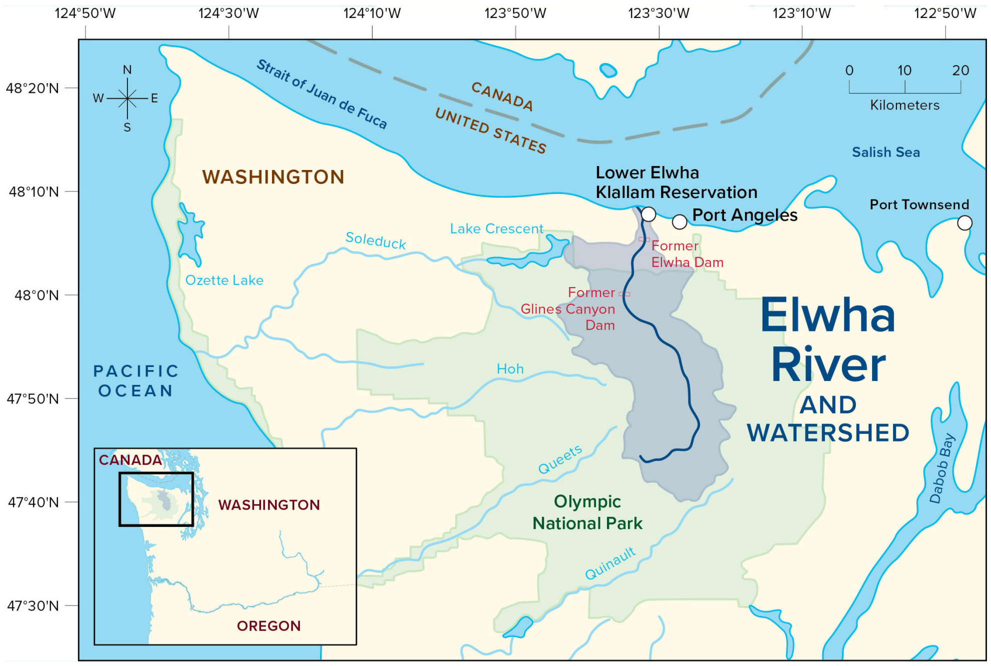

FIGURE 1
The Elwha (ʔéʔɬx̣ʷaʔ) River is located in Washington State, USA, on the Olympic Peninsula west of Seattle and south of the Strait of Juan de Fuca. Much of the watershed (smaller blue area) overlaps Olympic Peninsula National Park (larger green area), and the Lower Elwha Klallam Tribe's reservation lies to the east of the mouth of the River. Modified from Eitzel et al. (2023) under a CC-BY license; base map from iStock contributor Cartarium; Olympic National Park boundary from National Park Service map on Wikimedia Commons; watershed boundary from Fraik et al. (2021) under a CC-BY license.

world and its ecosystems, there are many elements of Indigenous Knowledge and management that overlap with some conceptions of CCS, particularly community-driven CCS (Tengö et al., 2021). In this sense, we acknowledge that the Lower Elwha Klallam Tribe has passed stories through the generations about their interactions with fish and wildlife, about their creation story along the Elwha River, and about their traditional fishing and hunting practices. We also recognize their early and consistent advocacy for the dam removals, their research (including their support of the Elwha ScienceScape group), and the cultural, emotional and economic cost to the Tribe of the ongoing fishery closure associated with the dam removals (Mauer, 2021).

In addition to the Klallam peoples' traditional and ongoing knowledge and relationship to the River, there have been other local residents who have advocated for the River and the fish. For example, Port Angeles local Dick Goin was a pulp-mill worker and fisherman who kept detailed fish catch records on the Elwha from the late 1950s–2010s. His extensive observations of natural history (e.g., species-specific run timing and spawning locations) are noteworthy because they demonstrated salmon declines over many decades. Dick's advocacy was particularly effective because he built relationships with many groups with differing perspectives and was able to motivate collective action.

2.3 Recent and current community and citizen science projects on the Elwha

During and since the dam removals, CCS participants have been involved in Elwha monitoring in a variety of ways, though none of the Elwha scientific literature mentions CCS as such (Eitzel et al., 2023). Explicit efforts facilitated community engagement at various points: prior to dam removal, the Elwha Nearshore Consortium (ENC, 2015) brought together local and regional scientists, citizens, and managers to understand and promote the Elwha nearshore. Recommendations from these meetings informed much of the nearshore work done prior to, during, and after the dam removals. Since 2022, the ScienceScape group that emerged around the Symposium events has been working on a more coordinated plan for Elwha CCS in the future. In the interim, however, there was not an overarching strategy or funding source for CCS in research and monitoring. This reflects the somewhat *ad hoc* nature of the monitoring effort in general, which began as a ground-up undertaking rather than a centralized directive.

Even without an explicit strategy for CCS, a diversity of different types of projects emerged (see Eitzel et al., 2023 for details). Projects varied in terms of number of participants from 1 to 2 people for vegetation sampling and plant identification, up to thousands for engagement with online biodiversity platform iNaturalist. Projects included several types of participants: K–12 students, undergraduate students, retirees, and tourists/visitors. Though most projects were biologically oriented, some were sediment-oriented. Projects also varied in terms of duration/longevity, with some projects running from the early 2000s (pre-dam removal) to present and some having begun in the summer of 2022. Some projects were designed to involve volunteers from the beginning and some benefited from serendipitous overlap of volunteer skills and availability. Future work could explore how these different types of projects have evolved over time.

A commonality among Elwha CCS projects is that many project leaders needed assistance engaging and managing volunteers. Some project leaders met this need through partnerships with other organizations who had volunteer management skills. Most volunteer projects were typically small-scale, with just a few people who were either already highly skilled (e.g., expert botanists) or who could be trained to do highly-skilled tasks (Figure 2). Reliance on skilled or knowledgeable individuals is unsurprising, as field science has long relied on the help of local experts (Vetter, 2016). Engagement in Elwha CCS often came in the form of both paid and unpaid internships, and/or as part of educational opportunities (largely K–12 or undergraduate students) – again unsurprising, as educational CCS projects in environmental science are common and well-studied (National Academies of Sciences, and Medicine, 2018). Each of these strategies (working with small numbers of volunteers, engaging with educators and their students, and/or using an internship structure) had key benefits for project managers: assistance in volunteer training, management, and engagement; easier data quality control; and built-in liability management for potentially hazardous activities. These strategies also offered benefits for participants in the form of compensation, work experience, and/or educational credit.

2.4 Proposed community and citizen science work on the Elwha

Even after 20 years of intensive study there are still many remaining questions as the Elwha River and its associated ecosystems continue to change. Maintaining long-term monitoring programs is essential to understand these changes, particularly in light of shifting baselines due to climate disruption (Lower Elwha Klallam Tribe, 2022). To support these needs, the ScienceScape group that emerged around the 2022 Symposium is now engaged in a systematic planning process around CCS in the Elwha watershed, reflected in Eitzel et al. (2023). As a result, the proposed projects we documented cover a wider range of topics and academic disciplines than the current projects have. The proposed projects require a range of different resources (e.g., volunteer management, data quality control, support for staff or volunteers, evaluation of tools for data collection) and differ in the stage of partnership development and planning (e.g., some are entirely new ideas and others are novel partnerships between well-established entities). The ScienceScape group is exploring what might be needed to sustain a more coordinated CCS effort (including supporting an Elwha CCS coordinator position), and future work could explore how CCS on the Elwha evolves with the benefit of

FIGURE 2
Participation in Elwha research is often small-scale (involving small groups) due to the technical and safety challenges of some projects. **(A)** NOAA researchers and student intern ford the Elwha to access a long-term benthic invertebrate monitoring station. (Image from Eitzel et al., 2023 under a CC-BY license.) **(B)** A volunteer from Clallam County BeachWatchers uses a radio-frequency identification (RFID) reader to locate tracers on the beach of the Elwha River delta in March 2009, prior to dam removal. (Photo by Ian Miller.)

more coordinated planning. Finally, there are also activities underway to enable the public to view the data they have collected, which can be another important form of positive feedback and benefit for participants (de Vries et al., 2019).

3 Discussion: lessons learned from Elwha community and citizen science

In this section we distill lessons learned from Elwha CCS, and identify possible areas for future development of Elwha CCS and ways that partners are, or could be, addressing barriers and challenges – many of which are common to CCS projects in other contexts (Burgess et al., 2017).

3.1 Current advances: what worked in Elwha community and citizen science

3.1.1 Lesson: partner organizations can help with volunteer coordination capacity

One theme among successful Elwha CCS projects was finding ways to address the additional administrative burden of managing volunteers. Some project leaders were able to overcome this limitation by partnering with external organizations with volunteer coordination expertise and capacity. In some cases, these long-term partnerships pre-dated Elwha dam removal monitoring. The Elwha coastal processes research of Miller et al. (2011) and Miller and Warrick (2012), for example, was made possible by connections with a local BeachWatchers program, which provided volunteer coordination and engagement services. Similarly, the Washington State Department of Natural Resources partnered with the Clallam Marine Resources Committee, The Coastal Watershed Institute, Peninsula College, Western Washington University and the University of Washington to work with volunteers to complete nearshore ecosystem and geomorphological studies (Parks et al., 2013; Parks, 2015). Many of the proposed Elwha CCS projects involve similar partnerships. The smaller size of the Elwha watershed and the relatively tight-knit community of researchers who work in the area lent itself particularly well to this type of informal relationship building. For other dam removal and restoration projects that span larger and potentially more demographically diverse regions, it could be particularly important to intentionally create opportunities for such collaborations before projects get underway.

3.1.2 Lesson: compensation for participants enables engagement

Supporting participants in various ways is important. Many Elwha project managers deliberately chose models in which participants were compensated in some way (e.g., financially, with academic credit, and/or training or resume-building activities). While some participants can afford to volunteer their time, labor, and skills, broader engagement includes supporting participation for those who cannot afford it. We note that compensation is an important form of reciprocity, which is key in research partnerships with communities (Wilmer et al., 2021) and often underlined by CCS researchers as critical to project longevity and ethical commitments. On the Elwha, programs including Washington Conservation Corps, AmeriCorps, and the Indian Youth Service Corps provide mechanisms for participant reimbursement.

3.1.3 Lesson: individuals committed to participatory work need support

We also note that many of the examples in Eitzel et al. (2023) were the work of specific individuals and organizations who highly value and have been committed to engagement with the public in their work. Some Elwha projects included planned participation by local citizens (Parks et al., 2013; Parks, 2015; Shaffer et al., 2017) and many additional unplanned CCS projects emerged despite the technical and liability challenges involved. This shows a commitment to community engagement on the part of scientists and an openness to the opportunities for collaboration that can arise in the course of long-term monitoring projects. It was often these individuals who – driven by their own commitments – jumped through bureaucratic hoops to develop partnerships and engage in CCS. This is an encouraging finding, but we feel this also points to the importance of broad multi-institutional support of CCS, as a way to remove barriers for individual scientists.

3.2 Future directions: opportunities for CCS research and practice

Though CCS on the Elwha contributed in critical ways to monitoring aspects of the Elwha system over the last decade, there are areas in which CCS could be expanded in scope and impact both on the Elwha and beyond.

3.2.1 Opportunity: plan ahead to expand beyond small-scale engagement

Fieldwork in the Elwha watershed and nearshore can require airplane, boat-based and in-water activities (wading, snorkeling, diving), wildlife interactions (e.g., fish identification and tagging), or hiking to remote locations – all of which can expose researchers to potentially hazardous conditions and may require specialized training (Hilperts, 2010). This often means that projects require significant planning in order to involve volunteers, and because many projects in the Elwha typically were not designed for CCS participants, these projects were often able to involve volunteers only on a small scale. This approach may miss opportunities to broaden engagement with diverse members of the public, thus limiting who can engage with science (Walker et al., 2021).

On the other hand, other large-scale environmental monitoring programs have demonstrated that systematic planning for CCS can help to expand participation. For example, in California's Marine Protected Areas, where CCS was an explicit priority within a broader monitoring framework, tens of thousands of people have participated across many different projects (Meyer et al., 2017; Freiwald et al., 2018; Meyer et al., 2022). While this example operates on a much larger scale than the Elwha watershed and coastal system, the wide range of project types (many different topics, approaches, and ways for participants to engage) is instructive, when considering some of the constraints described above: we underline that even in a highly technical context with safety concerns, there are still ways to plan ahead for larger-scale volunteer involvement. Likewise, there are opportunities to think specifically about including participation when planning watershed monitoring (Metcalfe et al., 2022), and guidance for how to do so (Meyer et al., 2020).

3.2.2 Opportunity: sustain research over generations through community co-production

Many Elwha scientists do not live on the Olympic Peninsula and many local residents hold nuanced forms of place-based knowledge. Maximizing opportunities for equitable interaction, engagement, and learning between scientists and residents can foster the co-production of knowledge in which diverse insights can support a thriving river and coastal system. Long-term engagement can assess the community benefits and potential negative impacts of CCS projects (Walker et al., 2021). At the same time, the timescales of biophysical change occurring in the watershed and adjacent coastal system last for multiple human careers and/or generations. We therefore point out that these forms of engagement can increase a sense of investment and ownership in the knowledge generation process, potentially sustaining monitoring efforts over the same multi-generational timescales.

3.2.3 Opportunity: engage participants throughout the research process

We note that much of the Elwha research and monitoring has been motivated by policy associated with the dam removals. Research therefore has been designed to test hypotheses related to the recovery of fish populations and restoration of sediment flow and other biophysical processes. While these issues may overlap to varying degrees with community interests, we note that this is not the same as a research and monitoring agenda that is actively shaped by community members. This therefore represents one potential growth area for Elwha CCS. Expanding participation means more than increasing the number of participants; it can also mean engaging them in more parts of the scientific process, including setting agendas and formulating questions (Shirk et al., 2012), as was done in the past with the Elwha Nearshore Consortium. The ScienceScape group made an important step towards assessing communities' current interests during the summer 2022 public event by asking event attendees to articulate questions of interest (Eitzel et al., 2023).

3.2.4 Opportunity: seek ways to build relationships with tribal community members

Tribal engagement is key in large-scale restoration projects (including dam removal) for justice and ethical reasons, as well as ecological and management reasons (via important Indigenous Knowledge about the system; Fox et al., 2017). However, attending to the way in which Tribal communities are engaged is essential to realizing the potential benefits for all involved. The ScienceScape group is currently working on more intentional engagement within the Lower Elwha Klallam Tribe. Though scientists working in the Tribe's Natural Resources Department do extensive research on all aspects of the Elwha River and some are Tribal members themselves, recent initiatives prioritize sharing research results directly with the community (e.g., outreach events on the reservation and articles in the Tribal newsletter). Finding forms of research communication that are accessible and of interest to community members is a key first step which could be followed by future efforts to engage Tribal members in additional aspects of research planning and monitoring processes.

4 Conclusions

Our exploration of CCS in the Elwha has uncovered the sometimes-hidden role that many kinds of participants have played in advancing knowledge about this system as it responds to a major restoration event. It also reveals the ways in which structural realities of professional monitoring – the policies, procedures, and physical realities of these projects – have shaped participation over more than a decade. On the Elwha River and coastal system, with no explicit long-term plan for public engagement in research and monitoring, the resulting CCS tended to include small numbers of people. But we found that CCS still happened, and contributed to Elwha science in important ways. Upcoming dam removal projects, take heed of this lesson: having a coordinated, intentional plan for CCS (e.g., following Meyer et al., 2020) – created in parallel with the political, economic, and engineering planning needed for removing the dam(s) – could expand the potential for CCS to benefit dam removals, for dam removals to benefit communities, and for communities to stay engaged in these long term management and decision-making processes.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

ME, RM, SM, AK, CJ, CB and HB contributed to conception and design of the paper. ME wrote drafts of the manuscript. All authors contributed to manuscript revision and read and approved the submitted version.

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Conflict of interest

The authors declare that the research 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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Challenges of implementing a multi-agency monitoring and adaptive management strategy for federally threatened Chinook salmon and steelhead trout during and after dam removal in the Elwha River

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Adaptive management, a process of planning, implementing, and evaluating management strategies, is often recommended for monitoring ecological systems. However, few examples of successful implementation and retrospective case studies exist. We provide a case study of adaptively managing hatchery-assisted protection and recovery for Chinook salmon (*Oncorhynchus tshawytscha*) and winter steelhead trout (*O. mykiss*) during and after the removal of two large mainstem dams in the Elwha River, WA. We summarize key aspects of the monitoring and adaptive management plan over the last decade and highlight successes, challenges, and complications during the plan's implementation. The Elwha Monitoring and Adaptive Management Guidelines included a trigger-based system for moving through four phases of recovery that included preservation, recolonization, local adaptation, and viable natural population, each with differing levels of hatchery production as the management actions. The monitoring component of the plan has been very successful, providing critical data to guide management actions that otherwise may not have occurred and, opportunistically, provided data for other native species in the Elwha River. Implementing adaptive management provided mixed results and was at times hindered by divergent management goals among project partners, the inflexibility of the Endangered Species Act regulatory requirements as implemented for this project, and conflicting information among guidance documents. We learned that some metrics and triggers in the plan were ill-defined or too difficult to measure in the field. In some cases, the performance indicators and/or triggers were successfully modified to incorporate what was learned; however, in other cases, we were unable to revise the values due to differing opinions among partners. The ability to reach consensus on revised triggers appeared to be influenced by the recovery trajectory of the species involved. The implemented adaptive management strategy resulted in substantial collaboration and learning, which resulted in revised management strategies, but was imperfect. Sufficient long-term funding is necessary to implement a well-designed monitoring program and could benefit from including a defined leadership position to shepherd and facilitate a multi-stakeholder adaptive management program. Additionally, incorporating adaptive management into legally binding conditions under the Endangered Species Act is feasible, but requires substantial pre-planning in close coordination with regulatory agencies.

KEYWORDS

adaptive management, dam removal, Elwha River, Chinook salmon, steelhead trout, restoration

Introduction

Adaptive management (AM), a special case of structured decision-making, is an iterative data evaluation and response framework often implemented for the management of dynamic ecological systems (Williams, 2011; Westgate et al., 2013; Deitch et al., 2021). The approach has been widely used across a range of ecological management scenarios, from small-scale single species projects to large-scale ecosystem management (Roux and Foxcroft, 2011; Melis et al., 2015). AM consists of a series of steps that include developing objectives, identifying and assessing options, and learning from monitoring and evaluation, and adjusting management as necessary (Argent, 2009). In theory, monitoring and evaluation information drives management actions through achieving targets which may produce subsequent iterations of a plan (Nie and Schultz, 2012). Examples of AM frameworks are abundant in the literature and provide a robust conceptual knowledge base for planning and implementing a new plan (Gillson et al., 2019). Forms of AM involving natural resources have existed for at least 65 years (Williams, 2011), across a diverse range of disciplines including climate change (Galappaththi et al., 2022), environmental flows (Wineland et al., 2022), landscape management (McCord and Pilliod, 2022), stream restoration (Bradford et al., 2023), and fisheries (Walters, 2007).

Several reviews have identified barriers and common pitfalls to effective AM implementation (Halbert, 1993; Keith, 2000; Walters, 2007; Runge, 2011; Williams, 2011; Williams and Brown, 2014). These issues range widely from intrinsic and institutional to purely technical (Williams, 2011). Elements of intrinsic and institutional issues are often grounded in unstable or dysfunctional working groups, or an inability to embrace uncertainty and alternative perspectives to achieve participatory decision making (Gunderson, 1999; Stankey et al., 2005), which may result in conflict that result in failed AM (Westgate et al., 2013). Technical issues often stem from a difficulty or inability to monitor changes, or ineffective monitoring protocols that fail to collect relevant information with tenable levels of precision to inform policy (McDonald-Madden et al., 2010; Runge et al., 2011). Despite these issues, AM is still preferred over other alternate management paradigms such as *ad hoc*, wait-and-see, and steady state (Westgate et al., 2013).

Several key elements for successful AM have also been identified (Keith et al., 2011; Gillson et al., 2019). One fundamental requirement is identifying variables that can be monitored and/or managed for a dynamic system (Williams, 2011). Effective monitoring and management actions require an engaged community of managers and researchers (Keith et al., 2011). Similarly, the AM process often applies a substantial temporal and fiscal burden to researchers and managers, where funding for involvement is repeatedly identified as imperative (Wilhere, 2002). Therefore, developing an approach to secure substantive long-term funding, such as integration of a plan into legal documents (e.g., Congressional acts, listed species reviews), can promote success (Doremus, 2001). However, codifying management plans into a legal framework can limit progress (Benson and Schultz, 2015). For example, a 2011 survey found over 70% of AM practitioners felt hampered by legal and institutional constraints (Benson and Stone, 2013).

Although a large body of literature exists surrounding AM plans, retrospective case studies of AM implementation are useful but uncommon (Roux et al., 2022). To address this issue, we provide a case study of monitoring and adaptively managing hatchery-aided protection and recovery of two U.S. Endangered Species Act (ESA) listed species after large-scale dam removal in the Elwha River. This retrospective analysis of the Elwha Monitoring and Adaptive Management Guidelines (hereafter EMAM, Peters et al., 2014) process provides an example for future AM planners to consider, particularly for dam removal projects. The EMAM includes performance indicators, with associated empirical trigger values that guide movement through four recovery phases (preservation, recolonization, local adaptation, and viable natural population), each with differing levels of hatchery intervention (details below). The EMAM also includes detailed monitoring protocols for the performance indicators. This plan was developed with considerations of the best available guidance, including incorporating monitoring and AM into regulatory documents. The objectives of this paper are to: 1) describe our monitoring and AM process, 2) describe the monitoring results for Chinook salmon (*Oncorhynchus tshawytscha*) and winter steelhead trout (*O. mykiss*) following dam removal and how these data were used for

AM, 3) identify factors leading to success, challenges, and unforeseen issues, and 4) provide recommendations to address these challenges.

An adaptive management framework for Elwha River Chinook salmon and winter steelhead trout during and following dam removal

Background

Understanding the historical context of the Elwha River, its fish populations, and complicated management regime resulting from multiple agencies with management authority (Box 1 for details) is critical to understanding restoration strategies employed during and after dam removal. Throughout the decades-long planning period leading up to the start of dam removal, several institutional processes occurred which set the context for potential management options considered for the Elwha River AM program (Supplementary Table S1). Dam construction led to significant habitat degradation upstream and downstream of the two dams (Pess et al., 2008) and associated salmon population declines. This in turn resulted in intermittent (1911–2022, (Johnson, 2013) and then continuous hatchery production for Chinook (1930's to present) and winter steelhead (1976 to present). Although Chinook salmon spawned naturally while their numbers declined, contemporary data indicate that a low proportion of the adults were progeny of natural-origin spawners, meaning the population was essentially sustained by hatchery production (Pess et al., 2024).

The license application for Elwha Dam (1968) and re-licensing application for Glines Canyon Dam (1973) by the dam owners to the Federal Energy Regulatory Commission, prompted Federal and State agencies (hereafter Agencies) and Lower Elwha Klallam Tribe (hereafter Tribe) to lobby for modifications to the projects to abate the degradation to commercially and culturally important anadromous fish and their habitat (see Winter and Crain, 2008 for detailed history). This was followed by years of administrative and legal challenges as the Tribe and Agencies argued that recommendations to restore fish passage and habitat conditions, including dam removal, should be considered. This resulted in a negotiated settlement among parties to lawsuits which was enshrined by passage of the Elwha River Ecosystem and Fisheries Restoration Act of 1992 (PL 102-495). The goal was restoration of the Elwha River's anadromous fisheries and ecosystem, and it essentially set the boundaries for AM development for the Elwha River dam removal project by establishing goals for the project through the production of several legal documents (Supplementary Table S1). These documents culminated in the development of the Elwha Fish Restoration Plan (Ward et al., 2008), multiple Biological Opinions (BiOps), EMAM (Peters et al., 2014), and ultimately the evaluation and recommendations determination document (NMFS, 2015) that governs Elwha Recovery, which is largely guided by the EMAM. A BiOp is a process of analyzing the effects of proposed activities to species listed under the ESA and their critical habitat. Three primary BiOps were completed for the Elwha restoration project, one governing dam removal (NMFS, 2012a) and two governing hatchery operations (NMFS, 2012b, 2015). The EMAM addresses all three BiOps, but management actions are largely focused on hatchery operations.

The primary goal of dam removal on the Elwha River was to eliminate migration barriers and restoration of native anadromous fish populations and the ecosystem that supports them (Wunderlich et al., 1994; Duda et al., 2008; Pess et al., 2008; Winter and Crain, 2008). The project was unique due to the height of the dams (64 m and 32 m), the massive amount of sediment stored in the reservoirs (21 million m^3), and the potential to restore connectivity for nine species of migratory fish into pristine spawning and rearing waters protected within Olympic National Park. This special opportunity to restore salmonid populations and their river ecosystem also presented management challenges ideally suited to an AM approach. A primary challenge was controlling the release of nearly a century worth of sediment accumulation into the river downstream (Randle et al., 2015), while protecting four fish species: Chinook salmon, steelhead trout, bull trout (*Salvelinus confluentus*), and eulachon (*Thaleichthys pacificus*) listed as threatened under the ESA. For these protected species, dam removal presented an interesting paradox (Stanley and Doyle, 2003). In the long term, dam removal could provide a tremendous benefit by providing access to approximately 187 km of mainstem, floodplain channel, and tributary habitats, mostly protected as wilderness inside the boundaries of Olympic National Park (Pess et al., 2008), and restoring natural processes to the lower river. However, in the short term, dam removal was expected to be a major disturbance, as nearly a century's accumulation of the river's annual sediment load was to be released during the two to four years of dam removal. This onslaught of sediment would increase channel instability and water column turbidity downstream of the two dams (East et al., 2015; Magirl et al., 2015), representing a significant threat to ESA-listed salmonids that depend on clean and stable spawning gravels, delivery of oxygen rich water for incubating eggs, and productive juvenile rearing habitats. This prompted a management strategy focused on the use of hatcheries to protect and restore salmon and winter steelhead trout during and following dam removal (Ward et al., 2008).

The use of hatcheries was identified as a significant component of stock preservation and recovery during and following dam removal (Department of the Interior et al., 1994; Ward et al., 2008). This approach was deemed necessary due to low population abundances of Elwha River salmonid stocks and uncertainties of the magnitude and duration of physical environment alterations resulting from dam removal. The use of hatcheries was also generally acceptable given the extensive history of hatchery intervention in the Elwha River. Hatchery managers generally avoided releasing non-local Chinook salmon into the Elwha River over the years (Brannon and Hershberger, 1984), and the steelhead hatchery program was established recently, in 2012, with native broodstock (Lower Elwha Klallam Tribe, 2011). However, the use of hatcheries also presented risk and uncertainty, related to documented genetic and ecological impacts of hatchery propagation (Naish et al., 2007; Anderson et al., 2020; McMillan et al., 2023), especially for stocks, like those in the Elwha, that had been reared in hatcheries for decades. Therefore, we developed the EMAM for monitoring and adaptively managing Chinook salmon and steelhead trout recovery following dam removal (Peters et al., 2014). The EMAM focused on Chinook salmon and winter steelhead trout because of their protected status and proposed management alternatives (i.e., hatchery conservation) required regulatory review that drove ongoing multi-agency efforts to monitor their populations during and following dam removal. The goal of hatchery intervention was to reduce extinction risk from high sediment loads in the short-term, when turbidity levels were expected to far exceed those known to be lethal to salmonids, and facilitate the colonization of newly accessible habitats upstream of the former dams (Ward et al., 2008). The strategy contained within EMAM was to phase out hatchery production incrementally as the stock's population progressed through the recovery phase after dam removal.

Five entities have management and decision-making authority for fish populations in the Elwha River. Olympic National Park was the lead agency for planning and implementing dam removal and manages fisheries for the Elwha River within the park. Washington Department of Fish and Wildlife and Lower Elwha Klallam Tribe co-manage hatchery production in the Elwha River, and fisheries for Elwha populations in both the marine and river environment outside of the park. These three managing entities are subject to oversight of actions that may impact ESA listed fish by National Marine Fisheries Service (NMFS) (Chinook salmon, steelhead trout) and U. S. Fish and Wildlife Service (bull trout). Thus, each entity approached Elwha fish recovery with a different management authority and responsibility. As a result, the group has generally worked through consensus, towards the goal of ensuring any decisions would not violate the decision-making authority of another entity. In some cases, the diversity of management and legal obligations among agencies led to the disagreements and challenges to implementing AM described below.

Guidelines for Elwha monitoring and adaptive management—methods to track progress through restoration

The overall AM strategy for listed Elwha River Chinook salmon and steelhead trout (Peters et al., 2014) mirrored the AM framework described by Roux and Foxcroft (2011). This framework included adaptive planning, implementation, and evaluation. Adaptive planning consists of vision development, objective setting, and the development of management options (Roux and Foxcroft, 2011). Adaptive implementation includes development of a detailed action plan, implementing the plan, developing monitoring protocols linked to measurable targets, and developing a strategy for regularly evaluating monitoring results. Adaptive evaluation is the process of evaluation and learning that occurs continuously throughout the process and is facilitated by addressing pertinent questions developed within the AM process (Roux and Foxcroft, 2011). Much of the adaptive planning portion of the project largely occurred during the Federal Energy Regulatory Commission and Environmental impact statement processes described above (Supplementary Table S1); however, some aspects were completed during EMAM development. The adaptive implementation and evaluation components were developed and described in the EMAM (Peters et al., 2014).

The EMAM was developed to promote informed, shared decision making, with each agency retaining management authority according to jurisdiction and legal obligations. This included management of fisheries (Lower Elwha Klallam Tribe, Washington Department of Fish and Wildlife, National Park Service), management of hatcheries (Lower Elwha Klallam Tribe, Washington Department of Fish and Wildlife), implementation of the dam removal project (National Park Service), and ESA oversight of these activities (National Oceanic and Atmospheric Association, U.S. Fish and Wildlife Service). A recognition of the inter-connectedness of these decisions inspired the development of the EMAM and heightened the sense of collaboration. The creators of the EMAM were agency (State and Federal) and Tribal biologists with varying responsibilities related to administration, management, and monitoring (Box 1). The development of the EMAM was largely a technical exercise conducted by fishery professionals, as public involvement and comment were incorporated during the Federal Energy Regulatory Commission and Environmental Impact Statement process related specifically to dam removal. Staff members from each agency updated the appropriate executive staff within their agency about progress and potential issues as necessary. The group generally worked through consensus, while ensuring legal authorities were not violated. Conflicts were typically addressed with respectful, sincere debate though none of the participants were trained facilitators, and agreement was not always reached. By soliciting, accepting, and considering input on issues pertaining to their management authority, each agency implicitly acknowledged the shared responsibility of promoting the recovery of Elwha River fish populations.

The EMAM works from broad to specific levels in a hierarchical manner. The main elements included setting goals, objectives, performance indicators, decision rules, triggers, and finally decisions (i.e., management/policy response), which was completed individually for Chinook salmon and steelhead trout (Table 1). Performance indicators, triggers, and management responses were developed for each objective and help determine the outcome of management strategies implemented.

Given the scope of the Elwha River AM project—dam removal with hatchery intervention—the EMAM prescribes a passive AM approach. In contrast to an active AM approach which is explicitly experimental in nature, a passive AM approach implements a single 'best' management strategy and evaluates the outcome (Walters and Holling, 1990). The passive approach was selected since the project involved dam removal in a single system, thereby limiting the range of management options that could be applied and evaluated. Because a passive approach was used, we implemented a structured decision-making process (Gregory and Long, 2009; Runge et al., 2013) along with intensive monitoring to collect data for evaluating fish recovery and the influential mechanisms. The structured decision-making process, of which AM is a special case (Gregory and Long, 2009; Runge et al., 2013), compensated for the passive approach by providing periodic decision points throughout the AM process when performance indicators were evaluated. This evaluation included a simple decision-tree process to determine the next course of action (see below and Figure 1). Monitoring was focused on data collection to evaluate empirical triggers for the selected performance indicators, as well as exogenous variables outside

TABLE 1 Definition of terms related to Elwha Monitoring and Adaptive Management guidelines developed by Peters et al. (2014).

Term	Definition
Adaptive planning	Development of the project vision and objectives, and the development of management options (Roux et al., 2022)
Adaptive implementation	Development and implementation of a detailed action plan, monitoring program, associated targets, and evaluating results (Roux and Foxcroft, 2011)
Adaptive evaluation	Evaluation and learning from the implementation phase and using the information to inform future management (Roux and Foxcroft, 2011)
Goals	Broad statements about what management hoped to achieve
Objectives	Broad quantitative targets that test questions/hypotheses, that once met, help achieve stated goals
Recovery phase	Relatively distinct, sequential, and biologically based phases of recovery that contain distinct goals and objectives. Movement from one recovery phase to the next is dependent upon performance indicators and phase-specific trigger values (HSRG, 2012)
Performance Indicators	Metrics to be measured by focused monitoring (e.g., adult abundance, juvenile productivity, and spatial distribution)
Triggers	Empirical criteria used in a structured decision framework to determine if the decision rule for the performance indicator has been met (e.g., 969 adult steelhead trout to move from Preservation Phase to Recolonization Phase)

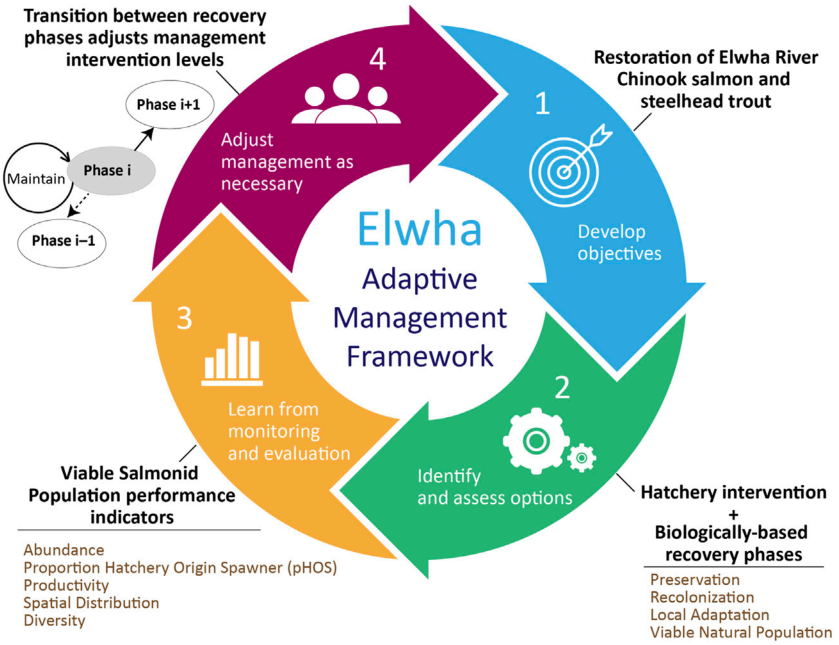

FIGURE 1
Conceptual diagram describing the adaptive management framework implemented for Elwha River Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*). The colored arrows show the four main elements of the framework, based on the adaptive management principles described in (Roux and Foxcroft, 2011). After developing objectives, it was determined that hatchery intervention would be required to mitigate the effects of the dams and their removal. The framework used biologically based recovery phases, which differed in levels of management intervention. Progress through the phases was determined by performance indicators exceeding "trigger values" derived for each species and based on viable salmonid population principles (McElhany et al., 2000). On an annual basis, monitoring data was used to assess whether the program would transition out of the current recovery phase.

of management control that could influence overall recovery. The purpose of this intensive monitoring program was to ensure data were available to understand observed recovery response and test hypotheses that may arise regarding why recovery was progressing in the observed manner.

Based on recommendations from the Hatchery Scientific Review Group (HSRG, 2012), the EMAM defined four recovery phases for both Chinook salmon and steelhead trout tailored to the specifics of dam removal and hatchery intervention, as well as the pre-dam removal status of Elwha River fish populations. These recovery phases—preservation, recolonization, local adaptation, and viable natural population—each had different goals and management strategies (Supplementary Tables S2, S3). Once the objectives, performance indicators, and associated triggers for a particular recovery phase were met in the same year, the AM program would move into the next recovery phase.

The preservation phase describes the period during and after dam removal when elevated suspended sediment concentrations were expected, at times, to be lethal to all fish in the river. This represented a high risk for complete or significant loss of extant fish populations or year-classes. The goal of the preservation phase is to protect the existing genetic and life history diversity of native salmonid populations until fish passage is restored and water quality impacted by the dam removal project returned to background levels. Hatchery management during this phase is maximum production and smolt releases directly from the hatcheries (Lower Elwha Klallam Tribe, 2011; Washington Department of Fish and Wildlife, 2012). In addition, adults volitionally entering the hatchery in excess of hatchery production needs were to be transported upstream of Elwha Dam and released into clean water refuges (i.e., tributaries unimpacted by dam removal) until turbidity returned to background levels (detailed in Liermann et al., 2017).

The recolonization phase describes the period following dam removal when passage was restored and access to refugia from lethal suspended sediment concentrations had been restored or suspended sediment concentrations were no longer lethal. The goal of the recolonization phase is to ensure that salmonids (hatchery-origin and natural-origin) are continually accessing habitats upstream of the former dam sites, with some fish spawning successfully and producing smolts. The EMAM proposed reduced hatchery production during this recovery phase based on adult abundance.

The local adaptation phase was the period when the already reduced releases of hatchery fish would be eliminated and the spawning of naturally produced adults would result in population growth. The goal is to maintain or increase life history diversity of natural spawning populations through their local adaptation to the Elwha River ecosystem. Hatchery production is eliminated at the end of this recovery phase when the triggers for final recovery phase (viable natural population phase) are met. This is the period when all aspects of the previous phases are met, and a viable natural population exists that can sustain recreational, commercial, and Tribal harvest without hatchery augmentation.

Performance indicators are specific metrics to be measured by focused monitoring and are used to define how recovery is progressing through the four recovery phases. Each performance indicator has an associated trigger representing target values for the phase being assessed (Supplementary Tables S2, S3). Performance indicator triggers were empirical targets based on published information, available active monitoring results from the Elwha River, and comparable watersheds that could be used as a potential reference (Peters et al., 2014). The performance indicators represented four viable salmonid population metrics (McElhany et al., 2000), including abundance, productivity, distribution, and diversity, plus managing for the proportion of hatchery-origin spawners (pHOS). We used a geometric mean calculated over a four-year period, representing the dominant age at maturity for both Chinook salmon and steelhead trout, to evaluate the status of each performance indicator.

The relationship between each performance indicator and associated triggers were typically evaluated annually. Once all trigger values within each phase were met in the same year, by one of the species, that species could proceed to the next recovery phase. Feedback mechanisms existed within each recovery phase, allowing for the regression to the previous recovery phase if an indicator's geometric mean dipped below the trigger value for the previous recovery phase. Thus, during each annual assessment, there were four potential management responses (Figure 1). Importantly, our approach allowed for the re-evaluation of triggers for each phase because they were based on a set of assumptions, with unknown accuracy.

Monitoring protocols were developed and are detailed in Pess et al. (2024). In general, timing of river entry and adult abundance were estimated using sonar estimates, weekly tangle net sampling, and carcass surveys to assess species composition and hatchery-origin return percentage, depending on the species (Denton et al., 2023). Productivity was assessed using sonar estimates of adult returns to the river, adult scale samples used to apportion adult estimates to brood year (i.e., adult productivity; Weinheimer et al., 2018), and both mainstem and tributary screw traps (i.e., juvenile productivity; McHenry et al., 2023b). Spatial extent was estimated using spawning ground surveys (McHenry et al., 2023a). The EMAM recognized that monitoring methods could change over time and recommended that revisions not occur until after the new methods had been evaluated and, if applicable, calibrated with the previous method to allow the development of comparable datasets. Finally, data standards were developed for monitoring data based on Crawford and Rumsey (2011) to ensure data quality was sufficiently accurate and precise to guide management decisions (see section 4.3; (Peters et al., 2014)).

The first decade (2012–2022) of results from the Elwha monitoring and adaptive management program

Adaptive monitoring to assess Chinook salmon and steelhead trout recovery

The monitoring component of the EMAM was deemed successful because monitoring data allowed for informed decisions based upon the recovery trajectory of Chinook salmon and steelhead trout through the EMAM recovery phases. The data also facilitated development and evaluation of hypotheses regarding the mechanisms influencing recovery.

The Elwha River Chinook salmon population consistently exceeded the preservation trigger value for abundance of naturally spawning adults and the recolonization trigger value for spatial distribution since 2016 (Figure 2). Productivity triggers are the same across all recovery phases, and while juvenile productivity has exceeded the trigger value since 2021, the trigger value for adult productivity (hatchery plus natural spawner-to-spawner) has not yet exceeded the preservation trigger value. In this case, the last assessment of the geometric mean of adult productivity was 0.96 for hatchery and natural-origin spawners, which was slightly less than the trigger value of 1.0. Thus, although the Chinook population exceeded all trigger values for the preservation phase at least once, they were not all met during the same assessment year as required.

Elwha steelhead trout also exceeded the preservation phase trigger values that could be measured (Figure 3). Adult abundance exceeded the trigger value for both the preservation and recolonization phases (since 2016). Adult productivity exceeded the trigger value (same value across all recovery phases) during the first potential assessment for the 2016 brood year (Figure 3). Winter

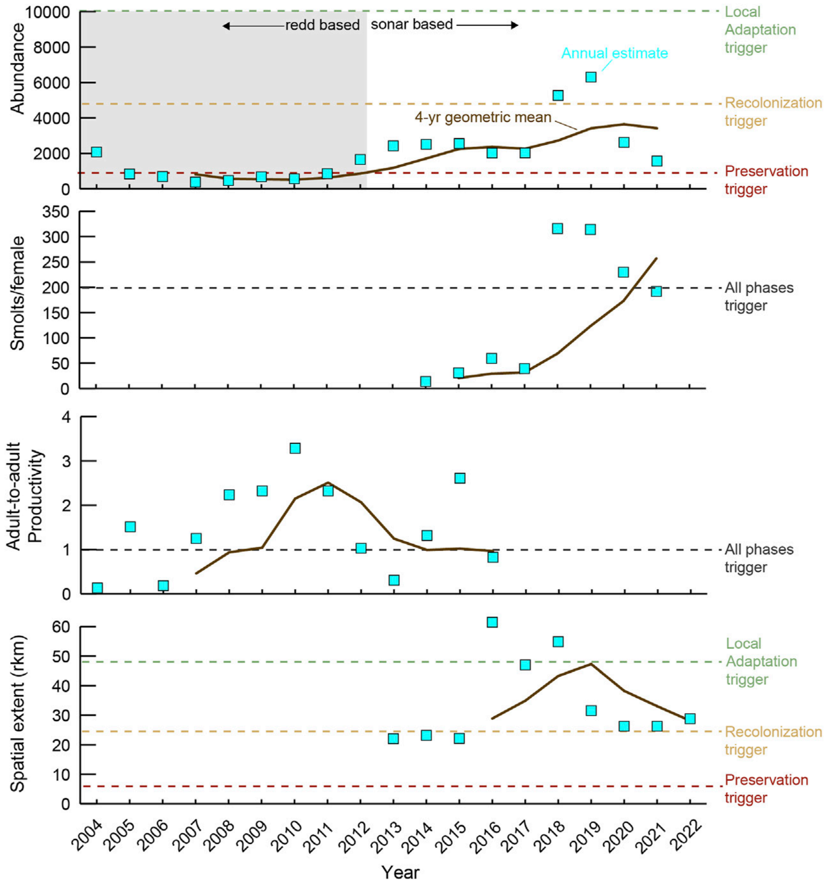

FIGURE 2
Quantitative assessment of performance indicators (abundance, smolts per female, adult-to-adult productivity, and spatial extent) for Chinook Salmon (*Oncorhynchus tshawytscha*) in the Elwha River from 2004 to 2022. Time period includes data before (2004–2010), during (2011–2014), and after (2015–2022) dam removal. Dashed lines represent performance indicator "trigger values" that when exceeded (4-year geometric mean) for all performance indicators during the same year represent completion of the current recovery phase. Note that abundance shifted from redd-based to sonar-based assessment at the start of dam removal (details in text). Data from Pess et al. (2024).

steelhead trout migrated upstream of both former dam sites and exceeded the distribution trigger for the recolonization phase, with some individual years surpassing the local adaptation trigger value. Finally, adult steelhead trout have been entering in January, exceeding the recolonization trigger value for run timing. The juvenile productivity trigger value was not met due to an inability to consistently capture enough steelhead trout smolts to estimate steelhead trout smolt abundance (McHenry et al., 2023b). Without this estimate, juvenile productivity could not be calculated, making it the only performance indicator whose trigger value was not exceeded for the preservation phase (but see below).

In addition to providing data to assess triggers, the collaborative interagency monitoring program guided by the EMAM has provided sufficient data to identify when monitoring methods needed to be adjusted. When problems were identified, scientists and managers worked together to make changes to the monitoring program. For example, at the inception of the EMAM, a channel spanning floating weir was a foundational method for estimating abundance, measuring pHOS, and describing run timing. However, river conditions during dam removal created high sediment and woody debris loads making it too difficult and labor intensive to safely and efficiently operate the weir, resulting in a low capture efficiency and insufficient data (Anderson et al., 2013). Recognizing the weir limitations, researchers pivoted towards using sonar methodology, which proved to be successful at estimating abundance and run timing despite challenging dam removal conditions. As a result, the weir was abandoned, and the sonar program expanded to include species composition netting, improving the precision of allocating image targets to species that overlapped in both size and run timing. Another example of adaptive monitoring included expanding the range and frequency of upper river summer snorkel surveys in response to the rapid expansion of summer steelhead trout (see Pess et al., 2024).

Adaptive management based on evaluating performance indicators

The EMAM monitoring program provided sufficient data to identify several modifications to recovery actions for Elwha River Chinook salmon and steelhead trout and to evaluate the quality of the performance indicators. The first case was removing a newly created fish passage barrier that might have gone unnoticed (or possibly delayed recognition) without intensive monitoring. After

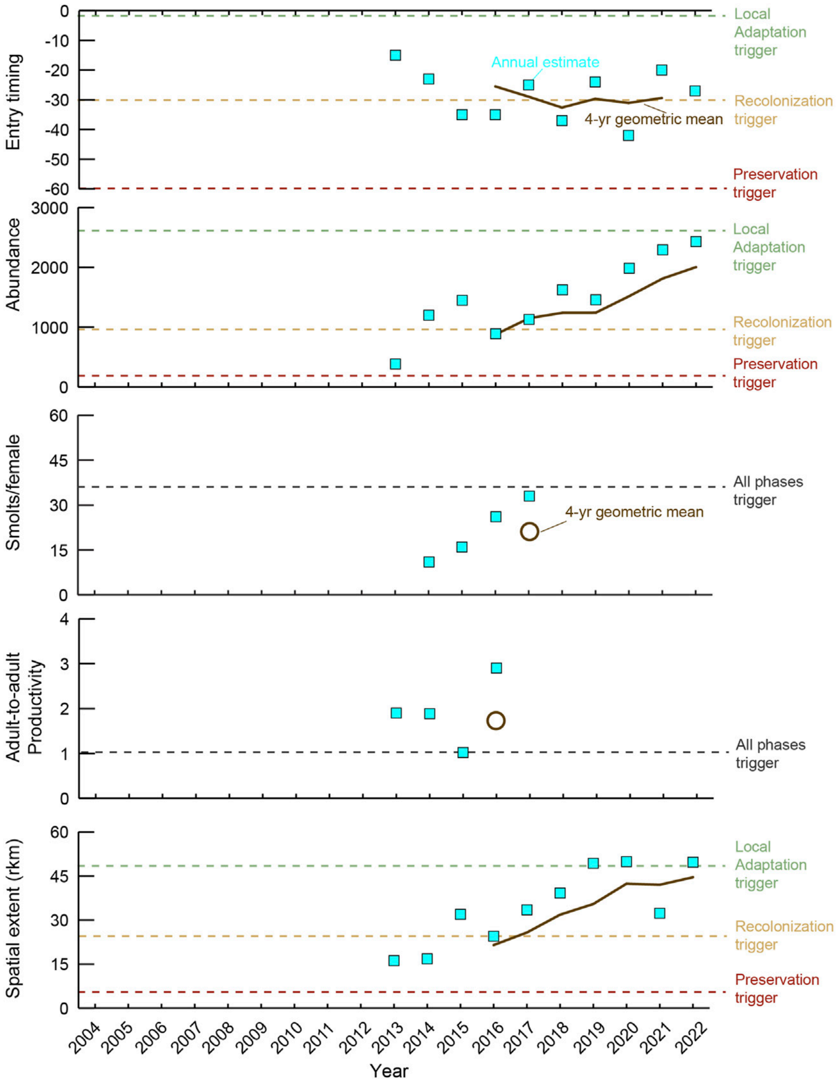

FIGURE 3
Quantitative assessment of performance indicators (entry timing, abundance, smolts per female, adult-to-adult productivity, and spatial extent) for steelhead trout (*Oncorhynchus mykiss*) in the Elwha River from 2004 to 2022. Time period includes data before (2004–2010), during (2011–2014), and after (2015–2022) dam removal. Dashed lines represent performance indicator "trigger values" that when exceeded (4-year geometric mean) for all performance indicators during the same year represent completion of the current recovery phase. Data from (Pess et al., 2024).

the complete removal of the Glines Canyon Dam in 2014, several species of anadromous fish were detected upstream of this site (Duda et al., 2021a), but data from a radio-telemetry study and spawning ground surveys in 2015 identified a fish passage barrier a short distance downstream of the Glines Canyon dam site. This prompted further investigation, which revealed that the barrier was the result of large boulders, likely portions of the canyon wall weakened during dam construction, falling into the channel shortly after dam removal was completed. In response, partnering federal agencies (National Marine Fisheries Service, Olympic National Park and the U.S. Army Corps of Engineers) conducted selective rock blasting to remove the boulders and reopen fish passage, which was completed by the autumn of 2016 (Ertle et al., 2019). The management action was successful in reestablishing fish passage upstream of Glines Canyon, with subsequent upstream detections and expanding spatial distribution of Chinook salmon and bull trout documented in 2016 and subsequent years (Duda et al., 2021b; Pess et al., 2024).

The second case of AM arising in the Elwha River EMAM project was adjusting the suite of performance indicators for steelhead trout. During the initial years of monitoring, during and following dam removal, insufficient numbers of steelhead trout smolts were captured and/or trap efficiency was too low to estimate entire basin steelhead trout smolt abundance in the mainstem, despite accurate estimates from two tributaries. The lack of data affected our ability to estimate the juvenile productivity performance indicator and to evaluate whether the trigger value had been met (Figure 3). Consequently, the interagency team recommended eliminating this performance indicator, a recommendation further informed by the observation that adult-to-adult productivity exceeded the trigger value throughout the monitoring period (Figure 3). The interagency team (i.e., stakeholders) concluded from adult productivity that the juvenile productivity trigger value had likely been exceeded. This recommendation has been evaluated for regulatory approval resulting in steelhead trout moving to the recolonization phase despite a lack of data to evaluate the juvenile productivity trigger, providing a prime example of AM.

The third example of AM actions was the hatchery production levels of steelhead trout. The removal of the juvenile productivity performance indicator from the EMAM for steelhead trout allowed steelhead trout to transition from the preservation phase to the recolonization phase of recovery. This led to management revisions in the spring of 2023 to reduce hatchery production of steelhead trout smolts from 175,000 to 30,000. This is an example of the goal of AM; using monitoring data to learn about a system and reduce uncertainty that results in updated management actions.

While the above are examples of successful implementation of AM principles, there were also missteps in application of AM for Elwha River Chinook salmon and steelhead trout. Differences existed in the timelines for development of the EMAM and drafting of the three BiOps for Chinook salmon and steelhead trout. As a result, draft values for performance indicators and triggers were incorporated into the BiOp (NMFS, 2012b), which were subsequently modified in the EMAM (Peters et al., 2014) (Supplementary Tables S2, S3). This conflict caused confusion among participants about which performance indicators and triggers should be used (Lower Elwha Klallam Tribe, 2011; Washington Department of Fish and Wildlife, 2012; Peters et al., 2014; NMFS, 2015). For example, the BiOp (NMFS, 2012b) list adult spawner escapement as natural-origin spawners, while the EMAM lists this as naturally spawning adults (i.e., hatchery- or natural-origin spawners). The EMAM was the final product of the scientists conducting the monitoring, yet it was not legally binding. NMFS has requested a memo to revise this language. However, the technical group has not reached consensus on all the trigger revisions for Chinook salmon and therefore have not submitted the memo, leaving this issue unresolved.

AM via the EMAM has also been hampered by some misguided performance indicators and triggers identified for the preservation phase. In retrospect, the established trigger values were too conservative in protecting fish from extirpation due to dam removal conditions. The river returned to levels where sediment levels were no longer a threat before the complete list of EMAM performance indicators could be assessed. Furthermore, performance indicators for river conditions directly impacted by dam removal, such as turbidity and channel stability, were not developed for the EMAM. This mismatch is highlighted by the recovery trajectory of Chinook salmon, which have fallen short of meeting the preservation phase triggers 10 years after dam removal (Figure 2). After about 4 years (2018), channel stability increased and turbidity no longer reached levels that were detrimental or lethal to fish (Magirl et al., 2015; East et al., 2018; Ritchie et al., 2018). Although Chinook salmon juvenile productivity has increased substantially in recent years, the adult productivity trigger value has not been met. Thus, despite reaching the overall conceptual goal for the preservation phase, Chinook salmon remain 'stuck' in the preservation phase, since adult-to-adult productivity did not exceed the trigger value during the last assessment, emphasizing the uncertainties of setting population benchmarks prior to a major, watershed-altering management action.

The issue of misguided performance indicators was recognized as early as 2017, and unsuccessful attempts to revise these triggers were made. The technical group developed draft performance indicators and triggers for Chinook salmon for the preservation phase. However, the technical group could not reach consensus on revised Chinook salmon performance indicators and triggers for the later recolonization and local adaptation phases. Thus, they have not submitted a request to the NMFS to revise the triggers in the BiOp. Since consensus could not be reached for Chinook salmon, no attempt was made to revise the performance indicators or triggers for steelhead trout.

Lessons learned from applying adaptive management principles to the Elwha River dam removal project

Like many others have found (e.g., (Keith et al., 2011; Runge et al., 2011; Williams and Brown, 2014; Roux et al., 2022), we experienced both successes and challenges in implementing AM. The adaptive monitoring component was successful, providing the data to understand the status and response of Chinook salmon and steelhead trout to dam removal and the role of hatchery-assisted protection and mitigation from short-term negative effects associated with dam removal. Given the unprecedented nature of Elwha dam removal, challenges in implementing the EMAM were expected; responding to these challenges would require both flexibility and a commitment to learning. Below, we discuss factors affecting successes and challenges in the context of lessons learned, including topics such as funding, leadership, communication and legal frameworks (i.e., ESA, BiOp, as implemented here) that others have consistently identified as essential for successful implementation of AM (Walters, 2007; Westgate et al., 2013; Dreiss et al., 2017; Edmondson and Fanning, 2022; Månsson et al., 2023).

Lessons learned about adaptive management

Lesson#1: salmonid recovery takes time, so choose performance indicators wisely

Ten years after dam removal, Chinook salmon and steelhead trout are still in the preservation (first phase) and recolonization (second phase) phases of recovery, respectively. Despite what is described as rapid recovery for steelhead trout by those monitoring this population, salmonid recovery takes time due to species-specific life history considerations such as age at maturity (i.e., 4 years for Elwha Chinook salmon and steelhead trout). However, this was also due to the performance indicators, triggers, and evaluation strategy initially selected requiring too much time before the first full evaluation could be completed. Therefore, performance indicators should be chosen that can be evaluated in as short of a timeframe as possible and be specific to the objectives for each recovery phase. This will allow progress to be assessed and hopefully observed more frequently throughout the AM program (Argent, 2009) to maintain momentum (i.e., progress). The EMAM included adult-to-adult productivity as a performance indicator for the preservation phase for both Chinook salmon and steelhead trout. Thus, the first potential progression from the preservation phase of recovery occurred 8 years (i.e., only two generations) after dam removal. However, the impacts from dam removal that raise concerns about the continued persistence of these two populations had largely subsided by this time (Warrick et al., 2015; East et al., 2018; Ritchie et al., 2018). In retrospect, the preservation phase should have been based on performance indicators with shorter evaluation periods that were more directly related to river conditions, allowing earlier evaluation and potentially more alternate management strategies that would have maintained observable progress through the recovery phases.

Lesson #2: adaptive monitoring requires dedicated funding

The monitoring component of the EMAM was very successful. In general, dedicated funding, a requirement for successful AM programs (Westgate et al., 2013; Newcomb et al., 2021; Edmondson and Fanning, 2022), allowed established teams to collect data to understand the status and response of Chinook salmon and steelhead trout to dam removal and hatchery production (Liermann et al., 2017; Munsch et al., 2023; Pess et al., 2024). Consistent and dedicated funding was made available for the project over 10 years by Olympic National Park to meet requirements in the BiOp (NMFS, 2012b). Although significant funding was provided, it was less than that requested for the program. In addition, no funding was provided after this 10-year period and the BiOP only addresses recovery through the recolonization phase. Thus, the future of the monitoring and AM program, which is necessary to determine when these two salmonid species have reached the local adaptation phase, is uncertain. Large projects requiring formal consultation or permit application could incorporate funding into legal documents to ensure dedicated funds are available (i.e., terms and conditions under Section 7, 10 of ESA, see Ruhl, 2004). Additional funding could be obtained by strategic and collaborative attempts to secure agency funding and/or agency staff dedicated to the program. The historic importance and visibility of the Elwha Dam removal project, coupled with the presence of species listed under the ESA, attracted funding support across a wide range of governmental, academic, and non-governmental organizations to conduct a variety of studies on the physical, biological, and ecological responses of the river and its freshwater and marine ecosystems (e.g., East et al., 2015; Ritchie et al., 2018; Brenkman et al., 2019; Duda et al., 2021a). We realize that the Elwha Dam removal project was unique in this regard, and future projects might not be able to attain funding to supply long-term data sets embedded within an AM framework. Yet, less than 10% of dam removals have been scientifically evaluated and most of these were of short duration or smaller dam removals (Bellmore et al., 2017). Thus, there is a scientific need for long-term evaluations of large dam removals. If funding is limited, attempting to implement an AM program would be more difficult and funding would be better spent implementing critical monitoring activities with an emphasis on data quality, since underfunded attempts to complete AM may be more costly over time to both financial and ecosystem resources (Rist et al., 2016).

In addition to understanding the response of Chinook salmon and steelhead trout to dam removal, the dedicated funds for monitoring enabled learning about unforeseen issues with fish passage and allowed collection of data for other species. One confirmed fish passage barrier, just downstream of former Glines Canyon Dam was identified and removed relatively quickly (Ertle et al., 2019). Finally, the monitoring program provided "value added" data for species and/or metrics that otherwise may not have been collected including key life history, abundance, and genetic information on coho (*O. kisutch*) (Liermann et al., 2017), chum (*O. keta*) and pink salmon (*O. gorbuscha*), Pacific lamprey (*Entosphenus tridentatus*) (Hess et al., 2021), bull trout (Quinn et al., 2017; Brenkman et al., 2019), and sockeye salmon (*O. nerka*) (Quinn et al., 2021).

Lesson #3: different species may progress through recovery phases at different rates

Steelhead trout recovery has progressed more rapidly than recovery of Chinook salmon. Except for the juvenile productivity trigger value, which could not be calculated due to an inability to capture enough steelhead trout smolts to estimate smolt abundance, all the steelhead trout performance indicators have exceeded the recolonization trigger values. Although three of the four Chinook salmon performance indicator triggers have exceeded the recolonization trigger values, the adult productivity trigger did not meet the preservation trigger value during the last assessment. Factors influencing the different trajectories observed in these two species may include spawning season and habitats, which likely favored steelhead trout (i.e., more tributary use), more influence of ocean fisheries on Chinook salmon returns, more limited hatchery intervention in the native-steelhead trout program, and the contribution of resident fish in the upper basin that likely contributed to steelhead trout recovery (Fraik et al., 2021; Pess et al., 2024).

The successes and challenges associated with revising the EMAM process appear to be related to the recovery rate of Chinook salmon and steelhead trout. Chinook salmon recovery lagged steelhead trout recovery. This difference may have led to the success/challenge by the interagency team in revising triggers associated with these species and submitting requests for changes to the NMFS resulting in the inability (for Chinook salmon) or ability (for steelhead trout) to revise performance indicators and/or triggers. This supports the recommendation by (Argent, 2009) to seek ways to observe progress and maintain momentum of the AM program. We did see progress in the AM process for steelhead trout, which led to adaptive management actions, whereas progress in the AM process for Chinook salmon stalled (i.e., inability to revise triggers).

Lesson #4: adaptive management requires clearly defined leadership

In contrast to the monitoring component, no funding was provided to fund a leadership position (and/or facilitator) to facilitate the adaptive implementation and evaluation components of the EMAM. Lacking directed funds, none of the agencies involved could afford to appoint someone to this leadership position, leaving the technical group to rely on several individuals to volunteer periodically (i.e., for annual meetings) to assume the 'leaders' role. This resulted in many of the challenges observed in implementing the EMAM. Strong and consistent leadership is a primary requirement for successful AM programs (Walters, 2007; Rist et al., 2016; Berkley and Beratan, 2021; Edmondson and Fanning, 2022). Lacking this steady leadership in the years following dam removal when monitoring from adaptive implementation was yielding actionable results, the EMAM suffered from a lack of communication among project partners, which negatively impacted collaboration, maintenance of common goals, and accurate implementation of selected management strategies. In addition, technical staff conducting the monitoring work were often not in decision making positions within regulatory agencies or the co-managers, which added another line of communication with regulatory and/or decision-making staff. Although significant learning occurred, that information has not been fully used to improve the adaptive evaluation component of the EMAM, including timely review and revision of performance indicators and associated triggers. Thus, an appointed leader to focus on continued communication and implementation of the adaptive evaluation component of an AM program would greatly enhance the AM success. The primary task would be communicating with participating agencies to ensure collaboration occurs to the extent possible, common goals are maintained, that issues identified through the AM process are addressed quickly, and that agreed upon management strategies are developed and implemented accurately. While there are no guarantees that having a dedicated leader would lead to success, it is hard to believe it would not have improved the situation since the group lacked a dedicated leader following dam removal. Although a decision charter would also solve these issues, this could not be accomplished in our case since it would be unlawful for the agencies involved to delegate their authorities.

A primary task of someone leading an AM program is goal setting, which itself is a primary activity identified in AM. Numerous authors recommend that all participants engage in this activity in a structured manner (Allen et al., 2001; Gregory and Long, 2009; Westgate et al., 2013; Berkley and Beratan, 2021; Edmondson and Fanning, 2022; Bamzai-Dodson et al., 2023). The value of common goals and the impacts of not maintaining/revising goals over time was highlighted while attempting to implement the EMAM. One individual led the planning and early implementation of this project, with a common goal existing throughout: remove the dams and develop a strategy to monitor and learn how fish respond to dam removal so that restoration actions beyond dam removal could be adjusted as needed. This common goal led to significant planning that resulted in the documents supporting dam removal (Department of the Interior et al., 1994; Department of the Interior, 1995; Department of the Interior, 1996) the fish restoration plan (Ward et al., 2008), and the EMAM (Peters et al., 2014). The common goal of learning has sustained an effective and collaborative monitoring program throughout the process, despite the lack of a single leader after the initial leader retired. However, divergent management goals and expectations among project partners developed after dam removal and with staff turnover at various agencies, leading to the emergence of different strategies for increasing Chinook salmon recolonization of the upper watershed. For example, the failure of Chinook salmon to consistently reach the upper watershed led to proposals to move adult Chinook salmon into the upper watershed (via helicopter). However, this view was not supported by all the technical team members and remains a point of contention. These divergent goals, expectations, and strategies impacted our ability to revise performance indicators and triggers for the recolonization phase for Chinook salmon, since no consensus could be reached. The group could not even agree upon a method for developing a distribution trigger value for Chinook salmon. As a result, Chinook salmon remain "stuck" in the preservation phase of recovery, although the consensus opinion among biologists involved in the project was that the lethal risk due to dam removal activities no longer exist. A primary leader or trained facilitator to facilitate communication and collaboration is necessary to maintain discussions that could result in the maintenance of common goals (Ebberts et al., 2018; Berkley and Beratan, 2021). It must also be recognized that the goals will evolve as projects progress and more information is obtained about the system being managed. Thus, the AM leader should maintain goal setting, regular review, and revision as a primary objective.

Lesson #5: how to adaptively manage within legal frameworks

The legal framework imposed by the ESA, as implemented in this project, put some constraints on the EMAM process. This resulted from the overall legal process and the lack of understanding of the process among managers and researchers. Managers and researchers did not understand the processes (i.e., re-consultation under ESA) required if the management options changed from those evaluated in the BiOp (e.g., hatchery production alterations not described in the initial BiOp). These issues occurred in the planning and design phase of the EMAM and proved to be problematic later. The issues with the design stem from incongruence between guidance and regulatory documents described above and a lack of diversity in management options (i.e., generally maximum on-station releases of hatchery fish). Our lesson learned was to maintain a consistent schedule and coordination among all guiding documents, to the extent possible. For the Elwha River, the only clear resolution to the current incongruence is to re-initiate the ESA consultation process, which has not been a popular choice. This is due, in part, to the litigious environment regarding the use of hatcheries in Elwha River recovery. Although the lack of flexibility resulting from how the ESA framework was implemented in this project was an impediment, it does not have to be the case for all projects. The ESA was implemented to protect listed species from the environmental impacts of dam removal and resulting use of hatcheries to protect and restore Chinook salmon and steelhead trout. In other cases, such as species reintroductions, there are several provisions that provide flexibility under ESA (Dunham et al., 2016).

Another issue imposed by the legal framework was the lack of diverse management options. Although we followed recommendations to include AM within legal frameworks (Ruhl, 2004; Garmestani et al., 2009), we did not understand how this could be done effectively under the ESA framework. Thus, only hatchery management, with varying levels of production for specific recovery phases were incorporated into the BiOp (NMFS, 2012b). This was partially due to the long planning period for dam removal in the Elwha. The management options (i.e., hatchery intervention) were largely laid out in the environmental impact statement process (Department of the Interior et al., 1994; Department of the Interior, 1995; Department of the Interior, 1996; Department of the Interior, 2005) completed one to two decades before the development of the EMAM. In addition, to improve the likelihood of understanding factors influencing progression, the EMAM authors reduced the management options listed in the Elwha fisheries recovery plan (Ward et al., 2008). As a result, maximum on-station hatchery production was listed in the EMAM as the priority management option during the preservation phase even though the Elwha fisheries recovery plan and ESA documents list additional management strategies that could have been employed. For example, fish relocation was listed in the Elwha fisheries recovery plan and ESA documents and was completed for steelhead trout and Chinook salmon (Pess et al., 2024). The EMAM suggested prioritization of a reduced number of alternative strategies to improve learning associated with monitoring. Including more management options for the preservation and recolonization phases within the ESA framework, such as a range of hatchery production given different levels of turbidity and/or natural production, or triggers to initiate fish relocation, would have provided more flexibility during the early phases of recovery. We still recommend incorporating AM into the ESA framework, when possible, since this approach has been successfully applied elsewhere (Ebberts et al., 2018). Incorporating the EMAM into the legal documents also provided the framework to monitor and adaptively manage recovery. However, some revisions to the process used for the EMAM are recommended, particularly the inclusion of multiple management options within each recovery phase.

Careful consideration is necessary to incorporate the flexibility essential for AM into legal documents (i.e., ESA), which requires clear and concise language and lengthy review. Incorporating AM into legal documents requires defining all potential management options using a phased approach for implementing these options (McDonald and Styles, 2014) and triggers in order to progress through recovery phases (Nie and Schultz, 2012; Kingsford et al., 2021). Although this was completed for the EMAM, the steps between recovery phases were too long, and in some cases included too many or flawed performance indicators. We originally identified four viable salmonid population performance indicators for the preservation phase. In retrospect, this could have been reduced to three, including distribution, natural produced smolts, and hatchery produced smolts. Revised triggers were proposed for Chinook salmon for the preservation phase but were not formally submitted to the NMFS for review, due to failed attempts to reach agreement on revised recolonization triggers. The proposed preservation phase revisions essentially ensure Chinook salmon migrate upstream of the former dams and that both natural and hatchery-origin smolts are produced in sufficient numbers to prevent extinction of the population. Successfully meeting triggers for these performance indicators would indicate that river conditions have improved to the point where natural production is occurring and extirpation due to dam removal is no longer a threat. These revised triggers were an attempt to adjust trigger values for the preservation phase and incorporate smaller steps and/or alternatives within each recovery phase, thereby allowing adaptation within a phase that would likely maintain progress and momentum (Argent, 2009).

Lesson #6: incorporate both physical and biological performance indicators

One limitation of the EMAM was the lack of monitoring specific to physical habitat and sediment, although these factors were a specific concern with respect to lethal conditions for fish during and immediately following dam removal. Turbidity, aggradation, and channel form monitoring occurred largely due to the requirement to maintain the City of Port Angeles domestic and industrial water supply (East et al., 2015; Magirl et al., 2015; Warrick et al., 2015; Ritchie et al., 2018). Physical monitoring was included in the EMAM to interpret recovery progress as observed but did not serve as performance indicators. In retrospect, performance indicators and associated triggers for physical variables including major habitat features, particularly at former dam sites, should have been included in the preservation phase since they are causally linked to the proposed performance indicators such as fish distribution and survival. Although this was lacking in the EMAM, fish passage was included in BiOps from the U.S. Fish and Wildlife Service and National Oceanic and Atmospheric Association covering dam removal (Crain and Brenkman, 2010; Olympic National Park, 2013) and the EMAM (Peters et al., 2014), while turbidity and geomorphic monitoring were identified within the sediment management plan (Bountry et al., 2018). Within the EMAM, viable salmonid population metrics served as proxies for physical monitoring and successfully identified a barrier (i.e., Ertle et al., 2019); however, the EMAM would have benefited from more direct inclusion of physical variables as performance indicators.

The EMAM recommended that the first assessment of trigger values and associated assumptions occur 8 years into recovery. This recommendation allowed for two full generations of Chinook salmon and steelhead trout to be completed prior to the assessment. In retrospect, the first assessment should have occurred sooner (i.e., 2–4 years) to better understand their utility for evaluating the rate of recovery. This likely would have increased the likelihood of identifying issues and successful revision of triggers that stalled progress through the AM process.

Lesson #7: AM provided monitoring benefits but management revisions were easier for non-AM species

In the Elwha case study, the EMAM was designed specifically for Chinook salmon and steelhead trout and was required under ESA. However, it did not address other key fish species including bull trout, eulachon, sockeye salmon, coho salmon, chum salmon, and pink salmon. Of the species not addressed in the EMAM, hatchery intervention occurred for coho salmon, chum salmon (intermittently), and odd-year pink salmon (2 cycles only). However, management actions have been taken to benefit species addressed and not addressed by the EMAM. Thus, the progression of these different fish species through recovery offers an opportunity to compare monitoring data collected and associated changes in management through recovery. The amount of data collected and corresponding links to management varied among EMAM (legal requirements) and non-EMAM (no legal requirements) covered species. Although significant information was collected for non-EMAM covered species (e.g., coho salmon: (Liermann et al., 2017; Munsch et al., 2023); bull trout: (Quinn et al., 2017; Brenkman et al., 2019; Duda et al., 2021a, 2021b), only coho salmon have similar amounts of monitoring data collected as seen in EMAM covered species. However, much of the data for non-EMAM covered species was largely collected opportunistically during work focused on Chinook salmon and steelhead trout. The exception to this is fish passage data collected for bull trout (BiOp requirement) (NMFS, 2012a) and the recent addition of adult abundance estimates for coho salmon based on SONAR. Management actions taken in response to monitoring data also varied among EMAM and non-EMAM covered species. For EMAM covered species, the only management change has been reduced hatchery production for steelhead trout implemented in 2023. Rock blasting to restore passage through the 2014 rockfall in Glines Canyon benefitted both EMAM and non-EMAM covered species but was initiated in response to monitoring related to Chinook salmon (EMAM) and bull trout (non-EMAM, but FWS required monitoring) (Ertle et al., 2019). For non-EMAM covered species, management changes have been suggested (coho salmon) or made (coho and pink salmon) based on information gained. Recommendations were forwarded that adult hatchery coho relocation upstream of former Elwha dam were no long necessary every year (Mchenry et al., 2022), a ceremonial and subsistence fishery for coho salmon conducted by the Lower Elwha Klallam Tribe occurred during the fall of 2023, and the pink salmon captive brood program was terminated. Thus, when data were collected for non-EMAM covered species, the information was used to revise management strategies despite the lack of a formal AM program. These management changes were also much easier to complete than those described in the EMAM that were bound by regulatory/legal frameworks resulting from their listing under ESA.

Conclusion

Although few successes of AM are reported in the literature (Runge et al., 2011; Westgate et al., 2013; Gillson et al., 2019; Edmondson and Fanning, 2022; Månsson et al., 2023), the framework is still believed to be better than alternative management paradigms such as *ad hoc*, wait-and-see, and steady state (Westgate et al., 2013). AM has been implemented for decades for numerous natural resource disciplines (Walters, 2007; Wineland et al., 2022; Bradford et al., 2023) and at various scales (Roux and Foxcroft, 2011; Melis et al., 2015). Numerous pitfalls and factors have been identified that lead to success and failure of AM programs (Walters, 2007; Williams and Brown, 2014), including the lack of retrospective analysis of implemented AM programs (Roux et al., 2022). By examining the AM program implemented for the removal of two Elwha River dams and associated hatchery intervention for the recovery of two fish species listed under the ESA, we have been able to identify factors leading to successes and challenges and provide recommendations to facilitate the successful implementation of future AM programs. Many of the factors leading to success and failure were similar to prior AM case studies. Funding was the most important factor leading to learning through a well designed and implemented monitoring program. The lack of a leadership position likely impacted the AM process by reducing communication, collaboration, and maintenance of common goals. The inflexibility of the ESA framework, as implemented, along with manager and researcher lack of knowledge of this framework and the lack of management options incorporated into guiding legal documents (i.e., environmental impact statement process), limited the flexibility of the AM program. This impact could have potentially been minimized by incorporating more management options into the BiOp analysis. The rate of recovery also appeared to influence participants' willingness to revise performance indicator triggers. To improve the likelihood of success, monitoring should be completed, and a leadership position should be established to shepherd the AM process through communication, collaboration, and maintenance of common goals. Finally, flexibility within the AM process should be maintained by identifying small attainable steps for the AM process that will require management actions that maintain momentum.

BOX 1 Understanding goals, values and backgrounds for effective collaboration.

Our experience adaptively managing Elwha River Chinook salmon and steelhead trout emphasizes the importance of recognizing the different goals, values and backgrounds of Federal, State, and Tribal governments, their agencies, and their representatives collaborating on a large-scale restoration project. Recognizing different perspectives helps explain situations where two professionals offer divergent opinions at a given decision point. Even further, an understanding and sincere effort to "put yourself in another's shoes" helps create a path toward finding common ground. Here we describe the diversity of goals, values and backgrounds in our Elwha working group, to help illustrate the challenges and critical importance of working collaboratively.

Our working group had a shared goal of restoring the health of the Elwha River ecosystem and increasing the abundance, productivity, and life history diversity of its fish populations. Individuals also had more focused goals aligned with agency and job responsibilities. Some were directly involved in the administration of dam removal and thus had a goal to manage the project to meet expectations and fulfill legal obligations. Others had a goal for dam removal to provide long-term sustainable fishing opportunities as a food source and cultural experience for local communities. Still others in the group were compelled to learn how the ecosystem and fish populations respond to dam removal to select, inform, and implement restoration projects elsewhere more effectively. Most everyone in the group identified with these various goals at some level, but individuals varied substantially in the extent to which they directly pursued them.

Divergent opinions on a given topic could often be traced to different value systems. One common source of debate was a spectrum of willingness for management intervention to support or accelerate fish reoccupying areas upstream of the former dams. We experienced divergent opinions over transplanting adult salmon to upstream areas with few salmon once water turbidity returned to pre-removal levels. Some felt that this action could only help recovery, with minimal risk if transplanted fish did not accelerate spatial expansion. Others emphasized the importance of fish expressing natural patterns of expansion past the former dams, allowing key ecological and evolutionary processes (e.g., habitat selection, life history diversity) to occur on a pathway towards the long-term sustainability of recovery. Our working group also had different views on the urgency of observing a fish response to dam removal. Some sought to observe shorter term increases in population status, whereas others expressed a willingness to wait longer. Often these differences were tied to professional roles and responsibilities, and the degree to which individuals were responsible for natural resources experiences in the communities they lead or represented.

A range of backgrounds in aquatic ecology, fish, and fisheries management were represented in our group. Some had extensive experience leading monitoring projects using a variety of methods. Our group also included leaders responsible for multiple natural resource management activities beyond Elwha dam removal, including managing lands, fishery harvest, and salmon recovery programs. For some, Elwha was one of many responsibilities, and they brought experiences from other watersheds elsewhere in Washington State and beyond. For others, most of their professional work was conducted in the Elwha watershed and adjacent aquatic systems on the North Olympic Peninsula. Some individuals were closer to regulatory requirements and legal obligations, some were involved in scholarly pursuits related to dam removal outcomes, whereas others were closer to day-to-day activities like monitoring in the Elwha River or producing fish in two hatcheries.

In summary, our group was most effective when we had open and regular lines of communication, which fostered the ability to learn from others doing different work and empathize with reasons behind divergent viewpoints. This was not always easy, and sometimes extended conversations were needed to reach mutual understanding. We did not always reach consensus or agreement on important issues. This may be due, in part, to the fact that we did not have a professional facilitator to lead our discussion. However, a shared respect for the relationships in our working group and sincerity in listening to alternative viewpoints laid the foundation for a healthy, productive collaboration.

Data availability statement

The datasets presented in this study can be found in an online repository at https://ecos.fws.gov/ServCat/Reference/Profile/163653.

Ethics statement

The animal study was approved by Washington Department of Fish and Wildlife sampling permits, U.S. Fish and Wildlife Service and National Marine Fisheries Service ESA sampling permits. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

RP: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. JA: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing–original draft, Writing–review and editing. JD: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. MM: Supervision, Validation, Writing–review and editing, Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources. GP: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing–review and editing. SB: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing–review and editing. JJ: Formal Analysis, Validation, Writing–original draft, Writing–review and editing. ML: Data curation, Formal Analysis, Investigation, Methodology, Writing–review and editing. KD: Data curation, Formal Analysis, Investigation, Methodology, Validation, Writing–review and editing. MB: Supervision, Writing–review and editing. PC: Funding acquisition, Project administration, Resources, Supervision, Writing–review and editing. HC: Data curation, Writing–review and 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 Klallam Tribe to collect data used in this study (SONAR).

The remaining authors declare that the research 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/fenvs.2024.1291265/full#supplementary-material

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Patterns, drivers, and a predictive model of dam removal cost in the United States

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Given the burgeoning dam removal movement and the large number of dams approaching obsolescence in the United States, cost estimating data and tools are needed for dam removal prioritization, planning, and execution. We used the list of removed dams compiled by American Rivers to search for publicly available reported costs for dam removal projects. Total cost information could include component costs related to project planning, dam deconstruction, monitoring, and several categories of mitigation activities. We compiled reported costs from 455 unique sources for 668 dams removed in the United States from 1965 to 2020. The dam removals occurred within 571 unique projects involving 1–18 dams. When adjusted for inflation into 2020 USD, cost of these projects totaled \$1.522 billion, with per-dam costs ranging from \$1 thousand (k) to \$268.8 million (M). The median cost for dam removals was \$157k, \$823k, and \$6.2M for dams that were< 5 m, between 5–10 m, and > 10 m in height, respectively. Geographic differences in total costs showed that northern states in general, and the Pacific Northwest in particular, spent the most on dam removal. The Midwest and the Northeast spent proportionally more on removal of dams less than 5 m in height, whereas the Northwest and Southwest spent the most on larger dam removals > 10 m tall. We used stochastic gradient boosting with quantile regression to model dam removal cost against potential predictor variables including dam characteristics (dam height and material), hydrography (average annual discharge and drainage area), project complexity (inferred from construction and sediment management, mitigation, and post-removal cost drivers), and geographic region. Dam height, annual average discharge at the dam site, and project complexity were the predominant drivers of removal cost. The final model had an R^2 of 57% and when applied to a test dataset model predictions had a root mean squared error of \$5.09M and a mean absolute error of \$1.45M, indicating its potential utility to predict estimated costs of dam removal. We developed a R shiny application for estimating dam removal costs using customized model inputs for exploratory analyses and potential dam removal planning.

KEYWORDS

dam removal, cost drivers, economics, river restoration, cost engineering

1 Introduction

Since the mid-20th century, the United States has been transitioning from a period of building dams to one focused on managing this aging infrastructure in the context of economic development, public safety, and environmental objectives (Juracek, 2015; McKay et al., 2020; Vahedifard et al., 2021). There are several factors contributing to this transition. With over 91,000 dams greater than 2 m in height in the national inventory (NID) (U.S. Army Corps of Engineers, 2023) and many times that number of smaller dams, many of the best dam sites have already been used. There is an increasing awareness of the impacts that dams have on freshwater and riparian ecosystems by decreasing aquatic biodiversity (Naiman et al., 2005; Collen et al., 2014; Reid et al., 2019), disrupting the lifecycles of migratory animals (Barbarossa et al., 2020; Waldman and Quinn, 2022), and changing natural temperature, sediment, and flow regimes (Bunn and Arthington, 2002; Poff and Zimmerman, 2010). At the same time, a portfolio of aging dams has created a need to reassess the demand for this infrastructure (Doyle et al., 2008). Some dams were built in a bygone era and no longer serve modern purposes. Others represent safety hazards, including low-head dams with downstream hydraulics that present drowning hazards to boaters and swimmers (Hotchkiss and Kern, 2023). Additional candidates for removal include older dams that need structural repair, are facing increasing operations and maintenance costs, or require expensive investments in mitigation for their negative environmental consequences. Severe reservoir sedimentation, a situation expected to increase in the future (Randle et al., 2021), may also lead to dam removal if the reservoir benefits are lost and only liabilities remain. With the growing opportunities to remove dams and reverse environmental degradation, dam removal has become a growing sector in the emerging restoration economy (Bernhardt et al., 2005; BenDor et al., 2015), with the requisite expertise to remove dams broadly expanding. This intersecting set of interests has led to the growth of dam removal in the United States and abroad as a method for both managing aging infrastructure and restoring ecosystems (Doyle et al., 2008; O'Connor et al., 2015; Foley et al., 2017; Habel et al., 2020).

Reliable estimates of dam removal project costs are important because unrealistic estimates can lead to elimination of dam removal as a feasible alternative, distrust among the public and affected parties, and delayed or derailed projects. Furthermore, dam removal cost estimates can be useful as decision criteria in strategic dam removal planning, particularly when a portfolio of dams are being evaluated. Although several decision-support tools for barrier removal planning exist (Branco et al., 2014; Hoenke et al., 2014; McKay et al., 2017; Guetz et al., 2022), the predicted costs of dam removals are rarely factored into prioritization exercises (Doyle et al., 2003). The incorporation of cost can enhance strategic barrier management planning which in turn can deliver and align economic and socio-ecological benefits (Zheng and Hobbs, 2013; Roy et al., 2018).

Estimating the costs of decommissioning and removing dams is a challenge, which makes it difficult to understand where dam removal may be a viable alternative to maintaining aging or problematic dams. A key difficulty is the wide range of factors that can affect price, along with limited and variable completeness of publicly available data to understand the impact of each factor on total cost. These factors can include the size of the dam and its impoundment, geographic setting (e.g., rural versus urban), the volume of stored sediment and its degree of contamination, the presence of sensitive species or infrastructure, requirements for post-removal site restoration (e.g., stabilization, revegetation), inherent regional differences (in permitting requirements, history of dam removal), needs to replace the function of the dam, and socio-economic dimensions (Born et al., 1998; Duda and Bellmore, 2022).

Cost estimation for civil infrastructure is commonly based on design-bid-build contracts, where the client hires the engineer and contractor under separate contracts and bids are based on unit prices, or how much time and material are required to complete specific tasks (e.g., Shrestha et al., 2012). The methods for unit price cost estimation are well established and include annually published manuals on rates (Mubarak, 2016) for typical cost components (e.g., mobilization/demobilization of heavy equipment, concrete, or electrician vs. common laborer). On the other hand, dam removals can be subject to substantial uncertainties, ranging from discovery of unknown structures or contaminated materials to unexpected high flows that erode coffer dams or result in exceeding water quality limits. As a result, more complex dam removals may be contracted as design-build projects in which the construction contractor maintains ownership of the process from start to finish, and typically bills for the whole project (i.e., fixed sum or guaranteed maximum price), rather than by unit prices. Design-build contracting is more common with complex, large projects that are subject to greater uncertainty, and these contracts tend to avoid change orders that occur with the discovery of some unexpected issue that can substantially impact project budget and timeline. (Park and Kwak, 2017). For design-build with a guaranteed max price, the contractor factors in uncertainty at the beginning based on their experience and knowledge of the project, and is the main reason these projects need a highly qualified design-build team. Further, design-build is often utilized to increase efficiency and get the contractor up to speed with the project faster because they are involved from day one. The continuity in leadership across the project, from start to finish, contrasts with design-bid-build, which can involve multiple contractors and limited oversight by the design engineer. Design-build with fixed sum contracting can result in better outcomes for complex projects but is also associated with some resistance among dam owners, consulting firms, and contractors to share their detailed cost data.

In addition to decommissioning surprises and paucity of publicly available data on project cost, dam removal can involve mitigation requirements that influence cost estimation. Many projects require restoration of the former reservoir footprint and/or other additional costs (e.g., movement or replacement of water intakes and treatment plants, fish hatcheries, drinking water wells) that often are not required with classic civil infrastructure projects (Winter and Crain, 2008; Bountry et al., 2013; Tullos et al., 2016; Duda and Bellmore, 2022). While the cost of site restoration actions and project add-ons can be estimated with unit-cost estimation methods, it can be hard to predict the scope and scale of these activities until the engineering reaches later design milestones. Thus, although removing dams often involves more than structural removal, it can be difficult to generalize the scope and scale of additional site-specific project components, particularly in early project planning stages.

With this paper we: (1) describe the compilation of a dam removal cost database (Duda et al., 2023) that includes cost drivers pertaining to sediment management, mitigation, and post-removal actions for completed projects in the United States; (2) contextualize the biogeographic trends and drivers of dam removal costs by creating common linkages with existing databases (i.e., the American Rivers Dam Removal Database, the Dam Removal Information Portal, and the National Hydrography Dataset Plus Version 2.1); (3) develop a predictive machine learning model to estimate the planning level cost of dam removal projects based on dam characteristics and prominent cost drivers, which is further packaged as an interactive and exploratory Shiny application for cost prediction (https://wrises.shinyapps.io/DamRemovalCostPredictiveModel/), and (4) conclude with a discussion of a detailed case study database (Tullos and Bountry, 2023) containing component-wise breakdowns of cost estimates to highlight the nuances and limitations entailed in cost estimation.

2 Methods

2.1 Compiling the dam removal cost database

We used the dams listed in the American Rivers dam removal database (versions 1–8; American Rivers, 2023) to search for dam removal cost estimates for inclusion in a dam removal cost database (Duda et al., 2023). For each dam, we used the search string, “dam name + removal + cost” or “river name + dam removal + cost” in the Google search engine to identify sources of project-specific cost information. Any source information that contained a cost estimate was reviewed and retained. Types of source material included technical reports, journal articles, websites, news articles, government documents, and blog posts. If no results were found after the initial search, we used contact information to request project cost from practitioners or project managers.

Once a source was identified as reporting the cost of a dam removal project, we extracted several pieces of information. First, we documented bibliographic information within a Zotero database including the type of source, the URL location, title, author, and year of publication. A screen image of the reported cost from the source material was saved as documentary evidence in case the URL became invalid or lost due to link-rot (Duda and Camp, 2008). Although most sources contained a reported cost for a single dam removal, some included a combined cost representing several dam removals (e.g., Aadland, 2010). When a cost estimate pertained to multi-dam removal projects, it was grouped under a unique identifier in the database to distinguish these cases and avoid double counting. When multi-dam removal projects contained a single reported cost for “n” number of dams, we used the proportional height of each dam “i” to partition the costs according to the size of each dam using the following equation:

$$Costdam_i = Combined\ \ Cost \cdot \frac{Dam\ height_i}{\sum_{i=1}^{n} Dam\ height} \tag{1}$$

2.1.1 Identifying potential cost drivers

Apart from the reported cost, we reviewed available source material and data sources to collate information on the characteristics and cost drivers of each dam removal project. We searched for any mention of why the dam was being removed, which typically fell into the categories of safety, river or ecosystem restoration, economics (e.g., it was more cost effective to remove the dam than conduct repairs, continue maintenance, or provide upgrades), or “other”. Next, we identified the presence of any cost drivers noted in the documentation of the dam removal. A total of 28 different cost drivers were identified and categorized into activities related to construction and sediment management, mitigation, and post-removal outcomes. *Construction and sediment* cost drivers (n = 6) related to whether: coffer dams or other site dewatering activities were needed; reservoir sediments were contaminated or not; river erosion or mechanical removal was used for sediment mobilization; sediment stabilization was required; and the use of a pilot channel through delta deposits was used. *Mitigation* cost drivers (n = 11) were related to activities needed to minimize the effects of dam removal, including: construction or enhancement of river habitat features; replacing or protecting water supply infrastructure; protecting levees or riverbanks; mitigating flood risk via property purchases; protecting or constructing bridges; protecting or constructing a fish hatchery; or protecting roads or wells. The *post-removal* cost driver category (n = 11) included: reshaping reservoir or downstream topography; revegetation; control of invasive species; fish passage; monitoring;

installation of stability berms or retaining walls; burial or removal of structures for safety; relocation or protection of utilities; creation of access roads; and installation of interpretive displays.

2.1.2 Compiling data describing dam and watershed characteristics

Next, we connected the dams with a reported cost to the Dam Removal Information Portal (DRIP) (https://data.usgs.gov/drip-dashboard; Wieferich et al., 2021) using the American Rivers identifier "AR_ID" for each dam. The DRIP tool has existing connections to the USGS Dam Removal Science Database (Duda et al., 2018) and the National Hydrography Dataset Plus version 2.1 (NHDPlus V2.1; Brakebill et al., 2020), allowing for access to additional dam and watershed characteristics including geospatial (latitude, longitude) and demographic information (height, length, construction material). Linkage to the NHDPlus V2.1 provided information about Strahler stream order (Strahler, 1957), drainage area upstream of the dam (km^2), and average annual stream flow (m^3/s). Some dams lacked available height and/or length information from any source. For dams that were missing length information ($n = 634$), we estimated the length of the dam using publicly available aerial imagery, distance rulers available in Google Earth Pro (version 7.3.4), and multiple measurements (2 or 3 depending on accuracy) by the same observer. However, only 298 dams had clear imagery of the entire channel both before and after the dam removal, thus allowing us to estimate the length of the dam. The other dams had channels that were obstructed, usually by canopy, making measurement impossible. For dams missing height information, project photos were used to determine whether the dam could be placed into the smallest height category (< 5 m) based on recognized scaling features (e.g., a human, a street sign) in the image ($n = 34$). If no such scaling was available, the dam was placed into the unknown height category ($n = 19$).

2.1.3 Indexing cost for inflation

We located a reported cost for dams that were removed during the period from 1965 to 2020. To adjust historical dam removal costs to their equivalent value in 2020 U.S. dollars (USD), we used the RS Means building construction cost index (Mubarak, 2016). RS Means is a widely used index that tracks changes in construction costs over time and was deemed more appropriate to estimate temporal dam decommissioning cost trends than other inflation indices (e.g., Consumer Price Index). Using 1992 as the base year (i.e., 100), the index ranged from 21.7 in 1965 to 234.6 in 2020. Price in 2020 USD for a dam removed in year i was calculated with the following equation:

$$Cost \ \ in \ \ 2020 = Cost_i \ \ x \ \ \frac{RS \ \ Means \ \ Index_{2020}}{RS \ \ Means \ \ Index_i} \tag{2}$$

2.2 Building the predictive cost model

2.2.1 Data preprocessing

We calculated a project complexity score as the sum number of cost drivers associated with construction and sediment management, mitigation, and post-removal actions. We then re-scaled the total score to a value between 0 and 1, where larger values corresponded to higher project complexity. Dam material, often listed as a combination of materials, was coded into one of three categories based on material durability: (i) concrete, masonry, and/or steel; (ii) wood and/or sheet piling; (iii) combination of both. The categorical variable of region (five categories) was one-hot encoded to dummy variables.

The dataset was also examined for data completeness. While a reported cost was available for every dam, dam height and length were missing for 56 and 335 records, respectively. For entries with missing height data that corresponded to a height category of "less than 5m" ($n = 34$), missing heights were imputed based on the median height of dams within the same height category (i.e., 2.1 m). The variables of dam length and age were excluded from model building due to a high proportion of missing data. To minimize model error associated with inherent variation in costs across states, dam removal costs were adjusted to a common-state standard using 2020 state cost adjustment factors developed by the United States Army Corps of Engineers (U.S. Army Corps of Engineers, 2022a). Since most dam removals have occurred in the state of Pennsylvania, all dam removal costs were computed to Pennsylvania standards based on individual state-based adjustment factors (see Supplementary Appendix A). This adjustment does not influence model results, but instead accounts for a non-informative source of cost variation in the model. To avoid model overfitting, the data was partitioned into training (80%, $n = 536$) and testing (20%, $n = 132$) data sets for model building and evaluation, respectively, using the "*createDataPartition*" function from the *carat* package (Kuhn et al., 2022) in R 3.03 (R Core Team, 2022). This function splits the data using random sampling while preserving the overall distribution of the data. The resultant split was also visually examined to make sure that test and train data points were distributed across dam removal cost and dam height ranges present in the database.

2.2.2 Data analysis

We modelled natural log-transformed cost data against six predictor variables shown in exploratory analyses to influence cost – dam height (m), average annual discharge (m^3/s), drainage area (km^2), project complexity, dam material, and region (one hot-encoded as five variables). We analyzed the relationships between dam removal costs and various predictor variables using stochastic gradient boosting (SGB; Friedman, 2002) with quantile regression, together called gradient boosted quantile regressions (GBQR). SGBs are a machine learning technique in which an ensemble of shallow and weak trees is successively built such that the performance of each tree is boosted by improving on the errors (residuals) of the preceding tree (Friedman, 2002). Unlike conventional regression trees that fit a single parsimonious model, SGBs incorporate the advantages of regression trees (i.e., handling mixed data types and missing data) while overcoming some of their limitations like poor predictive performance, lack of optimal tree structure, and high sensitivity to small changes in the data set (Elith et al., 2008). At each iteration, a tree is built from a random sub-sample of the dataset which incrementally improves model prediction accuracy while preventing over-fitting of the data. An advantage of the method is that predictor variables do not need to be transformed prior to analysis, since SGBs can fit non-linear relationships. Additionally, interactions between predictors do not need to be specified *a priori* (Elith et al., 2008).

To minimize overfitting, models were built based on a repeated 20-fold cross validation of the training data. We constructed GBQR models using the *caret* package using the following settings: interaction depth (i.e., tree complexity, which determines the maximum possible interactions) was set to 4 nodes; shrinkage (which controls the learning rate of the algorithm) was set to 0.002; iterations (or number of trees) was set to 5000; and the minimum number of observations in a node to commence splitting was 10. Finally, the bagging fraction, which controls the fraction of the training data randomly selected to build each tree was set at 0.7. To account for the uncertainties associated with cost predictions, we obtained median point predictions along with 50% and 95% prediction intervals by setting alpha values of 0.5, 0.25, 0.75, 0.025, and 0.975, respectively.

We created variable importance plots to visualize the relative importance of different predictor variables. Computed as the sum of squared improvements in error by each variable averaged over all trees (Hastie et al., 2001), the relative importance value of the most important predictor is assigned a value of 100 and the value of other variables are scaled proportionately. To examine the relationship between cost and each predictor variable, partial dependence plots (PDP) were constructed. We examined model performance using the relationship between the actual and predicted costs for the test dataset based on three metrics: the coefficient of determination or r^2; mean absolute error (MAE); and root mean squared error (RMSE).

The GBQR models were also integrated into a Shiny application to create an exploratory dam removal cost prediction tool, accessible at https://wrises.shinyapps.io/DamRemovalCostPredictiveModel/. The R code for model development and shiny application creation can be accessed via a GitHub repository (https://github.com/USACE-WRISES/DamRemovalCostModel).

2.3 Detailed cost for case studies

We compiled a second database containing detailed cost breakdowns of 15 individual dam removal projects (Tullos and Bountry, 2023). Projects were identified based on personal contacts with consultants working on dam removals, who then recommended additional contacts (i.e., snowball sampling). Detailed costs were acquired from bid abstracts and/or schedule of values provided by project technical leads and engineers. Costs were classified into six categories: construction, mitigation, design, litigation, stakeholder concern, and monitoring. *Construction* costs included pay items such as mobilization/demobilization, removal of the dam and appurtenances, sediment management, and restoration of the site. *Mitigation* costs included project components that were needed to replace the function of the dam and/or address impacts, such as hatcheries, pumping plants, replacement water supply wells, and levee improvements. *Design* costs (i.e., non-contract) were those pertaining to design, engineering, and permitting. *Litigation* costs involved any legal costs associated with litigation to keep or remove the dam. It is our expectation that this cost is underreported since project consultants usually were not involved with litigation. *Stakeholder concerns* comprised any additional studies, facilitation, site visits and other activities related to stakeholders and their project concerns. *Monitoring* included costs associated with required monitoring for water quality and other permits or project requirements, which does not include any costs associated with research-oriented monitoring. Detailed costs from each case study were compiled into the cost categories by each consultant with some guidance from the project team during follow up interviews, although the classification of several individual costs into these categories was subject to some individual discretion. Per the request of some information providers, names of some dams were removed to protect proprietary information.

In addition to detailed costs, 83 variables, including details on river and dam features (e.g., dam geometry and composition, stored sediment volume and composition, dam removal strategy, streamlining of permitting, mitigation measures) were documented based on interviews with project managers (Tullos and Bountry, 2023). These variables provide descriptive detail on features of the project that contribute to each cost category, such as the strategy for sediment management, degree of sediment contamination, need for replacement infrastructure, complexity of permitting, and other factors that could increase project complexity or cost.

3 Results

3.1 Dam removal trends from the cost database

Using the names and geospatial attributes of 1773 dams in the American Rivers dam removal database (American Rivers, 2023), we were able to locate reported dam removal cost for 668, or roughly 38% of the dams removed from rivers in the United States. The reported costs were for dams removed between 1965 and 2020 in 38 different states. We found 455 unique sources of information that contained a reported cost or information about the presence of cost drivers for the project (Table 1). The top categories of source information included governmental and non-governmental web sites (147), online news articles (117), unpublished reports and governmental documents (79; e.g., contract bids, budget reports), web blogs (41) and email communications with project contacts (26).

The total cost of the 668 dam removals indexed to 2020 dollars was $1.522B. Dam removal project cost estimates, including those where multiple dams were removed, ranged from $5k to $351.60M, which when adjusted for inflation to 2020 USD ranged from $6.0k to $402.56M (hereafter and in all tables and figures we report the indexed 2020 cost). When estimating the per dam cost of multi-dam projects with the proportional height calculation, cost estimates ranged from $929 to $268.80M (Figure 1).

Seventy-seven percent of reported costs (n = 518) were for projects where a single dam was removed, whereas 150 dams were removed as part of 53 multi-dam removal projects involving between 2 and 18 dams. There were far more small dams (< 5 m;

TABLE 1 Categories and descriptions of 455 bibliographic sources used to obtain cost estimates or cost drivers of dams removed in the United States between 1965 and 2020.

Type	Number	Description
Website	147	Webpage of governmental, non-governmental, or business organizations
Online news article	117	An online news article (e.g., Associated Press, local newspaper) or press release
Report	79	Unpublished reports
Web blog	41	Governmental and non-governmental organizations blog post
Email	26	Personal communication via email between study lead author and dam removal practitioner
Presentation	11	An online copy of a conference or power point presentation
Government document, conference paper, book	22	Government document, conference paper, book chapter, or journal article
Online magazine article	12	An online news or current events magazine (e.g., High Country News)

Some sources contained estimates for multiple dam removal projects.

n = 542) than medium height dams (5 m–10 m; n = 77) or large dams (> 10 m; n = 30) (Figure 1). The median dam removal costs were $157.30k, $823.48k, and $6.22M for small, medium, and large size dam removals, respectively. Only 19 dams with cost estimates did not have a height estimate. Given the median cost of dams with unknown height was $153.42k, it is likely that most of the dams lacking height information were dams less than 5 m tall.

The number of dams for which we located cost information varied regionally (Figure 2A). The number of dam removals with reported cost by region was highly correlated with the total number of dam removals (based on American Rivers data) per region (Pearson's r = 0.98, n = 5, $p = 0.002$), suggesting that our database was representative of dam removals in the United States. The Northeast and the Midwest had the highest number of reported dam removal costs (221 and 278, respectively), with small dams < 5 m being numerically dominant and representing a larger proportion of cumulative dam removal cost in these regions (Figure 2B). These two regions also had similar median costs for small, medium, and large dam removals (Table 2). In

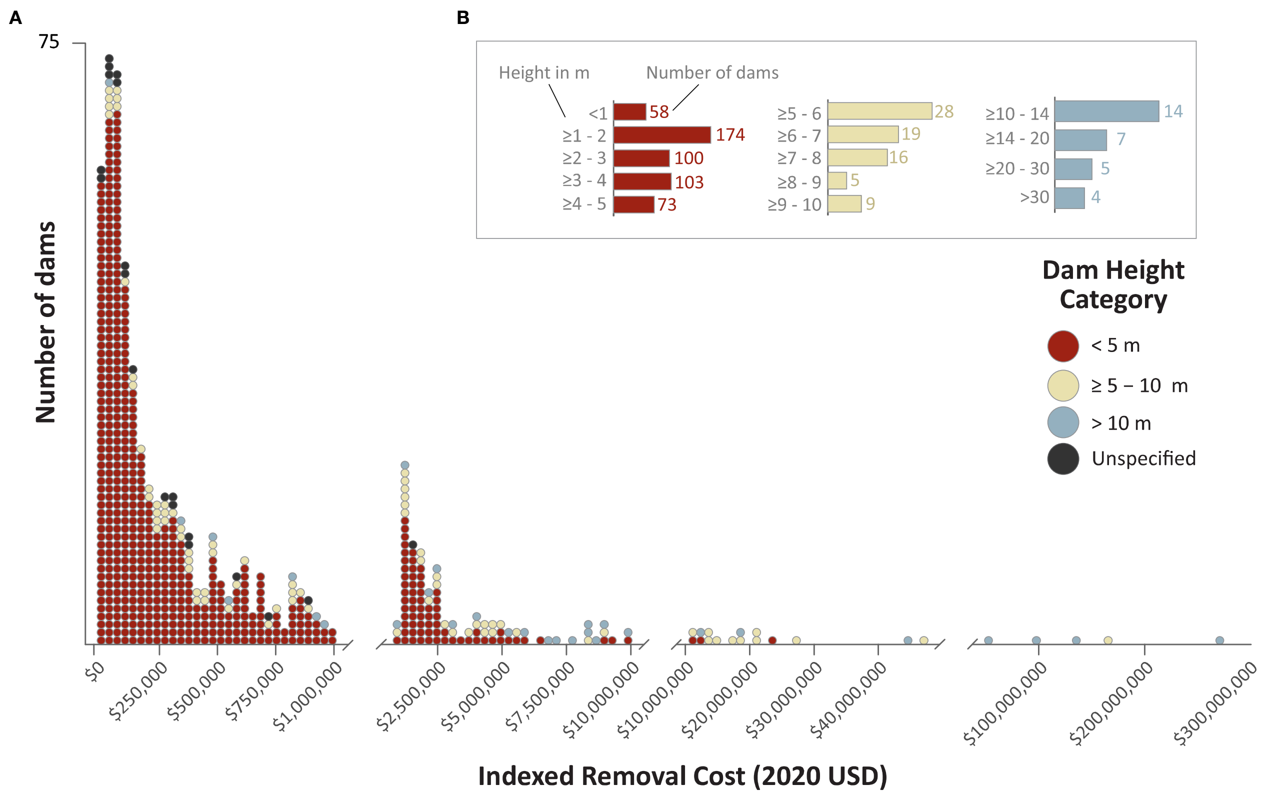

FIGURE 1
(A) Histogram of indexed cost estimates for 668 dam removals by height category. To represent the skewed data, the x-axis was broken into four non-equal divisions (<$1,000,000, $1,000,000 to $10,000,000, $10,000,000 to $50,000,000 and >$50,000,000) with the bin size for each division equal to 1/30th of the range of values. **(B)** Distribution of height per dam size category. For 34 dams in the less than 5 m category, height was visually estimated as being< 5 m from ancillary sources (e.g., photographs) but the exact height wasn't known. Another 19 dams with cost estimates were classified as unknown height.

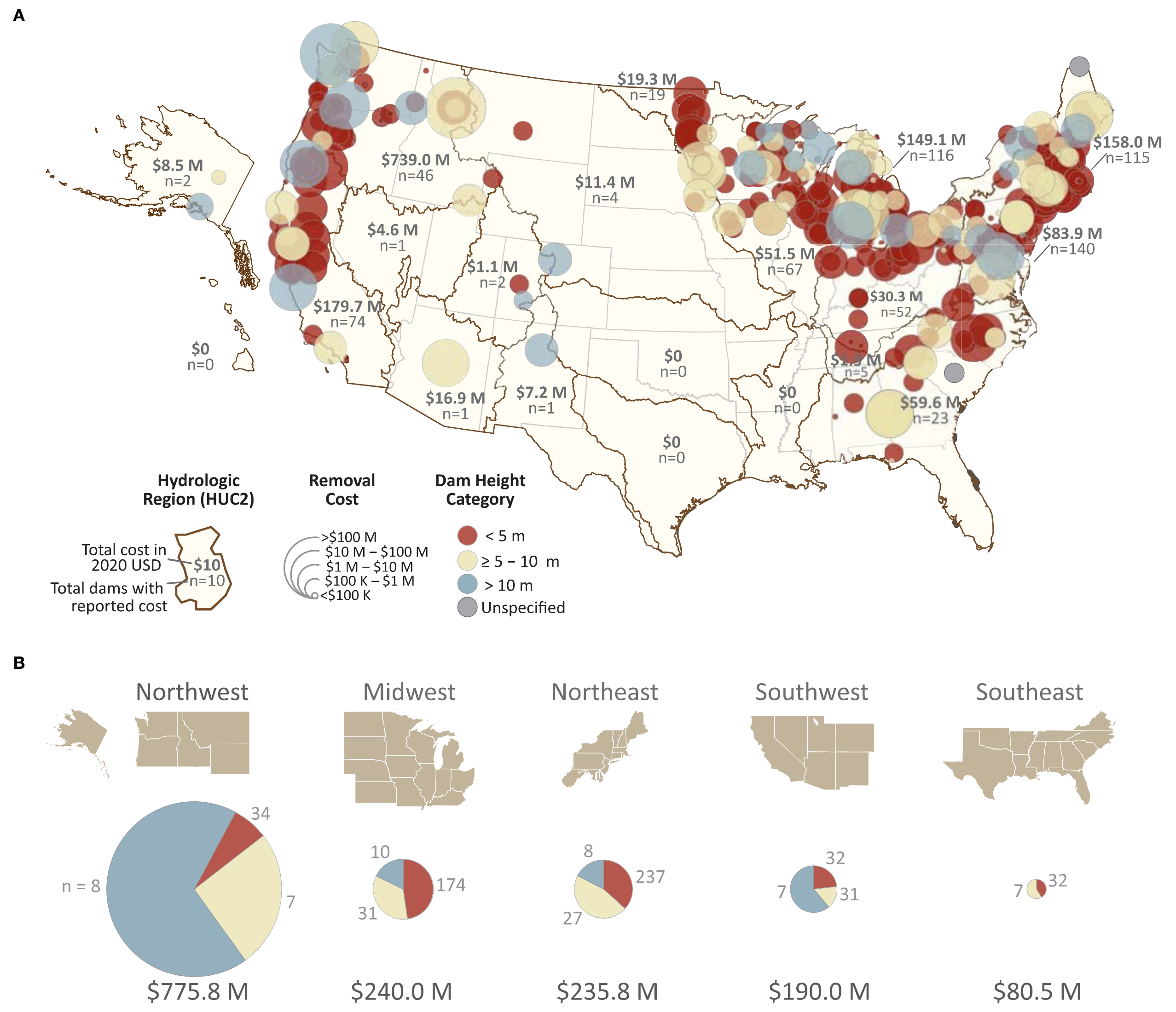

FIGURE 2
(A) Map visualization aggregating cost estimates of dam removals in the United States from 1965 to 2020. Dams depicted by height category (fill color) and cost bubbles (diameter) ranging across 5 orders of magnitude. Total number removed and total cost (calculated based on 2020 dollars using RS Means construction cost index) were aggregated to Hydrologic Unit 2 watersheds. **(B)** Regional cost estimates of dam removal by dam height category. Size of pie charts proportional to total cost for each region.

contrast, fewer dams were removed in the Northwest and Southwest regions (50 and 78, respectively) but the removed dams were larger (> 10 m), which accounted for a larger share of the cumulative regional cost for dam removal. The median costs of dam removals in these regions were similar for small and medium sized dams, but in the Northwest median cost for large dams was 3.4 times greater than in the Southwest ($26.42M vs. $7.82M), largely due to three expensive dam removals on the Elwha and Clark Fork rivers in Washington and Montana. If these dams are omitted, the median cost for large dam removals declines to $7.30M in the Northwest region, which is in line with large dam removal costs in the western United States (but still considerably higher than large dam removal costs in the eastern United States). Finally, the Southeast region had the fewest dams with reported removal cost, the least total dam removal cost, and no large dam removal projects (Table 2). The median cost for small dams in the Southeast was similar to the median cost in the Northeast, and for medium dams to the Northwest and Southwest.

For the dams where we located cost data, the stream and watershed characteristics differed by dam size category and in some cases by region. In each region, most removals were of small dams, averaging between 1.8 m and 2.7 m in height (Table 3). A trend of small dams being located on rivers with smaller stream order, upstream drainage area, and discharges was present in most regions compared with medium (5–10 m) and large sized dams (>10 m), although this trend did not hold in the Midwest region. For the large dam category, the western United States had, on average, taller dams removed (25.1 m and 24.9 m in the Northwest and Southwest, respectively) than the central and eastern United States (15.7 m and 14.2 m in the Midwest and Northeast, respectively).

TABLE 2 Dam removal cost by region and size category.

Region	States	n	Median cost (range) in millions of 2020 $USD per size category			Total cost in millions of 2020 $USD
			<5 m	5–10 m	>10 m	
Midwest	IA, IL, IN, KY, MI, MN, OH, SD, WI	222	0.223 (0.0063–8.82)	0.453 (0.031–20.61)	2.092 (0.020–12.23)	240.0
Northeast	CT, DE, MA, MD, ME, NH, NJ, NY, PA, RI, VT, WV	277	0.130 (0.0032–9.33)	0.750 (0.027–46.95)	2.254 (0.55–18.8)	235.8
Northwest	AK, ID, MT, OR, WA, WY	50	0.389 (0.060–23.41)	4.634 (0.057–162.49)	26.421 (3.941–268.80)	775.8
Southeast	AL, FL, GA, NC, SC, TN, VA	41	0.130 (0.014–11.87)	4.303 (0.082–19.11)	— —	80.5
Southwest	AZ, CA, CO, NM, NV, UT	78	0.0223 (0.001–5.99)	4.291 (0.84–16.90)	7.825 (0.95–98.19)	190.0
	Total for U.S.	668				1,522.1

There were 50 multi-dam removal (2–18) projects but only five had separate cost estimates for each dam removed within the project. For the other 45 projects, cost per dam was allocated proportional to each dam height in the project. If height was unknown, then the average per dam was used.
Only states with reported dam removal costs are listed for each region.

TABLE 3 Summaries by U.S. region and dam size categories of dam removal cost (median and range), upstream watershed size (average and SD), stream order (mode and range), annual flow in cubic meters per second (average and SD).

Region	Size category (m)	Number of dams	Average of dam height (m ± SD)	Average of upstream watershed size (km^2 ± SD)	Mode (range) of Strahler stream order	Average of mean annual flow (m^3s^{-1} ± SD)
Midwest	< 5	175	2.4 (1.1)	3007 (8279)	5 (1–7)	10.3 (16.1)
	5–10	31	6.3 (1.1)	1923 (3517)	4 (2–7)	7.6 (9.1)
	>10	10	15.7 (3.5)	871 (879)	4 (3–6)	7.0 (8.0)
	Unknown	6	na	412 (647)	3 (1–5)	3.5 (5.1)
Northeast	< 5	236	2.5 (1.3)	251 (478)	3 (1–6)	4.1 (7.5)
	5–10	27	6.9 (1.5)	1964 (5394)	2 (1–7)	36.8 (99.3)
	>10	8	14.2 (5.4)	1974 (4970)	3 (1–6)	36.4 (93.4)
	Unknown	6	na	372 (567)	1 (1–4)	7.6 (12.5)
Northwest	< 5	34	2.3 (1.1)	951 (2064)	3 (1–6)	7.3 (17.3)
	5–10	7	8.0 (1.1)	4736 (5996)	4 (3–7)	43.9 (32.2)
	>10	8	25.1 (18.7)	5546 (8573)	4 (4–7)	116.6 (147.7)
	Unknown	1	na	129 (na)	4 (4)	0.5 (na)
Southeast	< 5	32	2.7 (1.3)	1224 (2357)	5 (1–7)	19.7 (40.8)
	5–10	7	6.3 (1.0)	3631 (4243)	6 (2–6)	56.6 (74.2)
	>10	0	na	na	na	na
	Unknown	2	na	207 (na)	4 (4)	1.4 (1.4)
Southwest	< 5	65	1.8 (0.9)	239 (738)	2 (1–6)	2.9 (11.6)
	5–10	5	7.2 (1.4)	270 (486)	3 (1–5)	11.0 (24.0)
	>10	4	24.9 (6.0)	144 (142)	na* (1-5)	2.1 (2.2)
	Unknown	4		900 (1166)	na* (3–5)	12.9 (16.5)

*Selected streams have unique or missing data leading to a set of values with different stream order, there is no mode value.
Summaries based on a total of 668 dams, 524 of which were single dam removal projects. na, not applicable.

3.2 Reasons for dam removal and drivers of cost

We were able to identify at least a single reason for dam removal in all but 49 dams with a reported cost. Most dams had a single reason identified for dam removal, while 190 had two reasons (e.g., restoration and safety, safety and economics). Restoration of the aquatic ecosystem, often mentioning fish passage, was the most common reason cited for dam removal overall and within each size category (Figure 3). Removal of unsafe dams, including those in disrepair and in danger of failure or those that posed risk to swimmers and boaters, were the next most common reason for dam removal. Economics was the least commonly cited reason for dam removal

We were able to locate reference to at least one of the 28 different cost drivers for 239 (35.8%) dams in our dam removal cost database. Lack of identified cost drivers does not mean that drivers were not present, merely that they were not reported in the documentation we reviewed. Cost drivers related to sediment were present in 129 dam removal projects, with mechanical removal (n = 49) or river erosion (n = 37) of sediment the most common, followed by the use of coffer dams to dewater construction areas (n = 33), removing contaminated sediments (n = 26), reservoir sediment stabilization (n = 12), and use of a pilot channel (n = 7). Cost drivers related to mitigation elements for fish passage (e.g., grade control structures), water supply (e.g., water pumping or treatment), or habitat and infrastructure protection (e.g., bank stabilization), were associated with 118 dam removal projects. The most common type of mitigation driver (n = 73) was related to river channel features, like installation of rocks and boulders to create habitat, limit erosion/scour, and allow fish passage. Other cost drivers for mitigation included those intended to protect banks or levees (n = 49), replace or relocate water supply infrastructure (n = 27), or protect/replace bridges (n = 15). All other mitigation types were present in less than 6 dam removal projects each. Finally, potential drivers of cost associated with post-project elements associated with the dam removal site (i.e., post-removal drivers) and upstream/downstream features were present in 149 different dam removal projects. The most common was revegetation of reservoir and riparian areas (n = 93), followed by reshaping topography (n = 34), monitoring (n = 24), protection or removal of structures for safety (n = 25), and creation of interpretive facilities (n = 21). A total of 80 dam removal projects had a single

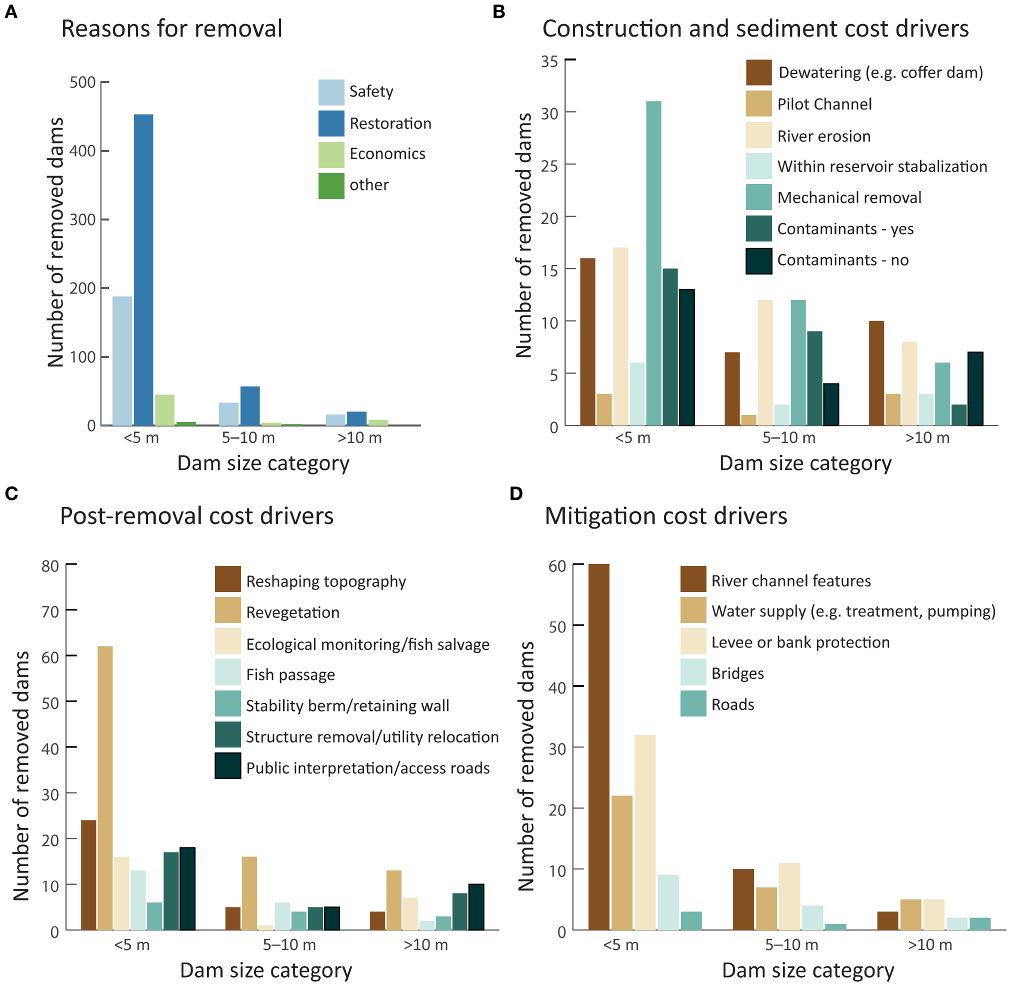

FIGURE 3
(A) Reasons for dam removal and **(B)** cost drivers related to sediment, **(C)** post dam removal activities and **(D)** dam removal mitigation needs. A dam removal project could have more than one driver identified.

identified cost driver, while 97 projects had two or three identified drivers. Only 62 projects had more than four drivers identified.

3.3 Predictive cost model

Dam height was the strongest predictor of removal costs, followed by average annual discharge, project complexity, and drainage area. Dam removals in the Southwest region, dam material, and other regional variables had a smaller effect (Figure 4A). Despite the differences in the strength of their effects, all variables were retained by the modeling process, showing at least some importance in predicting cost. The model explained 57.0% of the variance in dam removal costs for the training dataset.

The partial dependences of cost on the different predictor variables are depicted in Figure 4B. These plots represent the trend or nature of dependence between the predictor and response variables rather than actual values. In general, the strength of these effects was strongest for dam height and discharge (based on the scale of the y-axis in the partial dependence plots) and lowest for the Southwest region and dam material. Dam removal costs increased with dam height from < 1 m to 20 m, beyond which there was no cost increase after accounting for the effects of other predictor variables. It is likely that this reflects a paucity of reported cost data for larger dams in the data rather than a real effect. Similarly, discharge and project complexity resulted in increased removal costs up to approximately 100 m^3/s and 0.5 respectively. Beyond these threshold values, cost showed little dependence on these variables after accounting for other predictor variables. Drainage area had a nonmonotonic relationship with cost; as drainage area values increased from low levels to 20,000 km^2, cost first decreased and then increased. Beyond the 20,000 km^2 threshold, cost did not show any dependency of drainage area. Regional removal costs did not show any strong relationships except for the Southwest, where removal costs tended to be lower. Finally, cost of removal increased with the durability of dam material (Figure 4B).

The relationship between actual and predicted median cost values (n = 97) derived from model performance on the test dataset is shown in Figure 5. Due to incomplete or missing data for the predictor variables, we were able to predict model-based costs for only 97 of the 132 test data points. The coefficient of determination (R^2) was 33.8%, and the overall MAE and RMSE associated with predicted costs were $1.45M and $5.09M, respectively. Errors between predicted and actual costs were larger for larger sized and more expensive dam removal projects (Figure 6). For instance, predicted costs were much lower than actual costs for Savage Rapids, Fossil Creek, Embrey, Plainwell Dam #1, and Carbonton dams. Conversely, the trend was reversed for the Hidden Treasure and Boardman dams, where the actual costs were lower than those predicted. The relationship between actual and predicted costs was more accurate for dams less than 5 m in height, particularly when considering the 50% prediction interval. Yet even for the most extreme outliers, actual cost values were encompassed within the 95% prediction interval (Figure 5).

3.4 Case-studies from the detailed cost database

We also assembled in-depth case studies which provided detailed cost breakdowns from 15 dam removal projects, nine of which overlapped with the larger database. The removed dams varied in terms of location (occurring in 8 states across every region

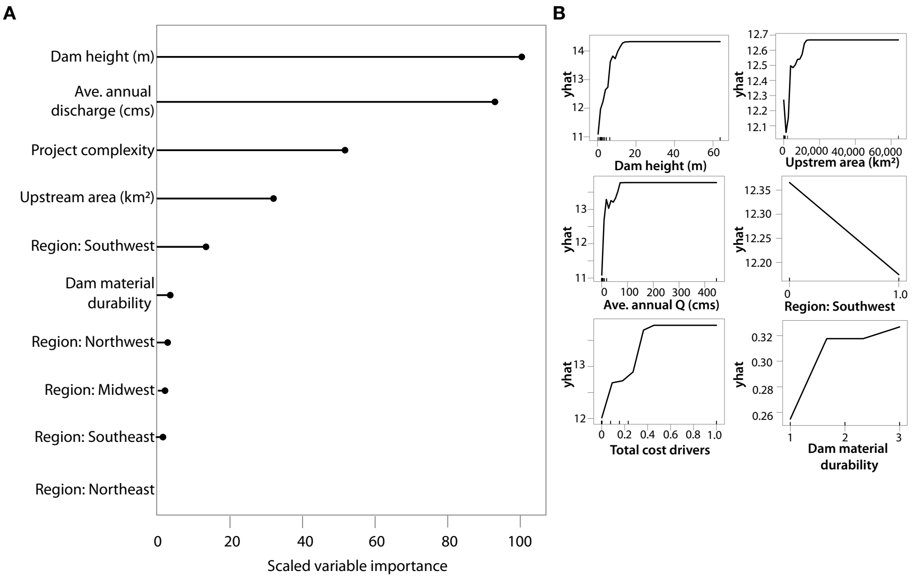

FIGURE 4
Results from a dam removal cost model derived from stochastic gradient boosted quantile regression showing **(A)** the relative importance of predictor variables scaled to the most important predictor and **(B)** partial dependence plots of the top 6 variables, showing the marginal effect (i.e., yhat) of the independent variable to the dependent variable. Note that the y-axis scales are different for each variable.

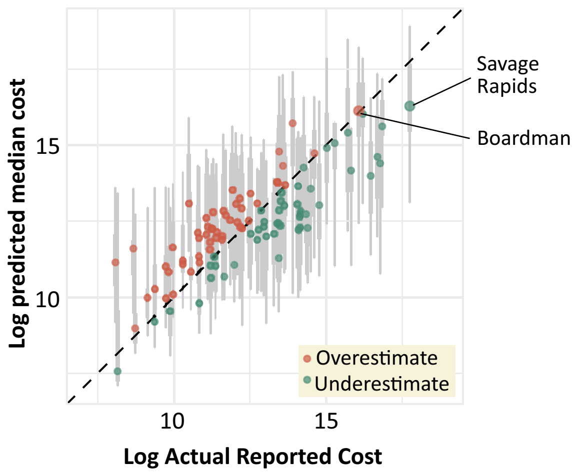

FIGURE 5
Actual versus predicted median cost of dam removal (shown in log-log scale) derived from stochastic gradient boosted quantile regression model. The model was derived from training data that contained cost and characteristics data (n = 536) and predictions were made on a test dataset of 97 dams. Gray bars and lines represent the 50% and 95% prediction intervals, respectively. The two labeled dams were those where interviews provided detailed cost estimates.

except the Southwest), height (1 m–64 m), drainage area (15 km^2–6,369 km^2), age (40 yr–288 yr) and overall cost ($75k–$263.73M). These dams showed that construction, mitigation, and design costs were the three largest contributors to total project costs (Figure 7). Across the 15 case studies, construction costs related to removing the dam and associated structures averaged 54% of the total costs (range = 6%–82%), and > 50% of the total cost in 9 of the 15 case-studies. The next highest dam removal project costs were for mitigation measures needed to replace lost functions or minimize effects from dam removal activities, which averaged 22% (range = 0%–80%). Only 3 of the 15 case-studies had mitigation costs exceed 50% of the total project costs (Elwha and Glines Canyon dams and Savage Rapids Dam). Design and permitting cost were the next largest expense, averaging 20% of the total project cost (range 7%–42%). The other three cost categories (litigation, stakeholder related, and monitoring) all had an average cost ≤ 3%.

4 Discussion

What has been lacking, but greatly needed, in the literature of dam removal is empirical data on the cost of dam removal projects and associated analyses about how the cost varies among dams, their characteristics, and the watersheds and regions in which they reside. Such data would illustrate important details on how the planning and engineering of dam removals vary across projects. To address this gap, we compiled cost data for 668 dam removals from a variety of sources, showing geographic trends in allocation of dam removal dollars across the United States over the past 5 decades. The total indexed cost of dam removals was $1.522B U.S. dollars. Assuming that these dam removal costs were representative of the 1,916 dams removed in the United States through 2022 (American Rivers, 2023), an algebraically derived estimate of the total cost for removing dams on U.S. rivers is roughly $4.4B dollars. Like the trends in dam construction and

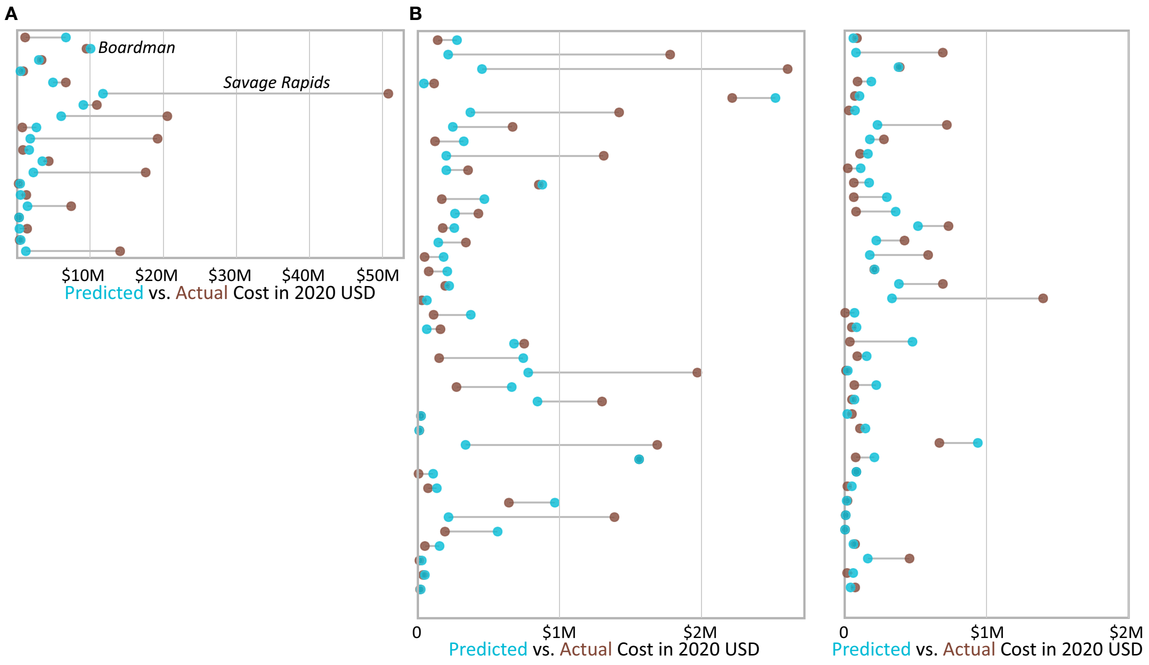

FIGURE 6
Dumbbell plot of actual (red) and predicted median (blue) costs of removal of individual dams in the test dataset that cost **(A)** greater than $10M 2020 USD or **(B)** less than $5M 2020 USD, with select case-study dams labeled for clarity. The length of the grey line between both points indicates the extent of difference between actual and predicted costs.

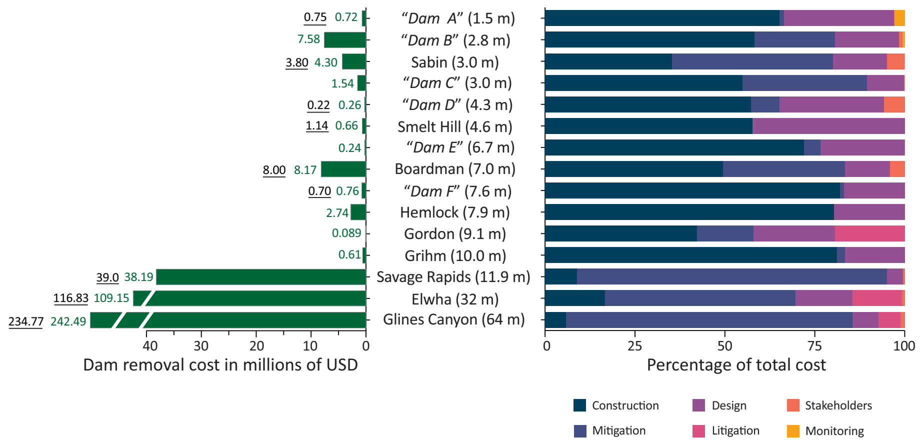

FIGURE 7
Total cost estimates (left) and cost category breakdown (right) for 15 dams with detailed cost estimates (Tullos and Bountry, 2023). Some dams anonymized to protect proprietary cost data provided by dam removal practitioners. Underlined numbers were reported costs independently derived from our dam removal cost database (Duda et al., 2023).

removal, the trends in reported costs were unequally distributed across the United States. In the Northeast and Midwest, proportionally more dam removal dollars were spent on small dams < 5 m in height, which are prevalent in these regions (Tonitto and Riha, 2016). The western United States, in contrast, had more money allocated towards larger and more expensive dam removals which were far fewer in number. In fact, two high-cost dam removal projects in the Northwest (on the Elwha and Clark's Fork rivers) were responsible for 73% of all dam removal costs in the region. Our predictive cost model showed that dam height, indicative of dam size, was the strongest predictor of removal costs. Costs also increased with river discharge and upstream watershed area, which could be indicative of larger and/or shallower reservoirs potentially trapping sediment from larger areas, resulting in larger areas to manage or restore at the time of dam removal. Project complexity was the third most important predictor and accounts for costs associated with additional activities necessary to manage construction and sediment management, mitigation, and post-removal activities related to the outcomes of dam removal. Regional differences and dam material were also significant but less important factors. Use of the dam removal cost database and the boosted regression model should be a helpful tool to conduct preliminary, planning level assessments of potential dam removal projects. An interactive shiny application based on the cost model has been developed (https://wrises.shinyapps.io/DamRemovalCostPredictiveModel/) as a tool to allow users to explore dam removal costs based on dam characteristics, location, and project complexity. When used with a dam removal prioritization methodology for watersheds in Northern California, our cost data were used to estimate the costs of candidate dam removal for projects in different feasibility categories (Jumani et al., 2023).

Examining the political, social, and historical dimensions of dam removal has revealed both socio-economic and geographic differences in the role that science, aesthetics, politics, regulations, and cultural identity have played in dam removal decision making and outcomes (Johnson and Graber, 2002; Poff and Hart, 2002; Fox et al., 2016; Magilligan et al., 2017; Roy et al., 2018; Roy et al., 2020; Germaine et al., 2021). Our results show that these geographical differences may have influenced where dam removal dollars have been spent across the landscape (Figure 2). Geographical differences can be explained, in part, by the presence or absence of factors related to the density of aging dams or those that do not serve any modern purpose, present a public safety risk, impede natural resources conservation or restoration goals, or economics (Magilligan et al., 2017). Some states, such as Pennsylvania and Wisconsin, have combined policy and regulatory mechanisms, stakeholder coalitions, and a combination of government and private funding to become leaders in removing dams that are aging, unsafe, or no longer serving their intended purpose (Born et al., 1998; Brewitt and Colwyn, 2020). Other states in the Northeast and Midwest, such as Massachusetts, New Hampshire, and Minnesota also have dedicated funding mechanisms and state agencies with staff focused upon dams and their safety, including offices or staff facilitating dam removal. Several projects in the database leveraged locally available funding with federal (e.g., NOAA restoration center) or private (e.g., Open Rivers Fund) programs to raise the necessary funds for dam removals. Other states where fewer dam removals have occurred may not have been afforded the "policy windows" to allow dam removal to be considered as an option for dealing with candidate dams (Doyle et al., 2003), have fewer aging dams, or a combination of both. Another factor that could be driving the geographic differences in dam removal is shifting regulatory and policy spheres at the state level, which can alter institutional structures such as permitting requirements from those that are confusing and excessive to those specifically designed to promote removal of old or unsafe dams (Lindloff, 2003; Lowry, 2005). Similar transitions have occurred at the federal level, for example the nationwide permit 53 from the Army Corps of Engineers for low-head dam removals (U.S. Army Corps of Engineers, 2022b).

Earlier studies have shown that safety was the most cited reason for dam removal, but the transition to environmental rationales starting in the 1990s (Pohl, 2002) has continued through the 2010s. Our results showed that safety and economics were less commonly cited as dam removal rationales compared with river restoration.

Twenty years ago, during a spate of dam removal research publications (e.g., Graf, 2002; Poff and Hart, 2002; Pohl, 2002; Stanley and Doyle, 2003), the lack of empirical information about project cost led some to conclude that decision makers consistently overestimated the cost of dam removal and underestimated the cost of retaining dams (Graf, 2002). It also limited the ability of researchers to build predictive cost models for dam removal (Orr et al., 2004). Despite this, empirical information of regional dam removals that had both cost and repair estimates showed that it was often less expensive to remove a dam than to repair or rebuild it (Born et al., 1998; Johnson and Graber, 2002). In their assessment of river restoration projects in the United States, Bernhardt et al. (2005) reported that in their database of over 37,000 river restoration projects, only 58% had information on project costs. We were able to find a reported cost for 38% of dam removal projects listed in the American Rivers dam removal database through 2020, showing that the "piecemeal" information about river restoration projects, including dam removals, may not have appreciably improved. Natural resources agencies, conservation organizations, and the dam removal community would benefit from the expansion and maintenance of existing dam removal cost databases, including in areas where such resources are lacking but the practice of dam removal is accelerating.

We surmise that, in most cases, the cost data represent an underestimate of the true and total cost of dam removal. There are several possibilities that could lead to inaccuracies (i.e., both under- and over-estimates) in our total cost data set. The factors contributing to underestimating total dam removal costs include non-reporting of in-kind costs (e.g., agency labor; Bernhardt et al., 2005), expenditures dealing with pre-project planning (e.g., litigation, stakeholder concerns), and post-project monitoring. Another source contributing to uncertainty is the potential for cost data to occur in information silos. Historically, dam removal costs were assembled from several sources, resembling "a patchwork quilt" of funding (Otto, 2000). We do not know whether sources used in our database accurately reported the entire pool of dam removal funding provided by all sources, or just those costs specific to a given funding source. It is also possible that the reported costs we found were based on initial bids or cost estimates and did not include change orders or other non-reported expenses that impacted the total cost. Comparing the seven overlapping cases of the Tullos and Bountry (2023) detailed case-studies with the Duda et al. (2023) dam removal cost database, the costs were highly correlated ($r = 0.99$, $df = 5$, $p<0.001$) with the largest absolute difference being 11.6% of total project cost.

The 15 individual case-studies compiled in Tullos and Bountry (2023) help identify how the breakdown of key cost components can vary, highlighting why cost estimation can be challenging. We compared two dams with detailed cost data that were of similar height but vastly different total costs and cost profiles (Figure 7). "Dam F" (name redacted to protect proprietary information) was a 7.6 m tall hydropower dam owned by a public utility district. The dam stored very little (~382 m^3) coarse, uncontaminated sediment which allowed permitting to be streamlined, resulting in a relatively straightforward and inexpensive ($0.75M) project dominated (82%) by construction related costs. In contrast, Boardman Dam was a 7 m tall (hydraulic height) dam owned by a local government. Although the dam's primary purpose was to deliver flow for irrigation, the project also operated a small hydropower plant. Project complexities, including construction of new roads, relocation of utilities, and construction of public interpretation facilities contributed to higher costs for the Boardman Dam removal (totaling $8.17M). Two key project requirements in the mitigation cost driver category elevated costs for Boardman Dam removal compared to the similarly sized Dam F removal. The first was associated with concerns about and activities related to managing the 460,621 m^3 of stored sediment. While about 40% of the sediment was eroded to the downstream reach, 30% was stabilized within the reservoir, and the remaining 30% was mechanically removed. In addition, a pilot channel was excavated through the reservoir sediment deposits and the reservoir drawdown rate was restricted to avoid slope failures. The second cost driver was associated with substantial mitigation activities at a cost of $2.7M (41% of the total cost), including levee/bank protection ($486.7k) and creation/mitigation of river habitat features ($610.5k). Finally, the Boardman project reported over $300k in required monitoring of reservoir erosion, water quality, and aquatic organisms including fish. Thus, despite two projects involving similar sized dams, lacking contaminated sediments and both having hydroelectric facilities and equipment present that had to be removed, the costs were 10.7x higher for the Boardman Dam project due to local concerns about the release of stored sediment that increased sediment management, flood control, and habitat mitigation costs. The complexities of the Boardman Dam removal were encapsulated within the project complexity score in the cost database (0.46), which explains the similarity between the actual and model predicted costs for this project (Figures 5, 6).

The Savage Rapids Dam on the Rogue River near Grants Pass, Oregon, is another noteworthy case-study where the large discrepancies between the actual ($50.80M) and predicted ($11.80M) costs of dam removal (Figures 5, 6) can be better understood by examining the component-wise breakdown from the detailed cost database. Savage Rapids was a 12 m tall diversion dam owned by a local irrigation district that was removed to improve both adult (upstream) and juvenile (downstream) anadromous fish passage. The reservoir was operated at a higher elevation using gates to seasonally divert water, such that reservoir sedimentation was only present in the permanent (lower) winter pool. The reservoir contained 542.8 m^3 of uncontaminated sand and gravel, and river erosion was used to erode and transport the deposit into the downstream channel. Although construction costs for decommissioning were not inexpensive ($3.40M) due to the requirement to utilize coffer dams (so that all work was performed, "in the dry" and fish passage was maintained throughout construction), it comprised a very small portion (9%) of the total costs. The construction did include creation of a pilot channel, revegetation of a newly created floodplain, and removal of a historical timber crib dam, but these items were minor costs and completed in just a few days. Instead, mitigation for the lost function of the dam (irrigation diversion) was the major cost driver. A new pumping plant and water conveyance pipe crossing was constructed at a cost of $32.87M, which represented 86% of the total cost and the bulk of design and construction effort. Further, litigation occurred to remove the dam, although these costs were not reported or represented in the database. Thus, Savage Rapids Dam reflects the type of project where project costs are not easily predicted solely by the size of the dam, the volume of sediment stored, or binary presence/absence indicators of project complexity. The high mitigation costs are likely a reason that our dam removal cost model underestimated the cost of the dams. The lack of information on the extent of influence of each cost driver may result in discrepancies between actual and predicted costs, particularly in such cases where one or more actions are associated with a large fraction of the total cost.

5 Conclusions

There is a pressing need to improve the volume and quality of empirical dam removal cost data to better inform dam removal planning. Given the large number of dams in the world and their finite lifespan, there is a strong likelihood that the practice of dam removal will continue (Stanley and Doyle, 2003). One recent estimate predicted that by 2050 between 4,000 and 32,000 more dams will be removed in the United States (Grabowski et al., 2018). Coupling cost information with the demographics of the dam (e.g., age, height), biogeographic information about the river (e.g., stream order, discharge), and estimates of cost drivers (e.g., mitigation requirements like reservoir revegetation and sediment management) is critical for contextualizing dam removal costs, determining geographic variability, and providing information for decision makers. As societies contemplate the future role of dams in the face of aging infrastructure and climate change (Beatty et al., 2017; Ho et al., 2017; Concha Larrauri et al., 2023), accurate data on dam removal cost are needed for decision makers and the public to assess whether a given dam should be removed, repaired, or rebuilt. Such data could be coupled with other emerging science and tools that describe how to prioritize, conduct, study, and manage dam removal projects (Hoenke et al., 2014; Wohl et al., 2015; Tullos et al., 2016; Bellmore et al., 2017; Bellmore et al., 2019; Curry et al., 2020; Jumani et al., 2023). Several of the factors in our cost model's partial dependence plots showed that more data are needed to improve the precision and applicability of the models. We encourage practitioners, funders, and natural resources agencies that participate in dam removal to develop consensus records of total project costs and make those available to data scientists. A national database of dam removal costs that included component cost breakdowns, the presence of cost drivers aside from construction costs, and accurate demographic data on the dams (e.g., location, age, height, sediment volume) would dramatically improve the ability to learn from past projects and predict the costs of future projects.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5066/P9G8V371 and https://doi.org/10.7267/h415pj58r.

Author contributions

JD – conceptualization, methodology, data curation, data analysis, original draft, review & editing, visualization, project administration, funding acquisition. SJ – data analysis, original draft, review & editing, visualization. DW – conceptualization, methodology, data curation, review & editing. DT – conceptualization, methodology, data curation, data analysis, original draft, review & editing, funding acquisition. SKM – conceptualization, methodology, data curation, data analysis, review & editing, funding acquisition. TR, AJ, and SB – conceptualization, methodology, review & editing, funding acquisition. BJ, RJ, EW, and KR – data curation, data analysis, review & editing. SW and EJW – methodology, data analysis, review & editing. JB – conceptualization, methodology, data curation, data analysis, review & editing, visualization, project administration, funding acquisition. All authors contributed to the article and approved the submitted version.

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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.2023.1215471/full#supplementary-material

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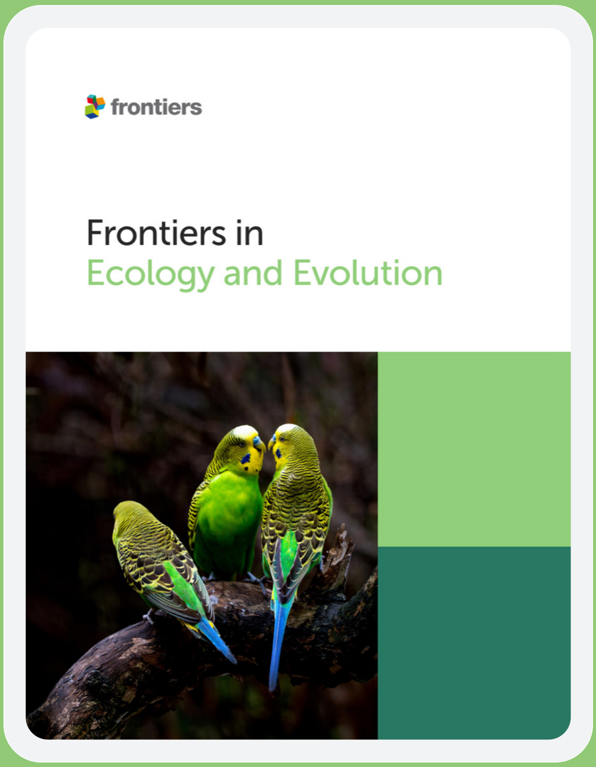
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