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RESEARCH ARTICLE

Assessing the Benefits of Valley-Bottom Restoration for Salmonids Using Spatially Explicit, Individual-Based Modeling

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ABSTRACT

As attention to valley-bottom or Stage-0 restoration increases, direct attempts to evaluate its effects on highly valued salmonid fishes remain rare. We evaluated a valley-bottom restoration project at Whychus Creek, Oregon, by simulating its effects on the abundance of both resident trout (native Rainbow Trout *Oncorhynchus mykiss* and introduced Brown Trout *Salmo trutta*) that currently occupy the site and anadromous Chinook Salmon *O. tshawytscha* that historically occupied the site. Specifically, we compared results from a spatially explicit, individual-based model for pre-restoration versus post-restoration conditions in a 650-m reach of stream within the larger restoration area. For both pre- and post-restoration conditions, we explicitly represented the entire areas inundated by the highest streamflow that occurred during a 15-year simulation period. The model represented the entire lifecycle of resident trout and the part of the lifecycle of Chinook Salmon that would occur at the study site, from the arrival of adults to the emigration of juvenile fish; simulations concurrently included all three salmonid species. The simulations indicated large benefits of restoration for all three species; model results for trout biomass corresponded with single empirical estimates of abundance before and after restoration. However, simulations also yielded year-class failures for both species of resident trout under both pre- and post-restoration conditions. This last result highlights the ability of mechanistic individual-based models to not only estimate the effects of restoration on populations of special concern, but also to place those effects in the context of the broad array of factors affecting populations.

1 | Introduction

The effectiveness and efficiency of restoration depend in part on the ability to forecast—at the planning and design phase of projects—the consequences of specific restoration alternatives for focal animal populations. Spatially explicit models in which population-level results emerge from the survival and reproductive success of individuals over time have clear potential as tools to forecast restoration effects, in part because they can rely on individual-level "first principles"—such as relations between physiology and temperature—which make them well-suited to address future environments likely to involve novel conditions (e.g., Ayllón et al. 2019), including altered climate (Beechie et al. 2013). In addition, such models naturally incorporate interactions among factors which are likely to be important in determining population dynamics (e.g., Harvey and Railsback 2007). Finally, process-based models grounded on the concept of individual fitness provide opportunities to better understand the mechanisms and causes underlying results.

Explicit inclusion of spatial and temporal variation in models used for the evaluation of restoration alternatives can be

critical, because restoration projects seeking to benefit animal populations of special concern must provide conditions necessary to continuously support individuals in those populations. Projects that achieve more general goals, such as increasing habitat complexity, may not sustain populations. Similarly, projects that meet specific narrow goals, such as increasing the quantity of habitat for one life stage, defined in terms of one or two parameters (e.g., water velocity and depth), may not meaningfully affect population dynamics because of the influence of additional habitat characteristics, the inability of individual animals to track and use available habitat, and/or the influence of processes affecting other lifestages. Approaches to habitat assessment that rely on random plots or snapshots in time can be effective for meeting some restoration evaluation goals (Hinshaw et al. 2022), but may not quantify habitat availability in ways that relate well to animal population dynamics.

Valley-bottom or Stage-0 restoration plans, which seek to create conditions that promote the development of multiple, complex channels connected to extensive floodplains (Powers et al. 2019), often include benefitting salmonid fish populations among their objectives. Considering that successful valley-bottom restoration typically yields profound change in topography and the spatiotemporal distribution of surface water (Cluer and Thorne 2014), complex effects on salmonid populations seem likely. While valley-bottom restoration typically increases floodplain habitat that can be valuable to salmonids (e.g., Jeffres et al. 2008), valley-bottom restoration could fail to benefit salmonid populations due, for example, to the effects of stranding (because it can produce broad areas of shallow habitat that could become isolated when flows decrease), increased predation risk from reduction of water depth (Harvey and Stewart 1991), or facilitation of invasive species. Spatially explicit, individual-based modeling can take into account the spatiotemporal dynamics of physical changes caused by valley-bottom restoration and their consequences for processes affecting fish populations. In this paper, we demonstrate the application of such modeling to the evaluation of consequences of valley-bottom restoration for fish, by simulating an existing restoration site both before and after restoration. We should note that estimates of water depth and velocity provided by both pre- and post-restoration hydraulic modeling of the site provided the foundation for fish population modeling. However, we did not have pre-restoration observations of additional habitat characteristics included in the fish model, so we assumed these could be estimated from those currently present in an adjacent unrestored reach.

2 | Materials and Methods

2.1 | Study Site and Restoration

Whychus Creek is a tributary of the Deschutes River in central Oregon which historically supported both Rainbow Trout *Oncorhynchus mykiss* and Chinook Salmon *O. tshawytscha*; however, the site is now also occupied by Brown Trout *Salmo trutta*, while Chinook Salmon cannot naturally access the site due to downstream barriers. Existing literature well describes both the stream and the restoration project (Powers et al. 2019; Flitcroft et al. 2022; Noone et al. 2025), carried out in part to benefit salmonid fish. The project included valley-bottom restoration over 2.5 km of stream length, completed in 2016. A variety of hydrologic and ecological responses to restoration at the study site have been measured (Edwards et al. 2020; Flitcroft et al. 2022; Noone et al. 2025), including large post-restoration increases in inundated area across all streamflows and specifically increases in wetted area with low water velocity possibly suitable for rearing of juvenile salmonids (Flitcroft et al. 2022).

2.2 | General Model Description

InSTREAM 7 is a spatially explicit, individual-based salmonid model in which population-level results emerge from the interaction of individuals and their environment (Railsback et al. 2021, 2023). Previous research has used the model and closely related models to evaluate habitat restoration (Railsback et al. 2013; Harvey et al. 2024; Hahn et al. 2025). As a process-based model that simulates individual fish—over their entire lifespans in the case of resident trout—the model does not impose demographic rates. Instead, population dynamics emerge from the survival and reproductive success of simulated individuals. Similarly, the model does not specify carrying capacities nor does it quantitatively use general measures of habitat such as "habitat suitability." InSTREAM 7 explicitly treats light as a factor controlling feeding success, predation risk, and therefore trout behavior; the daily light cycle is represented as four phases—dawn, day, dusk, and night. At each phase, model trout adaptively decide whether to feed or hide, and where to do so, mainly as a tradeoff between growth and predator avoidance. Food consumption by individuals reduces food availability for other fish in the cells those individuals occupy; the model assumes a size-based hierarchy in habitat selection and food consumption. Consumption of resources and the size-based hierarchy apply across species, such that, for example, food consumed by larger resident trout would be unavailable to age 0 Chinook Salmon.

The model represents stream reaches as sets of two-dimensional habitat cells. Water velocity and depth in habitat cells are typically estimated via hydraulic modeling. Both water velocity and depth affect both predation risk and feeding success through process linkages identified in the scientific literature (Railsback et al. 2023). Habitat cells have additional attributes important to the fitness of fish: (1) distance to cover, which affects predation risk for feeding fish; (2) availability of concealment spaces required for fish to use hiding behavior; (3) velocity shelter, which allows fish to use velocity variation to increase drift feeding efficiency; and (4) availability of spawning gravel. Habitat cells can vary in size and shape; they typically range 2–20 m^2.

InSTREAM 7 captures temporal variation in the environment important to fish by including daily or sub-daily variation in streamflow, temperature, and turbidity over multi-year simulations typically long enough to span multiple generations of fish. The model incorporates key process connections between physical conditions and fish: streamflow determines water depth and velocity in habitat cells and therefore feeding

success, spawning opportunities, and the probability of scour and desiccation of fish eggs and embryos in spawning gravel. Temperature affects bioenergetics, mortality, egg development, and spawning opportunities. Turbidity affects both drift feeding efficiency and predation risk. Dynamic environmental conditions typically yield annual variation in year class strength in model results.

As an individual-based population model that includes adaptive behavior and simulates the entire salmonid lifecycle, inSTREAM 7 is relatively complex. Separate submodels represent its various mechanisms, some of which are adapted directly from methods established in an extensive literature, while others represent processes that are less studied and more uncertain. The effects of valley-bottom restoration on salmonid populations are likely driven mainly by the submodels for drift feeding and salmonid energetics, both of which are based directly on extensive literature and existing models (e.g., Piccolo et al. 2014; Deslauriers et al. 2017), and predation risk, which is based on well-supported concepts but limited preceding research and modeling (Railsback and Harvey 2025). The credibility of these submodels and inSTREAM's submodel for how salmonids trade off growth and risk has been established via "pattern-oriented modeling" (Grimm et al. 2005). InSTREAM 7 and its predecessors reproduce a variety of patterns observed in real systems related to habitat selection (Railsback and Harvey 2002), population dynamics (Railsback et al. 2002), and diel variation in habitat and activity selection (Railsback et al. 2005, 2020). Railsback et al. (2023) provide a complete description and exploration of all submodels, including the scientific literature support for algorithms and parameters.

2.3 | Model Specifics Especially Relevant to This Application

2.3.1 | Food Availability

Trout and salmon in the model may feed on drift (food delivered by the current) or search for food. The submodel for drift feeding includes the effect of water velocity on food delivery rate, capture success, and the cost of swimming, producing dome-shaped relations between growth versus water velocity, which are also affected by other factors including fish size, temperature, turbidity, and water depth (Railsback et al. 2023). The availability of search food does not depend on the current. The availabilities of both drift (food/cubic meter of water) and search food (food/area/time) are calibration variables assumed to be constant in space and time.

2.3.2 | Mortality Sources

Juvenile and adult fish can die from: high temperature, stranding, starvation, and disease owing to low condition, predation by terrestrial animals, and predation by fish. In the simulations presented here, stranding occurs with a 50% probability when fish occupy habitat cells with zero water depth. This formulation recognizes that habitat cells with an average depth of zero may still contain wetted areas. Larger fish are less susceptible to stranding because they can move longer distances to avoid dry habitat (see 2.3.3 below). The probabilities of predation by terrestrial animals and predation by fish are affected by fish size and a variety of habitat characteristics, including cover, turbidity, and water depth.

Egg mortality can result from temperature extremes, dewatering, scour, or superimposition. Estimation of scour probability relies on the reach-scale model of Haschenburger (1999), which in turn relies on estimation of the Shields parameter. Increasing water velocity or slope and decreasing substrate particle size both increase the Shields parameter and consequently scour probability. In this application, we focused our estimates of scour probability for both the pre- and post-restoration scenarios on spawning areas identified by field observations. This effort, which depended on local topography, the hydraulic models, and field observations of substrate particle size, yielded similar pre- and post-restoration relations between Shields stress and streamflow.

2.3.3 | Individual Habitat and Activity Selection

Individual fish select their activity (drift feeding, search feeding, or hiding) and habitat (which cell to occupy) at each time step (i.e., four times per day). Juvenile and adult fish make these decisions by selecting the combination of activity and cell that provides the highest expected survival over a time horizon. This decision objective incorporates both the avoidance of short-term risks such as predation and the need to acquire energy to avoid starvation. Adult salmon do not feed, so they make this decision to trade off predation risk and the rate of energy loss, typically by seeking deep and slow cells. For juveniles, the decision objective includes a term representing the fitness benefits of growth, so they seek combinations of cell and activity that allow growth without undue risk, e.g., by feeding in moderate depths and velocities at night and in deeper habitat (or by hiding) in the daytime.

Fish select habitat from among all habitat cells within a distance of their current location which increases with fish length, although all fish are assumed to be capable of moving to cells adjacent to their current cell. In the simulations presented here, a 20-cm fish evaluated cells with centroids within 130 m of its current cell, while a 6-cm fish evaluated cells within about 12 m. As in nature, fish in the model needed a path of wet cells to move from one cell to another; in this application inSTREAM used the "path-to" method in the Networks extension of the NetLogo modeling environment to determine the existence of such paths.

2.3.4 | Spawning

Females may spawn in inSTREAM when a series of constraints are met. These constraints include: the age, length, and condition of the fish; a date window; a temperature range; a maximum streamflow; and a limit on recent variation in streamflow. Fish spawn on days when conditions allow, and a random Bernoulli trial for individual potential spawners meets or exceeds the value of a spawning probability parameter. This formulation produces a realistic temporal distribution of spawning within species-specific spawning periods.

2.3.5 | Resident v Anadromous Fish

The model represents the complete lifecycle of resident fish; in this case, Rainbow and Brown Trout. Simulations begin with initial populations that include individuals classified into three age groups: age 0, age 1, and age 2 and older. Persistence of resident populations requires successful reproduction in the simulated reach.

Even though anadromous Chinook Salmon currently cannot access the site, we simulated them to evaluate habitat restoration benefits if passage is restored in the future. For Chinook Salmon, the model represents the part of the lifecycle that would occur within the simulated reach. Adult Chinook Salmon are initiated in the reach during a pre-spawning period. The model then simulates adult survival to the end of the spawning period, redd site selection, spawning, incubation, emergence, and the lives of individual young fish before outmigration from the reach. Following methods in Railsback et al. (2013), age 0 Chinook Salmon outmigrate when the fitness value of migrating downstream—modeled as a logistic function of fish size—exceeds the fitness value of habitat available to them in the reach. Recently emerged fry migrate downstream only if expected fitness in the reach is very low. Fry able to locate good habitat in the reach tend to remain until they approach smolt size.

2.3.6 | Interspecific Differences Between Rainbow and Brown Trout

The model incorporates the difference in the timing of spawning of Rainbow Trout (spring) versus Brown Trout (fall). It also incorporates interspecific differences documented in the scientific literature in maximum and minimum spawning temperatures, the effect of temperature on egg development rate and mortality, and fecundity versus body length. Conversely, the simulations presented here assume a lack of differences between the two resident trout species in fish length versus mass, depth of egg deposition, movement capability, the effect of swimming speed on respiration, maximum swim speed versus length, and the effect of temperature on maximum swimming speed.

2.4 | Specific Methods Used in This Application

2.4.1 | Hydraulic Model

We used existing hydraulic models of pre- and post-restoration conditions at the study site described in detail by Flitcroft et al. (2022).

2.4.2 | Time Series for Physical Variables

We used streamflow data from the Sisters, Oregon, station (USGS 14076050) on Whychus Creek.

Year-round water temperature data were not available from Whychus Creek. To generate daily input for water temperature over the simulation period, we used measurements from a Whychus Creek site with observations for 40% of the simulation period and imputed missing data using the missMDA R package (Josse and Husson 2016) from relationships with streamflow and air temperatures measured nearby. This approach yielded a strong correlation between predicted and observed daily water temperatures ($r = 0.97$); however, the complete temperature record used in the simulations included extrapolation to fall and winter seasons that lacked water temperature measurements.

Few observations of turbidity were available near the study area. Therefore, we applied a linear relation between turbidity and streamflow, which produced turbidities similar to several spot measurements at the study site during high streamflow. The estimated turbidity input no doubt frequently differed from actual turbidity because the sources of turbidity at the study site include inputs not well linked to streamflow—specifically snow and glacial melt from high-elevation sites with abundant glacial sediments—but both estimated and actual turbidities at the study site were low enough to have negligible effects on simulated fish during the lengthy periods of low streamflow that dominate the hydrograph much of the year.

2.4.3 | Habitat Cell Delineation and Assignment of Habitat-Cell Attributes

Habitat cells were laid out considering ecological factors (capturing habitat variation, being no smaller than the area used by individual fish) and computational efficiency (avoiding unnecessarily small cells). For a 650-m reach within the restoration project and separately for the pre- versus post-restoration conditions, one person delineated habitat cells using aerial photography of the study area overlaid with cells from the pre- or post-restoration hydraulic models and cell-specific water depths and velocities across a range of streamflows (2.5 m^3/s [20% exceedance], 25 m^3/s [5% exceedance], and 58 m^3/s [< 1% exceedance]). Habitat cells for the fish model were delineated by aggregating cells from the hydraulic model, with the goal of minimizing within-cell variation in water velocity, depth, and distance to cover relative to variation in those variables among cells. Habitat cell delineation included the entire area covered by water at the highest streamflows during the simulation period. The process yielded 5263 habitat cells averaging 8.4 m^2 for the pre-restoration reach and 7664 habitat cells averaging 9.0 m^2 for the post-restoration reach (Figure 1). Water depth and velocity for fish-model cells were estimated as the area-weighted means of depth and velocity for the hydraulic model cells included in each fish model cell. Water depth and velocity were estimated for habitat cells across a broad range of streamflows to facilitate subsequent estimation by interpolation of depths and velocities at the simulated streamflows. To aid in the estimation of distance to cover and the number of concealment spaces, for the post-restoration model, the person making those estimates examined a series of recent on-the-ground photographs of the study reach in addition to the aerial photographs. Because information on model-specific habitat variables was not available for the simulated reach prior to restoration, we estimated distance to cover, the number of concealment spaces, and velocity shelter for habitat cells in the pre-restoration model using recent on-the-ground photographs of an upstream area with a single-thread stream similar to the stream in the simulated reach under pre-restoration conditions. Finally, we used pre- and post-restoration maps of spawning gravel provided by Paul Powers (personal communication) to estimate its habitat-cell-specific availability.

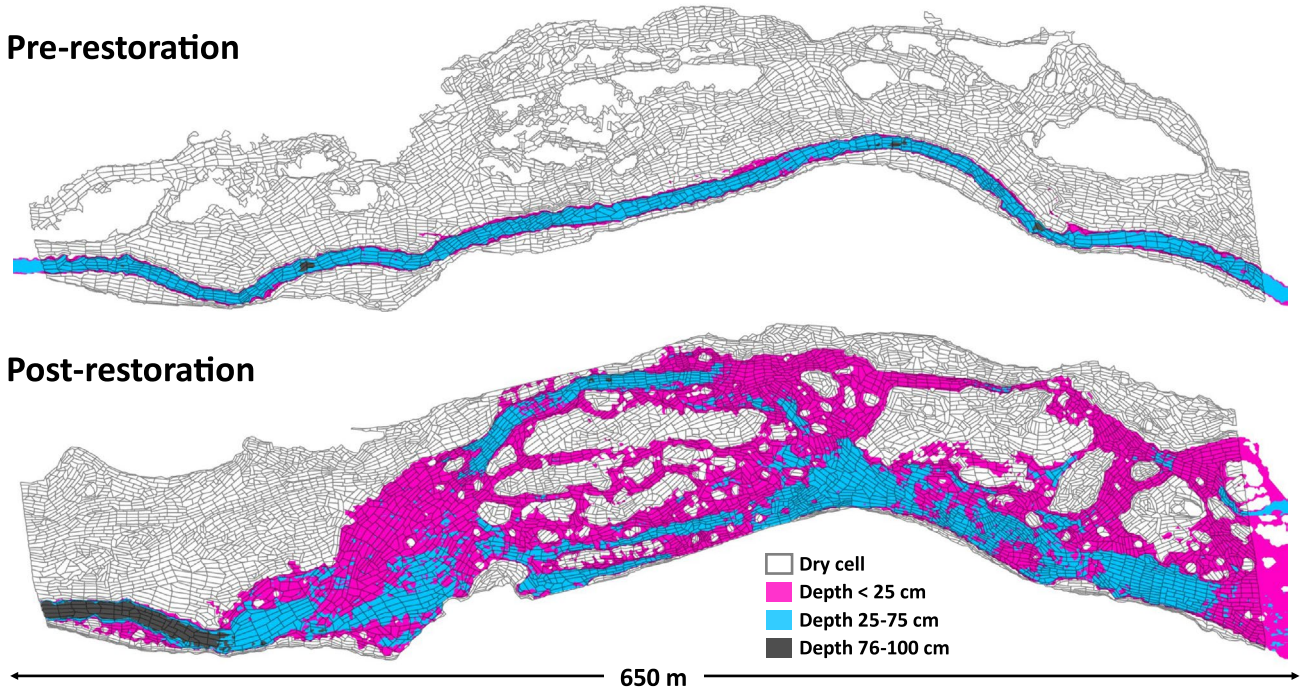

FIGURE 1 | The portion of a restoration site on Whychus Creek, Oregon, simulated for this study. Streamflow is 2.5 m^3/s (20% exceedance flow) in both the pre-restoration and post-restoration panels. Polygons indicate the habitat cells delineated for use in a spatially explicit, individual-based fish model (pre-restoration, 5263 cells; post-restoration, 7664 cells). For both scenarios, habitat cells cover the area inundated at the same maximum simulated flow. [Color figure can be viewed at wileyonlinelibrary.com]

2.4.4 | Calibration

We calibrated the model to the one fish sample within the modeled reach from the pre-restoration period, which included multi-pass electrofishing of a 200-m-long subsection of the simulation reach in 2015. We used the results of that sample as the target for average model results under pre-restoration conditions. We used the abundance and mean length of three age classes (age 0, age 1, age 2 and older, determined by frequency distributions) of both Rainbow and Brown Trout as calibration targets. We included four parameters typically included in the calibration of inSTREAM 7, those representing drift and search food availability and aquatic and terrestrial predation risk. We used prospective parameter values within ranges determined from previous applications of inSTREAM 7. We considered the absence of extensive observations for use in calibration not critical, and we did not conduct an extensive calibration, because here the emphasis was on contrasting two scenarios that used the same calibrated parameter values. Calibration values of food and risk parameters under pre-restoration conditions yielded mean annual values of the 12 abundance and length calibration targets that varied from the observed values in the 2015 fish sample by an average of 22%.

2.4.5 | Contrasts

We contrasted fish-abundance results from pre- and post-restoration simulations of the study area from 2005 to 2019. To reduce the influence of initial conditions, we ignored the first 3 y of simulation results. For the two alternative scenarios (pre- versus post-restoration), in addition to using the same values for the food and risk calibration parameters, we used the same initial fish populations and annual inputs of anadromous fish and the same daily inputs for streamflow, temperature, and turbidity. Therefore, differences in fish population results between scenarios stemmed specifically from their differences in physical habitat as represented by their separate hydraulic models and sets of fish-model habitat cells and habitat cell characteristics.

We also made limited comparisons involving the simulation results and both the single pre-restoration field sample of fish in 2015 and a post-restoration sample of fish in the same 200-m subsection in 2018. In particular, we compared total resident trout abundances and the relative abundances of Rainbow and Brown Trout in simulations versus field samples under pre- versus post-restoration conditions. We recognize that the comparison of simulation and field sampling results has a variety of limitations, including: the single field sampling events pre- and post-restoration, effects of fish planting in the study area on the field observations, and the lack of complete overlap in the simulated and sampled reaches.

3 | Results

Simulations of a 650-m reach of Whychus Creek and salmonid populations therein under pre- versus post-restoration scenarios indicated substantial benefits of valley-bottom restoration for resident trout. Higher abundance under post-restoration conditions persisted in every year, even as abundance exhibited substantial annual variation (Figure 2). Variation in annual reproductive success included complete year-class failures for both Brown Trout (2015) and Rainbow Trout (2017) under both scenarios. Inspection of the physical data input indicated that temperature and streamflow regimes combined to limit spawning opportunities in those years. The increase in abundance of trout age 1 and older under the post-restoration scenario versus the pre-restoration scenario

averaged about 5× in the simulations, similar to the ratio of about six for the 2018 field sampling (post-restoration) versus the 2015 field sampling (pre-restoration; Figure 3). The abundance of age 1 and older Rainbow Trout as a proportion of total age 1 and older resident trout was similar in pre- and post-restoration simulations; this pattern did not match a decline in the relative abundance of Rainbow Trout in the post-restoration (2018) versus the pre-restoration (2015) field samplings (Figure 4).

Results for Chinook Salmon in the same simulations that included resident trout did not suggest strong differences in spawning and egg incubation success in pre- versus post-restoration scenarios, but did indicate a strong increase in the post-restoration scenario in the ability of the reach to retain and provide growth opportunities for age 0 fish (Figure 5). Inspection of daily patterns suggested that the rapid loss of young Chinook Salmon from the reach under pre-restoration conditions did not depend on short-term peaks in streamflow, but on a general shortage of habitat for young fish during the post-emergence period. Under pre-restoration conditions, all age 0 Chinook Salmon died or outmigrated by the end of May, but under post-restoration conditions, outmigration from the reach typically continued into July (Figure 6).

Stranding of age 0 trout was substantially higher in the post-restoration scenario compared to the pre-restoration scenario, but was < 1% of both total mortality and abundance for trout in older age classes in both scenarios. Stranding accounted for about 24% of all mortality of age 0 Brown Trout in the post-restoration scenario and < 1% of mortality in the pre-restoration scenario, but this increase did not prevent consistently higher abundance of age 0 Brown Trout in the post-restoration scenario (Figure 2). Stranding accounted for 7% of mortality of age 0 Rainbow Trout in the post-restoration scenario and < 3% of mortality in the pre-restoration scenario, but higher stranding

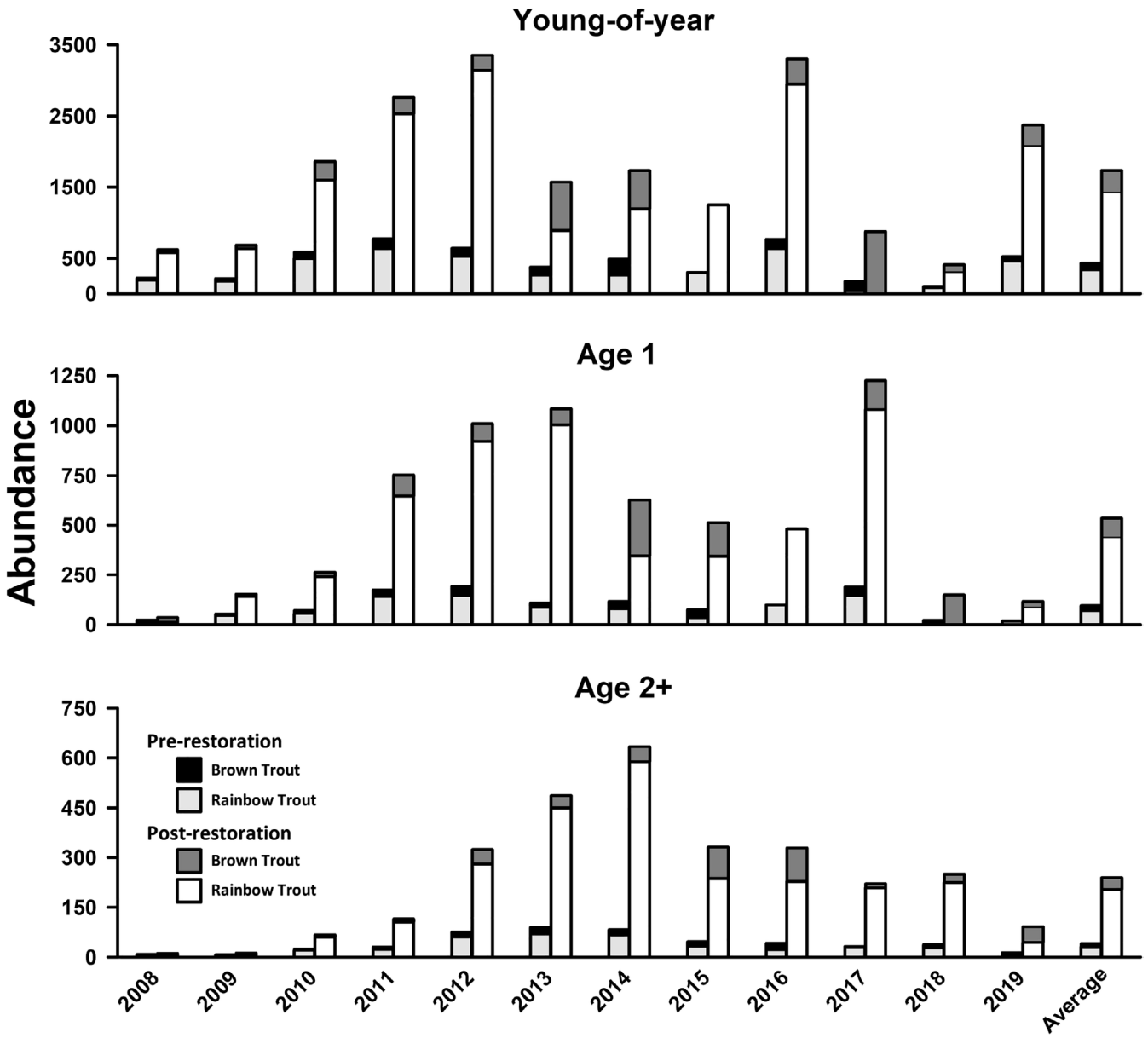

FIGURE 2 | Simulation results for resident trout under pre-restoration (left-hand bars) and post-restoration (right-hand bars) scenarios at a 650-m long site on Whychus Creek, Oregon, categorized by age groups and species.

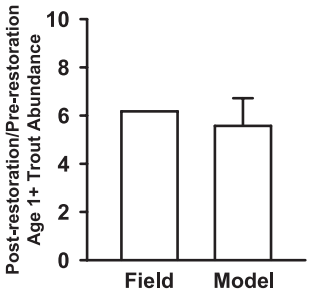

FIGURE 3 | Comparison of restoration effects in field results versus simulation results, expressed as the ratio of post-restoration to pre-restoration abundance of age 1 and older trout. Field results are derived from one pre-restoration (2015) and one post-restoration (2018) sampling of fish within a 200-m subsection of the 650-m simulation reach, conducted by multi-pass electrofishing. Model results summarize the last 12 years of 15-year simulations: 10 replicate simulations under pre-restoration conditions and 10 under post-restoration conditions. The model result is the geometric mean (and SD) of 10 ratios obtained by randomly pairing pre- and post-restoration replicates.

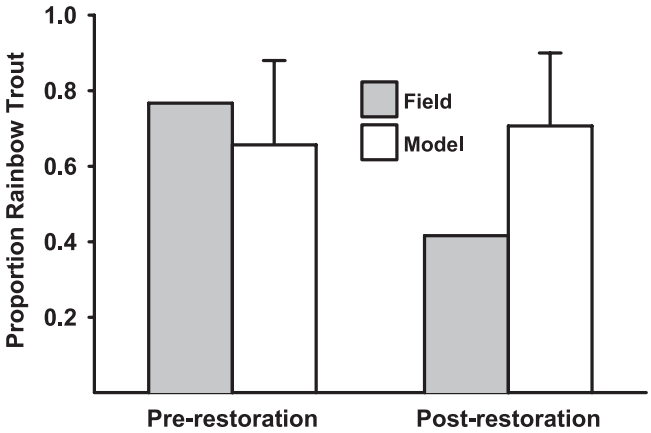

FIGURE 4 | Field and simulation results for Rainbow Trout age 1 and older abundance as a proportion of the total abundance of Rainbow and Brown Trout, under pre- versus post-restoration conditions. Field results were obtained by multi-pass electrofishing in 2015 and 2018 of a 200-m subsection of the 650-m simulation reach. Simulation results indicate the mean (and SD) for 10 replicate simulations. As suggested by Figure 2, simulation results also varied widely among years within replicates.

mortality also did not prevent large increases in the abundance of age 0 Rainbow Trout in the post-restoration scenario. No Chinook Salmon died of stranding in the simulations. However, while Chinook Salmon juveniles did not die from terrestrial predation in the pre-restoration scenario, terrestrial predation was responsible for 15% of predation mortality in the post-restoration scenario, probably in part as a result of Chinook Salmon occupying shallow water more often in the post-restoration scenario.

4 | Discussion

We illustrated the ability of a spatially explicit, individual-based fish model to translate reach-scale physical changes into consequences for populations, while incorporating the effects of external factors that can alter streamflow, temperature, turbidity, and the composition of fish assemblages. Continuous simulations of relatively lengthy stream reaches, involving virtual fish with realistic habitat selection capabilities, provide the opportunity to detect the influence of specific arrangements of habitat over time and space. Incorporation of external factors gives such models the potential to incorporate restoration measures beyond physical alteration of the valley bottom and stream channel, including, for example, streamflow enhancement and changes to fish passage. Incorporation of external factors also provides the ability to address the effects of climate change (Ayllón et al. 2019, 2021) and its potential interactions with restoration efforts.

The simulations presented here indicate substantial benefits of valley-bottom restoration for resident trout in the study area and potential benefits for Chinook Salmon. Model predictions of increased resident salmonid abundance corresponded with limited empirical observations at the study site, indicating a striking increase of more than 5×. These results are on the high end of observations elsewhere of favorable responses by salmonid populations to restoration that increases channel complexity, wetted area, and floodplain connectivity (e.g., Bouwes et al. 2016). In contrast to results for resident trout overall, model predictions about the relative abundance of Rainbow and Brown Trout did not correspond with a single post-restoration sample. We suspect that in addition to the constraints on comparisons between model results and single field samples described in Methods, the disparity in relative abundance results was also affected by the fact that the model does not include piscivory in its feeding submodels. Post-restoration, adult Brown Trout in particular may have benefitted from greater opportunity to consume juvenile fish. Both piscivory and the possible difference between Brown and Rainbow Trout in the propensity for piscivory (Yard et al. 2011) could readily be included in a revised model. Finally, the simulation result of a strong increase in the ability to support juvenile Chinook Salmon in the post-restoration versus the pre-restoration scenario could not be compared to any empirical data because of current limitations on the access of Chinook Salmon to the reach, but substantial benefits of floodplain habitat for Chinook Salmon have been observed elsewhere (e.g., Jeffres et al. 2008; Bellmore et al. 2013).

While persistent benefits of valley-bottom restoration for salmonid fishes emerged clearly from the simulations, occasional reproductive failures under both pre- and post-restoration scenarios indicated the influence of external factors on the capability of the site to support fish. Inspection of simulation results suggested that current combinations of streamflow and temperature regimes can constrain spawning success in some years, although more information on the capabilities of trout to spawn under challenging physical conditions would add confidence to this part of the model. Other applications of inSTREAM and related models (Ayllón et al. 2019, 2021) and many other studies (e.g., Jonsson and Jonsson 2009; Tonina et al. 2022; Kaeding 2024) show the importance of long-term trends in streamflow and temperature for the sustainability of salmonid populations and therefore to restoration planning.

Although here we used a spatially explicit individual-based model to evaluate a completed restoration effort, model

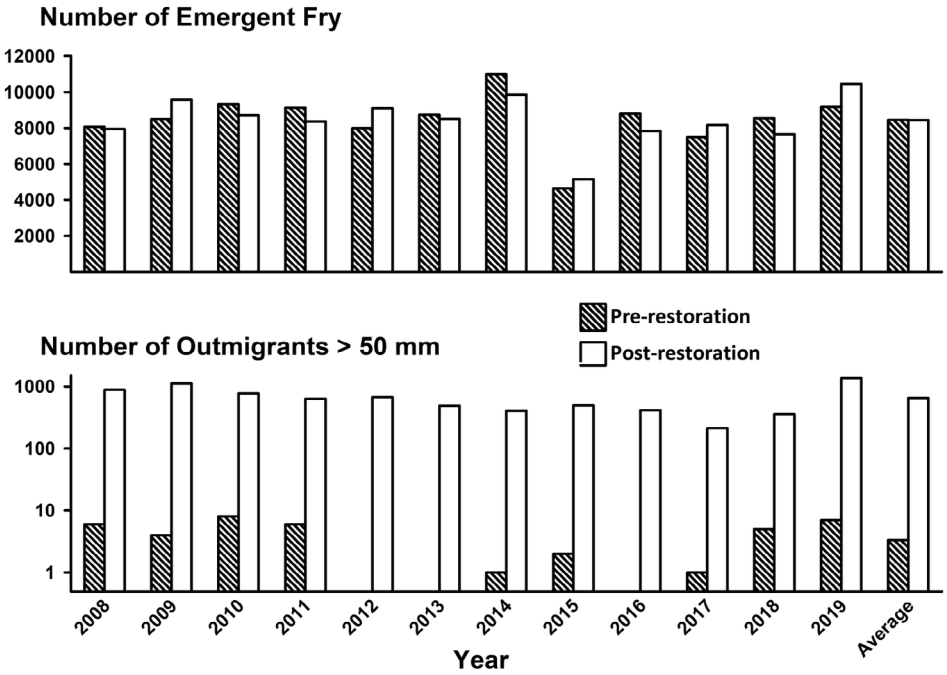

FIGURE 5 | Simulation results for Chinook Salmon under pre-restoration and post-restoration scenarios at a 650-m long site on Whychus Creek, Oregon. Note $\log_{10}$ scale of lower panel depicting the numbers of outmigrants > 50 mm fork length.

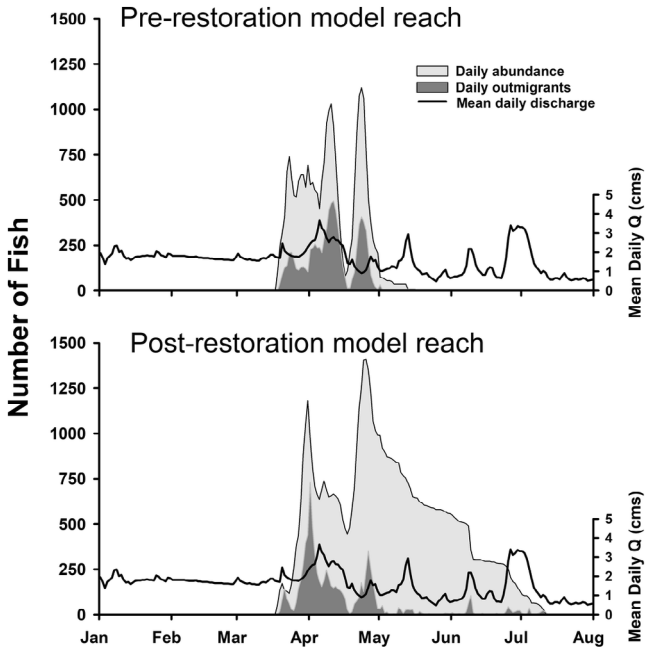

FIGURE 6 | Example pre- and post-restoration simulation results for Chinook Salmon, showing temporal patterns of abundance and outmigration.

simulations can have particular value in forecasting restoration outcomes, including comparisons of alternative designs. Methods to simulate prospective stream channels with the model we used are not especially challenging. Hydraulic models for alternative channel forms are readily generated. Here we made observations in a currently unrestored adjacent reach to inform simulation of the pre-restoration channel in the restored reach. Similarly, forecasting can use empirical observations at sites that exemplify anticipated conditions to supply reasonable distributions of values of model parameters that apply to individual habitat cells. Forecasting with the model we used also requires inclusion and consideration of larger-scale factors that should influence restoration planning, including anticipated temperature and streamflow regimes and the accessibility of restored areas to focal animal populations.

While the model we used includes substantial complexity, it also includes assumptions, such as spatial homogeneity of water temperature and food resources, known to be simplifications of natural conditions in complex stream channels (e.g., Bellmore et al. 2013; Flitcroft et al. 2022; Jennings et al. 2023). Given the importance of temperature and food to fish, it may make sense to add the capability to represent within-reach scale variation in these habitat characteristics to spatially explicit models such as inSTREAM 7, particularly where the extent of variation suggests that it will have meaningful ecological consequences (e.g., Majerova et al. 2020).

The example presented here also highlights the value of several modeling and monitoring activities now often associated with restoration efforts. Application of spatially explicit models such as inSTREAM almost always requires hydraulic modeling; existing hydraulic models of both pre- and post-restoration conditions at the study site were essential to the fish modeling we conducted in this study. Persistent, year-round monitoring of key physical variables (streamflow, temperature, turbidity) not only provides essential input for ecological modeling, but also often provides information useful in other ways. Finally, consistent pre- and post-monitoring of key response variables such as fish density, growth, and size distributions similarly provides essential information for the calibration and validation of ecological models, while also providing an ultimate form of assessment of restoration effectiveness.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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