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ARTICLE

Empirical and model-based evaluation of a step-pool stream restoration project: Consequences for a highly valued fish population

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Abstract

Objective: We sought to measure a step-pool restoration project's effects on a steelhead *Oncorhynchus mykiss* population and explore the capability of process-based modeling to enhance understanding of the results.

Methods: We used before-after–control-impact monitoring in combination with a process-based, individual-based, spatially explicit fish population model to evaluate a stream restoration project that reconfigured the channel and primarily added step pools to a reach of a second-order stream in northwestern California.

Result: Five years of monitoring both before (2012–2016) and after (2018–2022) restoration indicated that restoration caused substantial increases in the abundance and biomass of steelhead. Individual growth rates and retention of fish in the study reach did not exhibit consistent patterns, even in the first 2 years after restoration, when fish abundance and biomass exhibited extreme increases of about fivefold. Model simulations predicted about a twofold increase in the abundance and biomass of steelhead in the restoration reach, which corresponded with the empirical results 4–5 years after restoration. The model also predicted a similar increase in the production of steelhead out-migrants, a response we did not attempt to measure in the field.

Conclusion: Step-pool restoration benefitted steelhead. The model's correspondence with empirical observations indicates its potential applicability to more complex resource management questions in the study area, such as how restoration will combine with changes in climate to affect the sustainability of salmonid populations.

KEYWORDS

BACI, individual-based modeling, *Oncorhynchus mykiss*, steelhead, step pools, stream restoration

INTRODUCTION

After decades of extensive efforts to restore stream habitat, evaluations of those efforts allow few generalizations about their effectiveness (e.g., Bernhardt et al. 2005; Kondolf et al. 2007). Greater effort to evaluate and understand stream restoration is warranted by its history, which includes various practices unlikely to yield desired results. For example, Bernhardt and Palmer (2011) described the conceptual disconnect between carrying out reach-scale channel reconfigurations to address ecological responses actually controlled by watershed-scale processes. While efforts to monitor and evaluate stream restoration have increased (Wohl et al. 2015), great potential remains to improve understanding and methods; the variety and complexity of potential projects, environmental settings, and restoration objectives (e.g., O'Neal et al. 2016) create a strong need for useful evaluations to improve restoration practices (Wohl et al. 2015).

Among restoration practices involving channel reconfiguration, step-pool designs well-represent specific restoration actions in need of additional ecological evaluation. Stream restoration via the addition of steps pools—where large bed materials such as boulders are arranged perpendicular to the channel to create vertical drops that maintain downstream pools—is a widespread stream restoration technique. Step-pool restoration methods have a theoretical foundation in geomorphology (Chin and Wohl 2005; Chin et al. 2009), and the effects of step pools on macroinvertebrate assemblages—particularly in headwater streams—have received considerable study (Chin et al. 2009). However, the effects of step-pool restoration on fish have received little attention. Potential benefits of step-pool restoration for fish are suggested by the fact that less intensive but similar forms of restoration—construction of boulder and log weirs—have increased the abundance of salmonid fishes (Gowan and Fausch 1996; Roni et al. 2006), in some cases over decades (White et al. 2011; van Zyll de Jong and Cowx 2016). Also, limited evidence suggests that step-pool restoration may increase the density of benthic invertebrates and thus food availability for fish (Wang et al. 2009). On the other hand, consideration of step-pool restoration for fish in some settings may include the potential for steps to limit movement for some species (e.g., sculpins [family Cottidae] and dace [family Cyprinidae]; LeMoine et al. 2020) or for decreased stability of spawning gravel (Montgomery et al. 1999).

In this study, we used process-based, individual-based, spatially explicit modeling in combination with empirical monitoring to evaluate a step-pool channel reconfiguration project. The model provided the conceptual framework for monitoring and clear justification for specific monitoring measurements. Modeling allowed exploration of key process connections to enhance understanding and set the stage for better understanding of likely future scenarios that could include changes in temperature and hydrologic regimes or increased abundance of invasive species such as Brown Trout *Salmo trutta*. Our evaluation of restoration focused on a specific response of broad interest: the population dynamics of a highly valued salmonid fish.

Impact statement

Reach-scale stream restoration that primarily added step pools benefitted a steelhead population. Results from a spatially explicit, process-based model corresponded with real-world observations, suggesting that the model could help managers understand how restoration will interact with other environmental changes affecting fish.

METHODS

Study site

West Weaver Creek is a second-order tributary of the Trinity River in the Klamath Mountain Province in northwestern California. The drainage lies on the southern edge of the Trinity Alps Wilderness; the restoration project we evaluated (40.738900°, −122.967862°; elevation of 705 m) is about 3 km northwest of the town of Weaverville. The study included a control reach 1.7 km upstream (elevation of 800 m) from the restoration reach. The restoration reach drains approximately 20 km^2 of the West Weaver Creek watershed. The Mediterranean climate of the region is marked by a mild wet season (commonly October through May), with daily temperatures seldom averaging below 0°C and typical seasonal rainfall totals exceeding 900 mm. Although winter snow can accumulate at higher elevations, most (>95%) of the annual precipitation in the watershed falls as rain. The remainder of the year (June through September) yields little rainfall, and daily maximum air temperatures are frequently >30°C. The study area was subjected to intensive hydraulic gold mining in the 1800s. Mining-caused scarps and mounds of cobbles and boulders remain on the banks and floodplain, and the history of land-use disturbance throughout the watershed has produced a deeply incised active channel (in many places to bedrock), commonly with steep banks of coarse substrate. Gradient is 3.4% over the restoration site. The study area includes oak woodland and mixed coniferous forest. Riparian vegetation includes willows *Salix* spp., white alder *Alnus rhombifolia*, bigleaf maple *Acer macrophyllum*, Douglas fir *Pseudotsuga menziesii*, and ponderosa pine *Pinus ponderosa*. Mining, logging, and fire, including multiple fires since 2000, have altered the riparian vegetation.

West Weaver Creek in the study area supports steelhead *Oncorhynchus mykiss*, Pacific Lamprey *Entosphenus tridentatus* at low abundance, and occasionally Brown Trout. The study area is within the historic range of Coho Salmon *Oncorhynchus kisutch*, but none were captured during this study. West Weaver Creek also provides habitat for coastal giant salamander *Dicamptodon tenebrosus*, foothill yellow-legged frog *Rana boylii*, and tailed frog *Ascaphus truei*.

Restoration goals and description

The restoration project included floodplain and channel rehabilitation intended to improve conditions for salmonid fishes in West Weaver Creek (Environmental Science Associates [ESA] 2015). The goals of the project included improvement of fish passage through the project reach, improvement of instream conditions for salmonid rearing, and promotion of fine-sediment deposition on the floodplain. The design included construction of step-pool and boulder-cascade morphologic channel units, secondary channels, and lowering of the floodplain (ESA 2015; Rupp 2017 provides photographs). The project included 11 steps composed of large boulders over about 270 m of stream; step heights were typically 1–1.25 m. This study addresses the effects of restoration on stream channel morphology in the 5 years following implementation but does not include useful observations on sediment deposition on the floodplain or the evolution of secondary channels.

Study design

We used the original before-after–control-impact design, which compares the change, before versus after treatment, in the relationship between a control site and a treatment (or impact) site (Stewart-Oaten et al. 1992). We completed 5 years of sampling before the restoration project (2012–2016) and 5 years after (2018–2022) at both the control and restoration sites. We quantified fish abundance, biomass, growth, and retention in the 106-m control reach and in the upper 125 m of the approximately 270-m restoration reach. We also sampled a second control site (127 m long) between the restoration site and the original control site in 2015, 2016, and 2018–2021 to assess the assumption of the before-after–control-impact design that the primary control site represented temporal variability in the study area; fish biomass at the two control sites varied similarly across years ($r = 0.86$).

Fish sampling

To estimate fish abundance, biomass, growth, and retention, we sampled with a backpack electrofisher at the beginning (late spring to early summer) and end (late summer to early fall) of the dry seasons of 2012–2016 and 2018–2021. We also sampled in late spring or early summer of 2017. In 2022 we sampled only in the late summer. Collections normally consisted of two-pass depletion sampling, but when the second-pass catch exceeded 25% of the first-pass catch, we employed a third pass. In 2018, immediately following the channel reconfiguration in 2017, water depth in a single pool in the restored reach prevented effective backpack electrofishing. In response, in 2018 we snorkeled the deep pool and counted steelhead, distinguishing two size-classes designated as age-0 and post-age-0 fish. We used the depletion data to generate maximum likelihood abundance estimates (Van Deventer and Platts 1989) for the study reaches, adding the snorkel estimates to the depletion estimates for the restoration reach in 2018. We also measured length and mass of all collected vertebrates except in the restoration reach in 2018, when unusually high capture numbers along with logistical constraints prevented measurement of every individual. In that case, we recorded a hand count by size-class (age-0 and post-age-0 fish) of the unmeasured individuals. We inserted PIT tags into the body cavities of all measured and untagged steelhead >75 mm FL on all sampling occasions to quantify individual growth rates and retention of fish on the reach scale. Biomass estimates for the reaches incorporated the measured mass of all captured fish and an estimate of the mass of uncaptured and any unmeasured fish.

Fish model

To better understand the consequences of the restoration project for fish, we simulated both the pre- and post-restoration stream channels using a spatially explicit, individual-based model of salmonids (version 7 of inSTREAM; Railsback et al. 2023) modified to include the out-migration of smolts (Railsback et al. 2013; Harvey and Railsback 2021). The spatially explicit aspect of the model relies on site-specific delineation of habitat cells and hydraulic modeling. We separately represented all individuals within the simulated river reaches across multiple generations. Simulations included the annual arrival of adults with the potential to spawn in the reach and the incubation and emergence of their progeny. To represent the openness of the population, simulations also included annual spring or early summer immigration of age-0 fish. The model incorporates the ecologically important spatial and temporal complexity of real rivers. The model relies on delineation of two-dimensional habitat cells that together cover all areas wetted at the highest streamflows included in simulations. Habitat cells within the bank-full channel typically range from 4 to 16 m^2, while floodplain cells are larger. Each habitat cell has its own specific dimensions and values for parameters representing the availability of cover that influences short-term avoidance of predators, cover that allows long-term concealment behavior, velocity shelter that influences the benefits of feeding on drifting prey, and spawning gravel. Hydraulic modeling relates water depth and velocity within habitat cells to streamflow. The use of time series input for streamflow, water temperature, and turbidity in continuous simulations spanning multiple generations leads to fish in the model facing daily variation in environmental conditions, including changes in depth and velocity with any change in streamflow. In this application, model simulations relied entirely on site-specific empirical observations of habitat cell characteristics and physical regimes and site-specific hydraulic modeling before and after restoration. The model includes four daily time steps: night, dawn, day, and dusk. On each time step, individual fish select a habitat cell and activity (drift feeding, search feeding [any food acquisition that does not depend on water movement to transport prey to the fish, including surface feeding in low-velocity habitat], or hiding). A bioenergetics submodel then determines growth or weight loss of the fish, given its selection of habitat and activity. The model then determines whether the fish survives or dies from a series of habitat-, activity-, and size-dependent mortality risks, including predation and starvation.

In the model, fish use adaptive behavior to select habitat cells and activity. Fish determine growth potential and mortality risk for all combinations of habitat and activity available to them and also use their growth and mortality risk experience over three preceding time steps to select a combination of habitat cell and activity that best balances growth and risk (Railsback et al. 2021, 2023). When such habitat is available, fish typically select habitat and activity combinations that allow some growth and otherwise minimize mortality risks (Railsback et al. 2020). To represent anadromous steelhead life history, the model treated downstream migration as an additional habitat selection alternative, following methods in Railsback et al. (2013). On each time step, in addition to evaluating the value of the combinations of habitat cells and activity available to them within the area of the reach, individuals evaluated the fitness value of migrating downstream. The fitness value of migrating downstream is modeled as a logistic function of fish size. Because of the logistic function, newly emerged fry migrate downstream only if expected fitness in their current location is very low. Fry able to find productive habitat tend to stay and rear until they approach smolt size.

Railsback et al. (2023) provide a full description of a closely related resident-salmonid model. Here we note several of its characteristics especially relevant to this application. Food availability is assumed constant in space and time, and both drift concentration and area-specific search food availability are determined by calibration. Model scenarios that use the same drift concentration and the same input for streamflow provide the same level of drift food, but model scenarios in which the same level of streamflow yields different amounts of wetted area will yield different levels of search food. However, whether drift or search food in particular habitat cells is actually consumed by fish is determined by fish density and the trade-off decisions fish make in selecting habitat. For example, search food in an extremely shallow habitat cell lacking cover is unlikely to be used by larger juvenile salmonids because of relatively high predation risk in shallow water (Harvey and Stewart 1991) included in the model. For a second example, small juveniles may not occupy a relatively deep cell with water velocity favorable for drift feeding because of the presence of larger fish consuming drift food in that cell. Light level affects the reactive distance of drift feeding fish and predation risk but has negligible effects on both processes over the range of daytime light levels resulting from different amounts of riparian canopy. Habitat features and fish characteristics combine to affect the risk of predation; water velocity, water depth, the availability of cover, and fish size all influence the risk of predation by avian and terrestrial predators. Therefore, deep habitat cells with cover, such as those at the base of boulder steps, provide particularly safe habitat for fish in the model.

Field methods for modeling

We followed methods in Railsback et al. (2023) to delineate habitat cells and determine their model-specific parameter values. We used the same methods to represent the prerestoration scenario (in 2012) and the post-restoration scenario (in 2018), which included field identification of cross-stream transects and delineation of habitat cells along those transects (completed once for each scenario during late spring) and observations of cell-specific depths and velocities at four streamflows. Cell depths and velocities were modeled using PHABSIM's "IFG4" approach (Bovee et al. 1998), as implemented in RHABSIM software (Thomas R. Payne & Associates 1998). In calibrating the hydraulic model, we followed the recommendation of Railsback (1999) to emphasize matching observed cell depths and velocities over matching flows at the transect scale. Simulation of the prerestoration scenario included 268 habitat cells along 25 transects to represent the upstream 125 m of the restoration reach. Simulation of the post-restoration scenario used 347 habitat cells along 31 transects to represent the same reach. We did not attempt to represent the modest annual changes in channel form within the 5-year pre- or post-restoration periods. We also made hourly, year-round measurements of streamflow, temperature, and turbidity using methods described in Harvey et al. (2014) to produce daily mean values used as model input.

Model calibration

We calibrated the model of the prerestoration scenario to six empirically observed values: the mean fall abundances and lengths of three age-classes of steelhead (age-0, age-1, and post-age-1 fish) over the 5 years preceding restoration (2012–2016). Calibration simulations included 2009–2011 (and actual streamflow, temperature, and turbidity observations from that period) to eliminate the effect of initial conditions on model results. We used for calibration the four parameters that together represent food availability (drift concentration, search food availability) and predation risk (risk from terrestrial predators, risk from aquatic predators). We selected these parameters for calibration because they are uncertain, difficult to measure, and strongly influence model outcomes. We then used the calibrated values for food and risk determined from prerestoration measurements and simulations in all simulations of the post-restoration period. Prior applications of the model (Railsback et al. 2020) informed our choices of parameter values to include in calibration. The ranges of drift concentration and search food availability included in calibration also incorporated the assumption that large juvenile steelhead select drift feeding under most conditions. A relatively coarse calibration that included all combinations of four levels of drift concentration and three levels each of search food and the two risk parameters yielded a parameter combination with mean age-specific abundances and sizes within 8% on average of the six observed values.

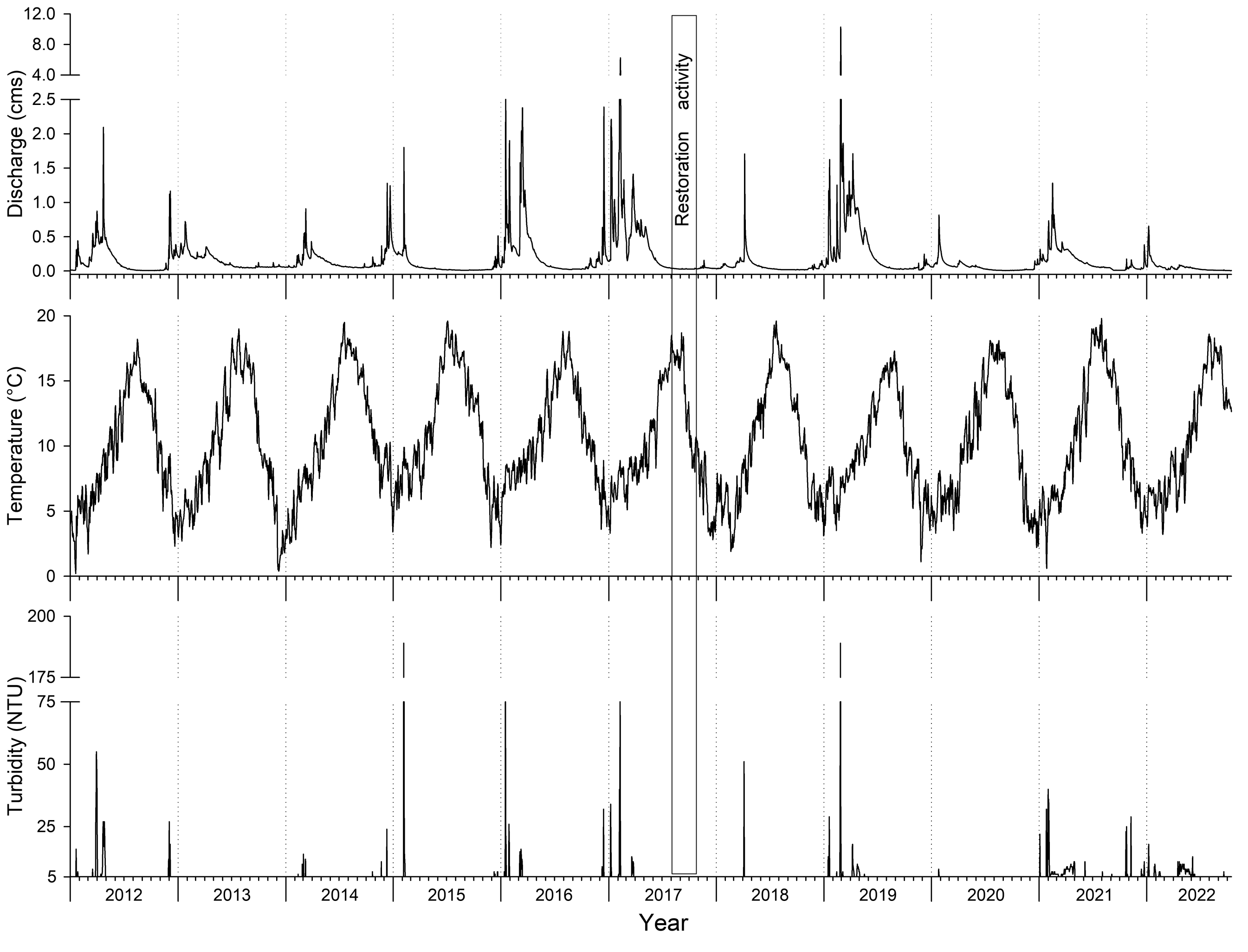

FIGURE 1 Physical regimes at the West Weaver Creek, California, restoration site during evaluation of a channel-reconfiguration restoration project conducted in 2017.

Analytical approach

To contrast pre- and post-restoration scenarios, we conducted simulations that differed only in the representations of the physical habitat developed from field observations and hydraulic models under pre- versus post-restoration conditions. We focused on results for the post-restoration period (2018–2022), but simulations included the prerestoration period to eliminate the effects of initial conditions on reported results.

To assess credibility and better understand the simulation results, we compared the activity selection (drift feeding, search feeding, concealment behavior) of fish in the model under pre- and post-restoration scenarios. Finally, to explore the potential for variation in food availability to affect results, we simulated the post-restoration scenario across a range of food availability.

RESULTS

Physical conditions

Streamflow, temperature, and turbidity regimes remained suitable for steelhead throughout the study, with no marked differences before versus after restoration (Figure 1). After restoration, the upper 125 m of the project area included in fish sampling and model simulations included eight

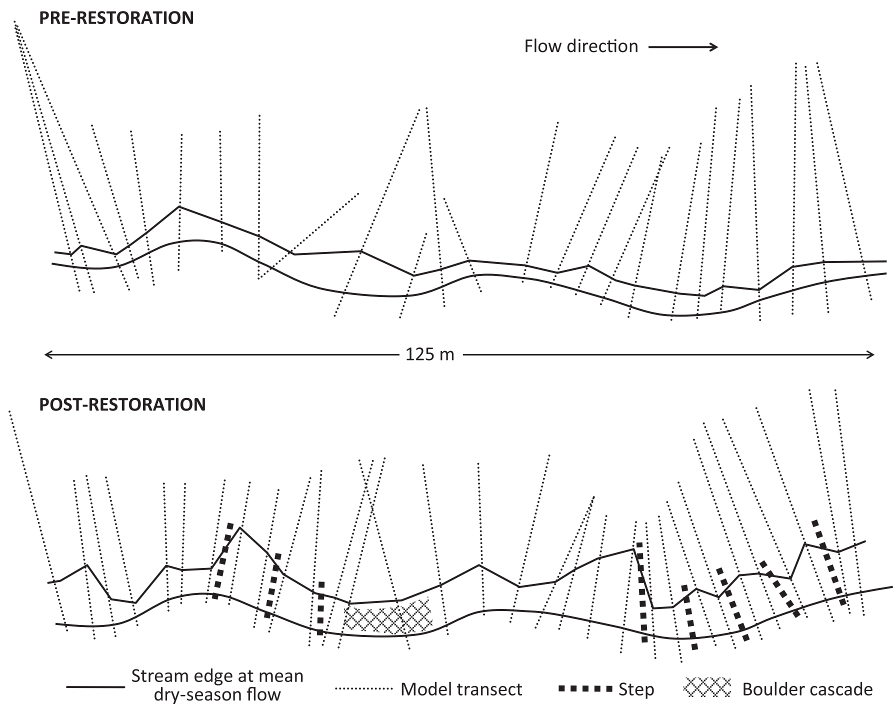

FIGURE 2 Diagrams of the pre- and post-restoration channels in a 125-m reach of West Weaver Creek, showing stream widths at the mean streamflow (0.03 m^3/s) for July–September, 2010–2022, and transects used for hydraulic modeling and habitat simulation. Transects extended approximately to the valley walls.

TABLE 1 Habitat areas (m^2) in various categories under pre- and post-restoration scenarios within a 125-m-long reach on West Weaver Creek, California, as determined from on-site habitat cell delineation and hydraulic modeling completed to support simulations using a spatially explicit, individual-based fish model. We used the 2012–2022 mean streamflow for July through September (0.03 m^3/s) to represent the dry season and the mean streamflow for April through June (0.20 m^3/s) to represent spring.

	Dry-season streamflow		Spring streamflow	
Habitat	**Before restoration**	**After restoration**	**Before restoration**	**After restoration**
Total	335	546	433	594
Depth ≥20 cm	129	287	253	426
Depth ≥20 cm, distance to cover ≤30 cm	38	57	73	108
Depth ≥20 cm, velocity ≤15 cm/s	113	260	83	303

constructed step pools (Figure 2). At typical dry-season streamflow, restoration caused about a 60% increase in the total wetted area of the stream and about a 120% increase in stream area with depth > 20 cm (Table 1). For typical spring streamflow, post-restoration total wetted area was about 35% higher and stream area with depth > 20 cm was about 70% higher. Restoration also increased relatively deep areas with relatively short distances to cover (Table 1).

Fish

The biomass and abundance of steelhead in the study reach exhibited dramatic increases in the first 2 years following restoration, followed by general decline (Figure 3). However, 5 years after restoration, the biomass of post-age-0 steelhead remained 3.8 times higher than in the control reach, after averaging 2.2 times higher

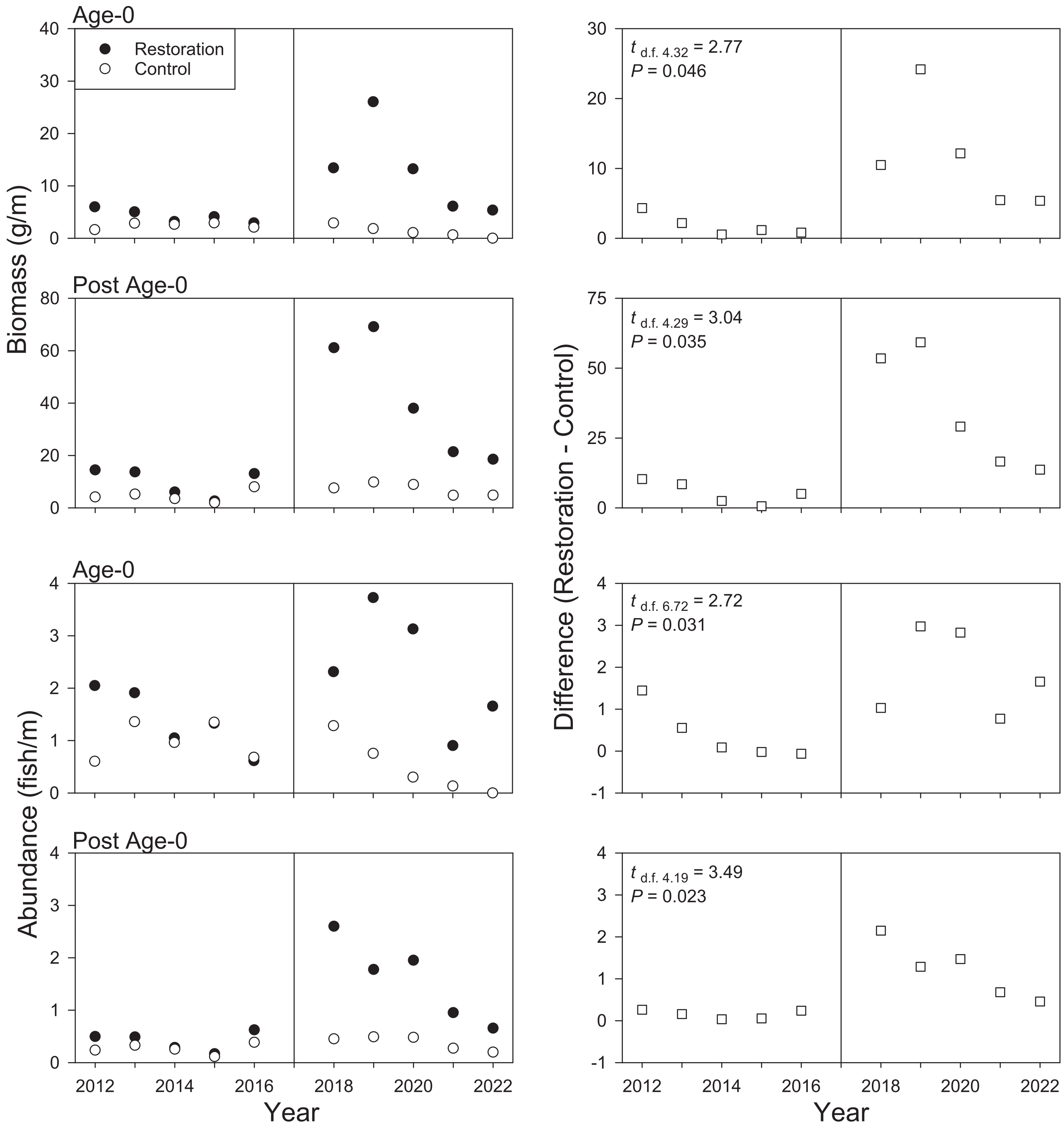

FIGURE 3 Biomass and abundance of steelhead, by age-class, determined from fall sampling in two reaches of West Weaver Creek, California, before and after restoration of one of the reaches in 2017. Panels in the right column depict the differences between restoration and control that provided the before–after contrast analyzed with the Satterthwaite *t*-tests included on the figure.

during the 5-year prerestoration period. Sustained benefits for age-0 fish were also evident (Figure 3). In contrast to the change in fish biomass and abundance after restoration, individual growth rates and retention of fish exhibited lesser change in the differences between restoration and control reaches before versus after restoration (Figure 4). However, post-restoration growth rates in the restoration reach persistently exceeded growth rates in the control reach in both the dry and wet seasons, even in 2018 and 2019 when the restoration reach supported especially high biomasses of fish. Perhaps contrary to expectation, high fish biomass in the restoration reach in 2018 and 2019 was not consistently accompanied by low retention of fish; the restoration reach exhibited

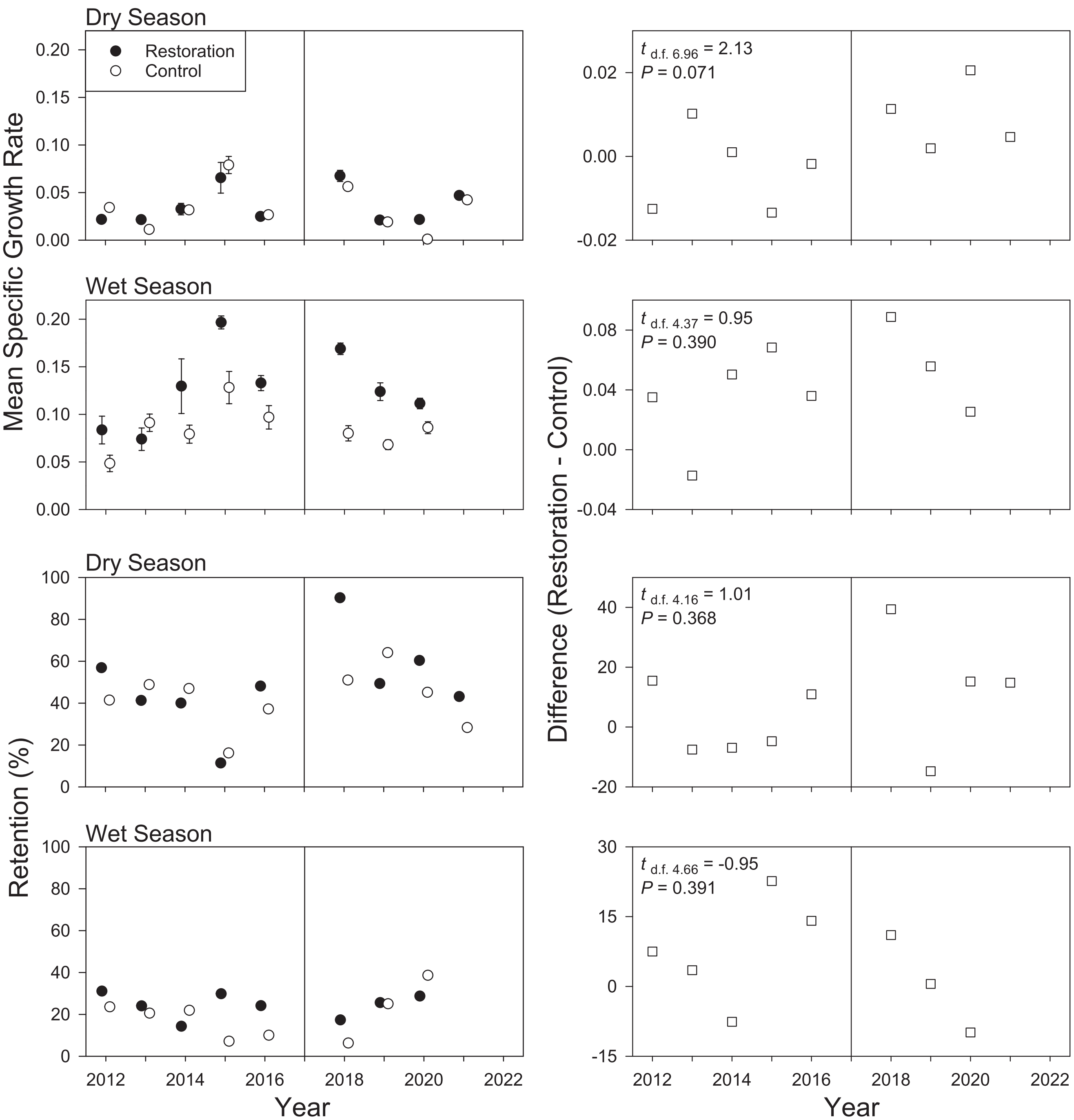

FIGURE 4 Growth and retention of steelhead >75 mm FL, determined from spring and fall sampling in two reaches of West Weaver Creek, California, before and after restoration of one of the reaches in 2017. Wet-season growth and retention results for a given year relied on fall samples from that year and spring samples from the next year (e.g., wet-season results for 2016 depended on spring samples in 2017). Panels in the right column depict the differences between restoration and control that provided the before–after contrast analyzed with the Satterthwaite *t*-tests included on the figure. Growth rate error bars indicate ±1 SE.

relatively high retention of fish over the dry season in 2018 and low retention in 2019 compared with subsequent years with lower biomass.

Comparison of individual-based model simulations of the pre- and post-restoration reaches also indicated benefits from restoration (Figure 5). Simulation results for the five post-restoration years indicated 2.1 times more biomass of post-age-0 steelhead on average in the post- versus prerestoration scenario. Simulated age-0 biomass averaged 2.2 times greater in the post-restoration scenario. While simulation results for the post-restoration scenario did not reflect the initial, dramatic increase in fish biomass observed following restoration, simulations corresponded with empirical observations 4 and 5 years after restoration (Figure 5). Simulation results also indicated that restoration would benefit the production

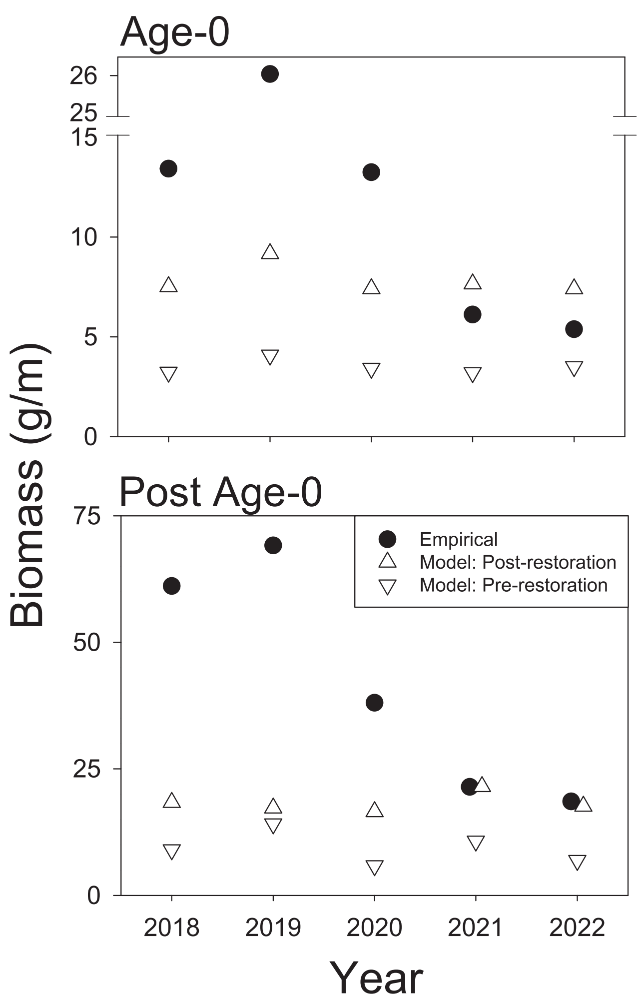

FIGURE 5 Comparison of empirical observations and individual-based model results for steelhead biomass under pre-versus post-restoration models of the stream channel. Simulations of the two scenarios began on the same date, using the same initial fish populations and the same streamflow, temperature, and turbidity input for all dates in the simulations (shown in Figure 1). Simulation results are the means of 10 replicate model runs.

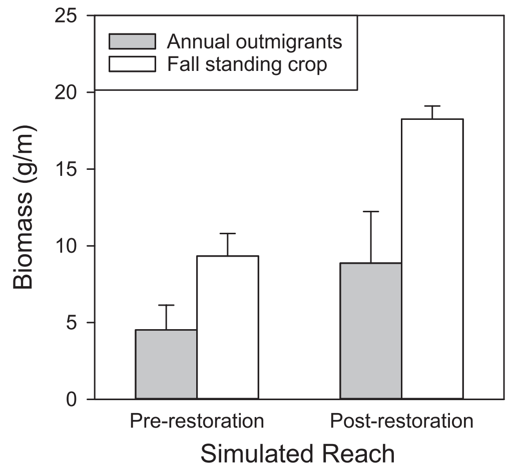

FIGURE 6 Mean biomass of steelhead over five simulated years under pre- and post-restoration scenarios at West Weaver Creek, California. Error bars indicate 1 SE.

of out-migrants in parallel to the benefits observed for standing fish biomass within the reach (Figure 6).

Comparison of fish behavior in simulations of the pre- and post-restoration scenarios, on the same simulated days and therefore with the same streamflow, water temperature, and turbidity within each comparison, revealed reasonable differences and similarities between the two scenarios (Figure 7). Restoration yielded greater availability of relatively deep water with low velocity, which explains the consistently higher proportions of fish selecting search feeding in the post-restoration scenario. Higher streamflow on the spring date compared with the summer date explains the higher proportion of drift feeding in the former, under both pre- and post-restoration scenarios.

Simulation of the post-restoration scenario across a range of food availability indicated the potentially strong influence of food at the population level. The simulations suggested that—with all else equal and with the assumption that all fish biomass stemmed from the survival and growth of age-0 fish within the simulated restoration reach—a twofold increase in food availability would have been needed to account for the observed large increase in fish biomass immediately after restoration (Figure 8). The predicted increase in the fish population was greater than proportional to the increase in food. Subsequent overprediction of fish biomass under increased food scenarios in later post-restoration years suggests only a temporary increase in food following restoration.

DISCUSSION

Both empirical observations and ecological modeling indicated persistent benefits for a salmonid population of

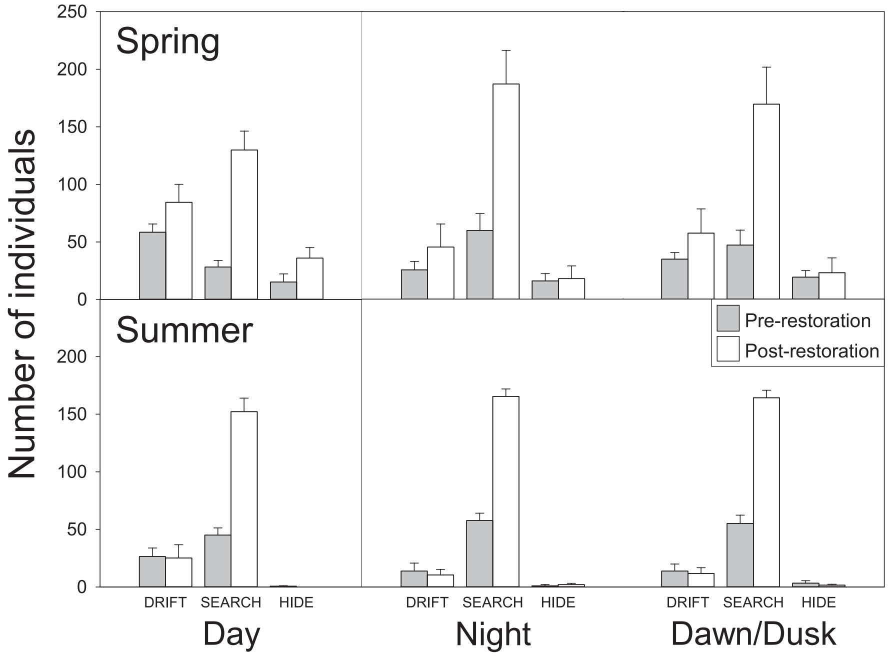

FIGURE 7 Behavior of virtual post-age-0 fish in simulations of the pre- and post-restoration conditions in a 125-m reach of West Weaver Creek, across different times of day, on two specific dates in spring and summer. Drift feeding, search feeding, and hiding are the three behavior alternatives virtual fish select among on each model time step (four time steps per day). Greater overall numbers of individuals in the post-restoration scenario in this graph reflect the larger fish populations under that scenario.

a step-pool channel reconfiguration project in a second-order stream. Stream restoration projects in general (O'Neal et al. 2016) and channel reconfiguration projects in particular (Bernhardt and Palmer 2011) have produced mixed results for a variety of ecological responses. In contrast to many prior restoration projects involving channel reconfiguration, the project at hand included several characteristics likely to contribute to measurement of a positive outcome. During this study, the watershed supplied the project site with high-quality water, a water temperature regime favorable for salmonid fish, and a natural flow regime. Also, the project immediately increased high-quality habitat for a vagile focal species (steelhead) at a readily accessible site. Finally, the project received considerable pre- and postassessment, thereby increasing the potential to detect change.

While ecological analyses of step-pool channel reconfigurations have previously focused on benthic invertebrates (Comiti et al. 2009), particularly in headwater streams (Purcell et al. 2002; Wang et al. 2009), this study illustrates the potential value of step pools for salmonid fish. This result corresponds with previous observations of positive effects on the abundance of juvenile salmonids with installed boulder weirs (Roni et al. 2006) and of relatively high densities of juvenile salmonids in natural step pools. For example, in multiple years of sampling in a California coastal stream, Caspar Creek, step pools held two times the average reach-scale density of post-age-0 steelhead (R. J. Nakamoto, unpublished data). Model simulations presented here incorporated multiple ecological process connections that likely contributed to the benefits of restoration, both in nature and in the model. In the model, increased water depth and cover provided by step pools constructed at the study site increased habitat with relatively low predation risk, particularly for post-age-0 salmonids (Harvey and White 2017) during low streamflow, when survival can be relatively low (Berger and Gresswell 2009). Virtual fish simultaneously considered both risk and food acquisition in habitat and activity selection, so lower predation risk also had positive consequences for food acquisition. Restoration resulted in more wetted area at a given streamflow and therefore an increase in total search food availability, given the assumption of constant area-specific search food in the model. In both the model and in nature, the depth gradients in the constructed step pools provided opportunities for physical separation of age-0 and post-age-0 fish. Such separation could be beneficial to age-0 fish via both reduced competition and reduced risk of cannibalism by larger fish.

We cannot readily explain the extreme initial response of the salmonid population in the first 2 years following restoration. Given that canopy reduction can have trophic benefits for stream salmonids (e.g., Kaylor and Warren 2017) and the strong influence of food availability in the model we used (e.g., Railsback and Harvey 2011), we explored the potential for a change in food availability

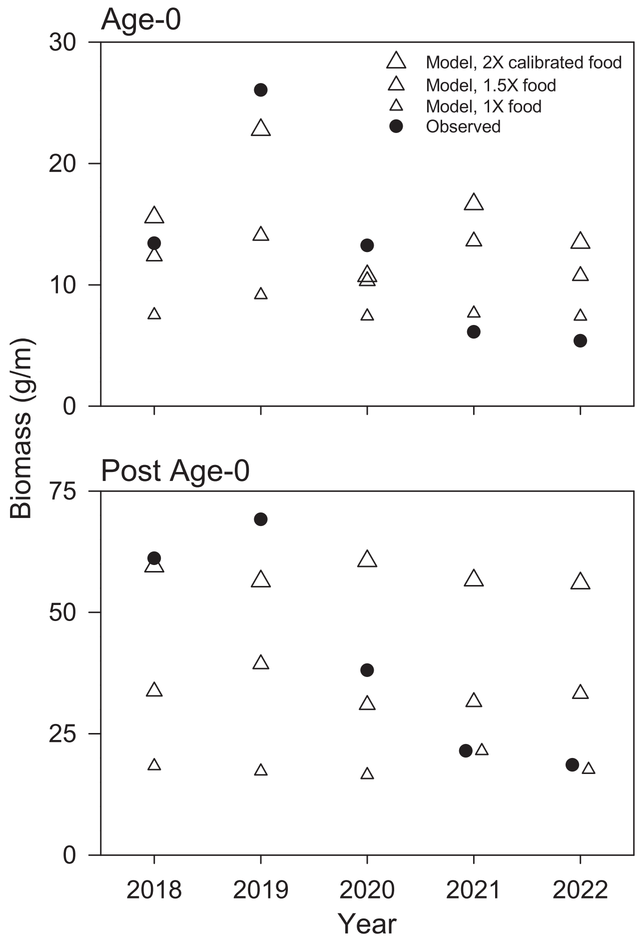

FIGURE 8 Comparison of individual-based model results from simulations of the post-restoration stream channel and sampling period, across a range of food availability. Triangle sizes distinguish scenarios with different levels of food availability that were multiples of the food availability determined by calibration of a model of the prerestoration scenario over the 5 years of prerestoration sampling (2012–2016).

to account for elevated fish biomass immediately following restoration. The simulations we conducted suggested that a doubling of food availability could account for the initial extreme increase in fish biomass, although this result relies on simplifying assumptions about spatial and temporal homogeneity in food availability. It remains unclear if a food availability hypothesis conflicts with the subsequent decline in fish biomass we observed in years 3 to 5 after restoration. Stream shading modestly increased in the 5 years following restoration, and it seems unlikely that instream primary production would have declined by 100% as a result, although previous research suggests that small differences in the canopy can affect fish through instream trophic pathways (Heaton et al. 2018; Kaylor and Warren 2018). On the other hand, increases in riparian vegetation from low levels might lead to increased food availability for salmonids from terrestrial inputs (Rosenberger et al. 2011). Beyond food availability, stream shading may affect fish feeding through effects on prey capture efficiency (Wilzbach et al. 1986), but this mechanism also seems incapable of explaining the decline in fish biomass over the 5 years following restoration, considering the relatively high light levels throughout the post-restoration period of the study.

The preceding paragraph makes clear the general point that better understanding of factors affecting food availability could improve our understanding of stream restoration effects on fish (and stream fish ecology in general). For example, the assumption of spatially and temporally constant food availability as drift per unit volume and search food per unit area in the stream fish model used here is clearly wrong, but current knowledge did not offer clearly better alternatives. However if, for example, a relationship between drift concentration and streamflow existed (Rashidabadi et al. 2022), it could significantly influence the consequences of restoration for fish and therefore be beneficially included in models.

This restoration evaluation highlights the importance of study length; in this case an 11-year study provided useful results but still left some questions unanswered. Our results indicate that a study limited to 1 or 2 years post-restoration would have been misleading, but persistent increases in fish abundance in the 5 years after restoration suggest that the project's design and implementation provided persistent ecological benefits. However, postproject streamflows have yet to challenge the sustainability and resilience of the project, although the increased connection of the stream channel and floodplain included in the restoration design gives reason for optimism as does the fact the restoration design included consideration of the potential for channel evolution (ESA 2015). Along with channel form, stream canopy cover will continue to change over time (Dyste and Valett 2019), with likely consequences for food availability and feeding conditions for fish (Hoover et al. 2007).

The process-based, spatially explicit model provided a useful framework for evaluating the consequences of habitat restoration. The model focused the evaluation on the response of greatest interest, a salmonid fish population, and provided an estimate of the most fundamentally important response variable for that population, the production of out-migrants, which would have been costly and difficult to measure in the field. The model also provided a clear rationale for a specific monitoring plan, including measurement of habitat characteristics with direct connections to the fitness of individual fish (e.g., velocity shelter and distance to cover) and continuous measurement of ecologically important physical variables of stand-alone interest (i.e., streamflow, water temperature, and turbidity). Model results for fish corresponded with empirical results 4 to 5 years after restoration, suggesting that modeling could provide useful forecasts of biological results where future environmental scenarios of interest can be quantitatively described. The approach to modeling and monitoring applied here can address the complex problems faced by resource managers, such as the need to better understand and predict the consequences of restoration efforts under likely future scenarios that could include more abundant invasive species and changes to streamflow and temperature regimes.

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CONFLICTS OF INTEREST STATEMENT

Authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

This study adhered to the American Fisheries Society's *Guidelines for the Use of Fishes in Research* (Use of Fishes in Research Committee 2014).

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