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Beyond sticks and stones: Integrating physical and ecological conditions into watershed restoration assessments using a food web modeling approach

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ABSTRACT

Watershed assessments have become common for prioritizing restoration in river networks. These assessments primarily focus on geomorphic conditions of rivers but less frequently incorporate non-geomorphic abiotic factors such as water chemistry and temperature, and biotic factors such as the structure of food webs. Using a dynamic food web model that integrates physical and ecological environmental conditions of rivers, we simulated how juvenile salmon (*Oncorhynchus* spp.) biomass responded to restoration at twelve sites distributed across the Methow River (Washington, USA), ranging from headwater tributaries to mainstem reaches. We explored responses to three common river restoration strategies: (1) physical habitat modification, (2) nutrient supplementation, and (3) increased riparian vegetation cover. We also simulated how different food web configurations that exist in salmon-bearing streams, such as the presence of 'non-target' fishes and 'armored' predation resistant invertebrates, could mediate restoration outcomes. Some locations in the river network experienced relatively large increases in modeled fish biomass with restoration, whereas other locations were almost entirely unresponsive. Spatial variation in restoration outcomes was primarily controlled by non-geomorphic environmental conditions, such as nutrient availability, water temperature, and stream canopy cover. Restoration responses also varied significantly with different food web configurations, suggesting that as the structure of food webs varies across river networks, so too could the outcome of restoration. These findings illustrate that ecological responses to restoration may exhibit substantial spatial variation within river networks, resulting from heterogeneity in environmental conditions that are commonly overlooked—but which can and should be considered—in restoration planning and prioritization.

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1. Introduction

When the outcome of restoration is successful at one location in a river network, it is natural to want to apply the same technique in other locations (Hilderbrand et al., 2005; Montgomery, 2006). This assumes that expected outcomes of restoration are roughly similar across river networks. It is well-known, however, that rivers exhibit variability in both abiotic and biotic conditions across space. From this, it follows that expected outcomes from specific restoration techniques can vary accordingly. Fluvial geomorphology and stream ecology have helped elucidate how the physical and ecological conditions of rivers vary (e.g., Montgomery, 1999; Power and Dietrich, 2002; Vannote et al., 1980), but knowledge from these fields has not been applied equally to restoration planning and prioritization. Restoration assessments have primarily focused on the geomorphic context for restoration (Fryirs and Brierley, 2013; Rosgen, 1997), such as the structure of river channels and floodplains. Although there are notable exceptions (Beechie et al., 2012; Bellmore et al., 2017; Justice et al., 2017), there has been limited consideration of how non-geomorphic abiotic factors, such as water chemistry and temperature, and biotic factors, such as community and food web structure, influence restoration outcomes.

From the field of fluvial geomorphology, watershed-scale geomorphic assessments have become common for prioritizing river

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restoration based on spatial variation in geomorphic conditions (see Buffington and Montgomery, 2013). Locations deemed to have high recovery potential are frequently those with detectable anthropogenic alterations to geomorphic processes (Beechie et al., 2010; Roni et al., 2002) or habitat structure (Rosgen, 1997), such as incised river channels that are disconnected from adjacent floodplains (Pollock et al., 2014), or segments that lack structural complexity, such as large wood (Wohl et al., 2019). These assessments, however, generally do not explicitly account for numerous other abiotic conditions, such as water temperature, turbidity, and nutrient availability, which can also mediate restoration outcomes (but see Beechie et al., 2012). For example, if water temperatures are outside the thermal optimum for target species, or if ambient nutrient concentrations strongly limit aquatic productivity, then ecological recovery may fall short of expectations defined by geomorphic conditions alone (McHugh et al., 2017; Sanderson et al., 2009). Furthermore, many restoration approaches that seek to ease conditions limiting target fish populations, such as riparian vegetation restoration, nutrient augmentation, and nonnative species removal, cannot be adequately evaluated by geomorphic assessments because these approaches do not directly modify the physical structure of the stream.

In the related field of stream ecology, there has been a longstanding focus on how food webs and the carbon sources that fuel aquatic productivity vary across space within river networks (Junk et al., 1989; Power and Dietrich, 2002; Vannote et al., 1980). Despite this existing knowledge, however, river restoration assessments rarely consider how food webs may affect restoration outcomes. Underlying this omission is the assumption that geomorphology directly affects the ecological structure and function of rivers (Wipfli and Baxter, 2010), including food webs; therefore, quantifying geomorphic characteristics is adequate for assessing ecological recovery potential. This assumption is likely to be only partially correct.

Geomorphic conditions do indeed influence the availability of carbon resources that support the base of river food webs. For example, the height and aspect of river valleys control the availability of light necessary for autochthonous primary production (Julian et al., 2008; Yard et al., 2005). The width and height of floodplains influence the structure of riparian vegetation that contributes allochthonous energy to the stream in the form of leaf litter and terrestrial invertebrates (Naiman et al., 2010; Stanford et al., 2005). And the morphology and hydraulics of river channels influence the physical retention of these organic matter sources (Bellmore et al., 2014; Wohl et al., 2018). However, the pathways and efficiency by which this basal energy is *routed* through food webs to species and trophic levels depend on the structure or the topology of the food web itself (Vander Zanden et al., 2016).

The topology of riverine food webs can be driven by the presence and abundance of different species that strongly regulate the pathways and efficiency of energy flows (Bellmore et al., 2013; Benke, 2018; Cross et al., 2013). For instance, aquatic predators, such as some fishes and amphibians, can modify the behavior and control the abundance of their prey (Layman and Winemiller, 2004; White and Harvey, 2001), and, in some cases, this top-down predation can indirectly affect the abundance of organisms at lower trophic levels via trophic cascades (McIntosh and Townsend, 1996; Power, 1990). Conversely, species that occupy lower trophic levels, such as primary consumers, can influence the efficiency of energy flow up to higher levels. For instance, the presence of armored grazers that are resistant to predation, such as some cased caddisflies and snails, can redirect energy flows into "trophic cul-de-sacs," which reduces prey availability to higher trophic levels (Vinson and Baker, 2008; Wootton et al., 1996).

Although geomorphic conditions *partially* control the presence and abundance of species by regulating basal resource availability and physical habitat niche space (Chessman et al., 2006; Vannote et al., 1980), the communities and resultant food webs that occupy different river segments are also strongly regulated by temperature and flow regimes, organism dispersal, resource subsidies, species invasions, antecedent conditions, and numerous other factors (Cross et al., 2013; Kendrick et al., 2019; Naman et al., 2016; Thomson et al., 2004; Wipfli and Baxter, 2010). Because all these factors vary across space, river networks are composed of a heterogeneous mosaic of food webs (Bellmore et al., 2013; Cross et al., 2013), each of which is likely to exhibit unique responses to restoration actions (Bellmore et al., 2017). Thus, understanding what ecological outcomes to expect from restoration and how they vary within river networks requires expanding restoration assessments beyond an appraisal of geomorphic conditions to include other abiotic factors, such as water and nutrient availability, as well as biotic conditions, such as the structure and dynamics of river food webs.

Here we used a simulation modeling approach to explore how spatial heterogeneity in abiotic and biotic conditions within a river network influences ecological responses to reach-scale restoration. We conducted model simulations for the Methow River in northern Washington State, USA (Fig. 1), where multiple restoration approaches are being applied to recover imperiled populations of Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*). We explore two key questions with our model analysis: (1) How does spatial variation in abiotic environmental conditions (specifically channel morphology and hydraulics, flow and temperature regimes, nutrient and light availability, and water turbidity) influence fish response to reach-scale restoration?; and (2) how might variation in the structure of local food webs mediate fish response to restoration? To explore these questions, we employed a food web simulation model, the Aquatic Trophic Productivity model (ATP model; Bellmore et al., 2017). We used the model to simulate responses to three alternative river restoration strategies, common to salmon recovery efforts in the region, that influence river ecosystems and fishes via different mechanistic pathways: (1) Increasing the quantity of habitat that is suitable for fish rearing (physical habitat restoration); (2) Increasing food resource availability by augmenting the stream with salmon carcasses; and (3) Altering inputs of terrestrial organic matter and light via restoration of riparian vegetation. Our main goal was to illustrate that ecological responses to restoration exhibit substantial spatial variation within river networks, resulting from spatial heterogeneity in environmental conditions that are commonly overlooked in restoration planning and prioritization.

2. Methods

2.1. Study area

The Methow River is a major tributary to the upper Columbia River in northern Washington State. It has experienced long-term declines in salmon and steelhead populations, leading to the Endangered Species Act listing of spring Chinook salmon and summer steelhead (NMFS, 2016). Restoration to recover these imperiled populations includes physical habitat improvements, salmon carcass augmentation, and planting of riparian vegetation. To explore how responsive different locations of the river network might be to these restoration alternatives, we selected 12 reaches (sites) across the watershed, ranging from 2nd order tributaries to 5th order main channel sites, for our model analysis (Fig. 1). These sites were selected because they have strong differences in physical and chemical conditions (Table 1, Appendix A; Mejia et al., 2019). Also, the environmental data necessary to conduct our model analysis were readily available from previous research. Each site was a part of the Columbia Habitat Monitoring Program (CHaMP)—a monitoring program aimed at establishing relationships between habitat conditions and juvenile salmonid productivity (ISEMP/CHaMP, 2018).

2.2. Model description and parameterization

We used the ATP model to explore how juvenile salmon biomass responds to restoration (Bellmore et al., 2017; Whitney et al., 2019). The ATP model is a dynamic food web simulation model, whereby the capacity of river ecosystems to sustain fish is explicitly tied to transfers

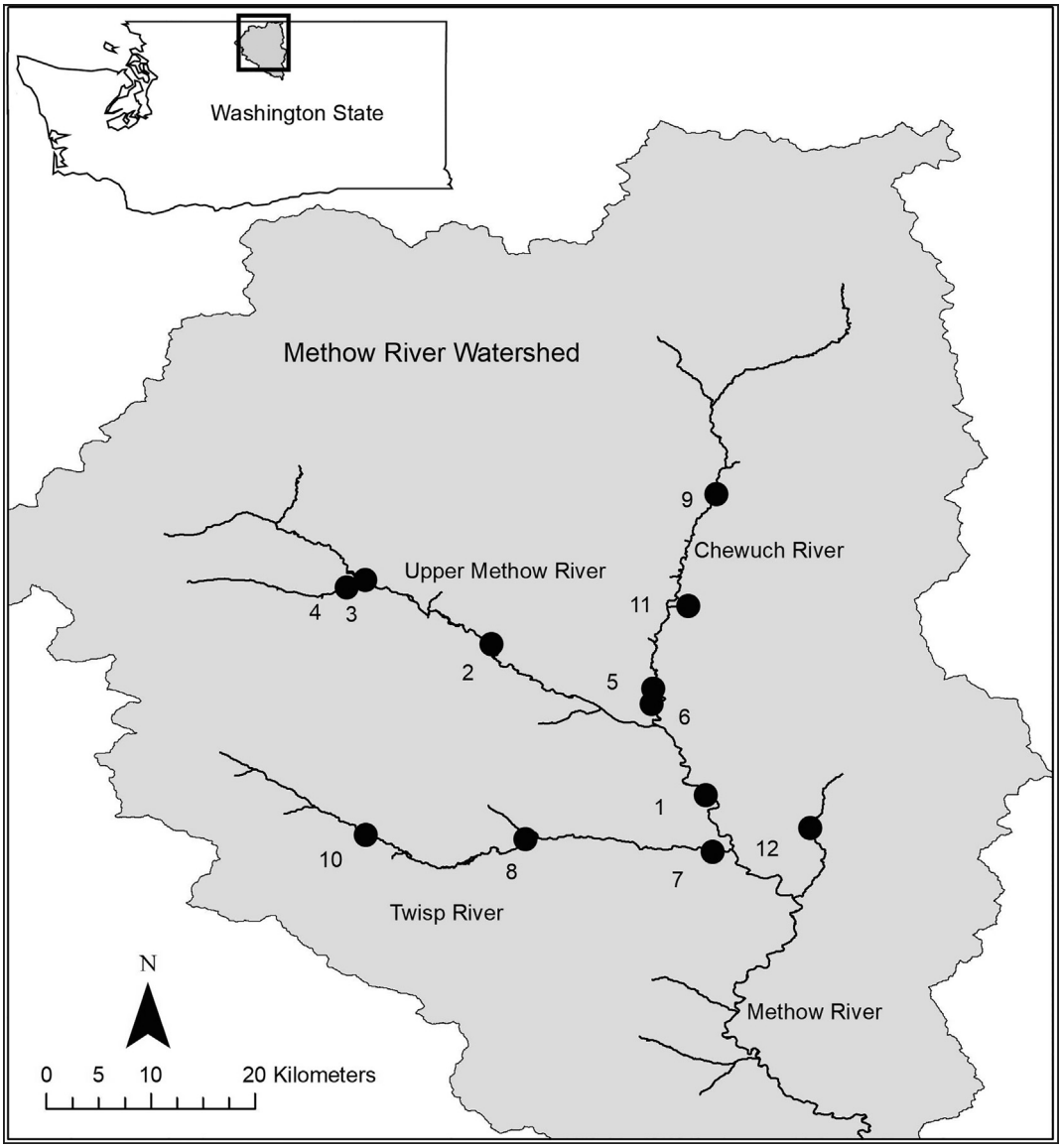

Fig. 1. Map of the Methow River watershed located in northern Washington state, USA, with case study sites (black circles). Labeled from largest average annual discharge (site 1) to smallest average annual discharge (site 12).

of organic matter between different components of a simplified river food web (Fig. 2). At the base of the food webs are biomass stocks of periphyton (e.g., attached algae) and terrestrial detritus (e.g., leaf litter from riparian vegetation), which are consumed by aquatic invertebrates. In turn, these aquatic invertebrates and terrestrial invertebrates that enter the stream from the riparian zone, are consumed by fish, which in this model analysis are represented as juvenile salmonids.

The model mechanistically links the food web dynamics, and the resultant performance of different web members, to (1) the physical conditions of the stream, (2) inputs of terrestrial organic matter and organisms from the adjacent riparian zone, and (3) marine-derived nutrient subsidies delivered by naturally spawning adult salmon or dead salmon that are purposefully added to the stream as part of nutrient supplementation efforts. In the ATP model, physical conditions, such as the turbidity of the water and nutrient concentrations, influence the amount of light and nutrients available to periphyton. Temperature mediates the bioenergetics of organisms and decay rates of organic matter. Stream discharge and channel hydraulics affect water depth, width, velocity, and shear stress, which in turn affect parameters such as habitat area and retention of organic matter. Riparian vegetation contributes to organic matter and invertebrates, as well as affects stream shading. Additionally, adult salmon returning from the ocean to spawn in freshwater affect the system through trophic and non-trophic pathways including providing food and nutrients and bioturbation of the stream bed during nest building. The model includes feedback loops that allow for interactions between the food web members and the site conditions. For an annotated description of the model structure, including visuals see Whitney et al., 2019. The modeling framework assumes that the general dynamics of the river food web can be predicted if the dynamics of these environmental factors are known. Following this assumption, the model can be used to explore how environmental changes influenced by restoration or changes to the structure of the food web itself (e.g., adding species or functional groups) might affect the overall dynamics of the food web and the performance of specific web members.

The model runs on a daily time step and tracks the biomass of periphyton, terrestrial detritus, aquatic invertebrates, and juvenile fish through time in units in grams of ash-free dry mass (AFDM). The

Table 1
Average environmental parameter values for each of the 12 sites in the Methow River Watershed. Sites are numbered based on decreasing average annual discharge. DIN = Dissolved inorganic nitrogen. SRP = Soluble reactive phosphorus. Data sources indicated by superscripts.

Parameter	Site 1	2	3	4	5	6	7	8	9	10	11	12
Discharge (m^3/s)[a]	30.9	20.1	16.8	10.9	10.8	10.8	7.2	6.8	6.2	3.5	1.4	0.7
Temperature (°C)[b]	7.2	7.3	6.9	5.1	7.6	7.2	6.5	6.3	6.9	5.3	6.8	6.7
Turbidity (NTU)[c]	6.4	6.0	6.1	5.8	7.2	7.2	7.1	6.1	6.4	5.8	7.9	8.7
Shading (%)[b]	25.2	39.8	53.0	56.1	32.6	49.0	54.8	49.6	52.1	82.7	61.2	64.3
Substrate size (D50, m)[b]	0.13	0.09	0.13	0.13	0.06	0.13	0.09	0.06	0.09	0.09	0.18	0.06
Channel width (m)[d]	40.6	41.2	40.5	22.2	28.5	26.4	19.6	25.4	27.1	14.5	6.3	6.6
Channel depth (m)[d]	0.69	0.50	0.57	0.57	0.58	0.45	0.40	0.45	0.36	0.37	0.26	0.22
Wetted area suitable for fish (%)[d]	37.8	29.7	40.1	24.0	46.2	33.0	27.6	37.2	34.5	29.6	21.4	22.9
Slope (m/m)[d]	0.004	0.005	0.005	0.011	0.004	0.009	0.006	0.001	0.005	0.013	0.045	0.016
DIN (mg/L)[c,e]	0.12	0.05	0.06	0.06	0.05	0.05	0.07	0.06	0.03	0.07	0.04	0.26
SRP (mg/L)[c,e]	0.003	0.002	0.002	0.001	0.002	0.002	0.001	0.001	0.003	0.002	0.007	0.010
Proportion of the stream covered by vegetation[f]	0.05	0.05	0.05	0.1	0.05	0.1	0.1	0.1	0.05	0.15	0.3	0.3
Number of returning salmon[g]	18.8	18.1	21.6	1.8	14.6	12.5	5.0	7.0	14.5	3.2	1.1	1.0

[a] Mastin, 2015.
[b] ISEMP/CHaMP, 2018.
[c] Zuckerman, 2015.
[d] Bureau of Reclamation, 2012, 2015.
[e] Washington Department of Ecology, 2016.
[f] Calculated based on the assumption that vegetation overhangs stream channel one meter on each bank.
[g] Calculated based on assumed density of 0.001 salmon/m^2 (Snow & Frady, 2013) and stream length.

model was constructed and executed in Stella Architect™ version 1.9.4 (isee systems, Lebanon, New Hampshire, https://www.iseesystems.com). This version of the ATP model was specifically structured to explore how juvenile salmonids respond to changes resulting from restoration actions or shifts in food web structure (Whitney et al., 2019). A thorough description of the model structure, parameter values, sensitivity analysis, and a comparison of model values to empirical data have been previously published (Bellmore et al., 2017; Benjamin et al.,

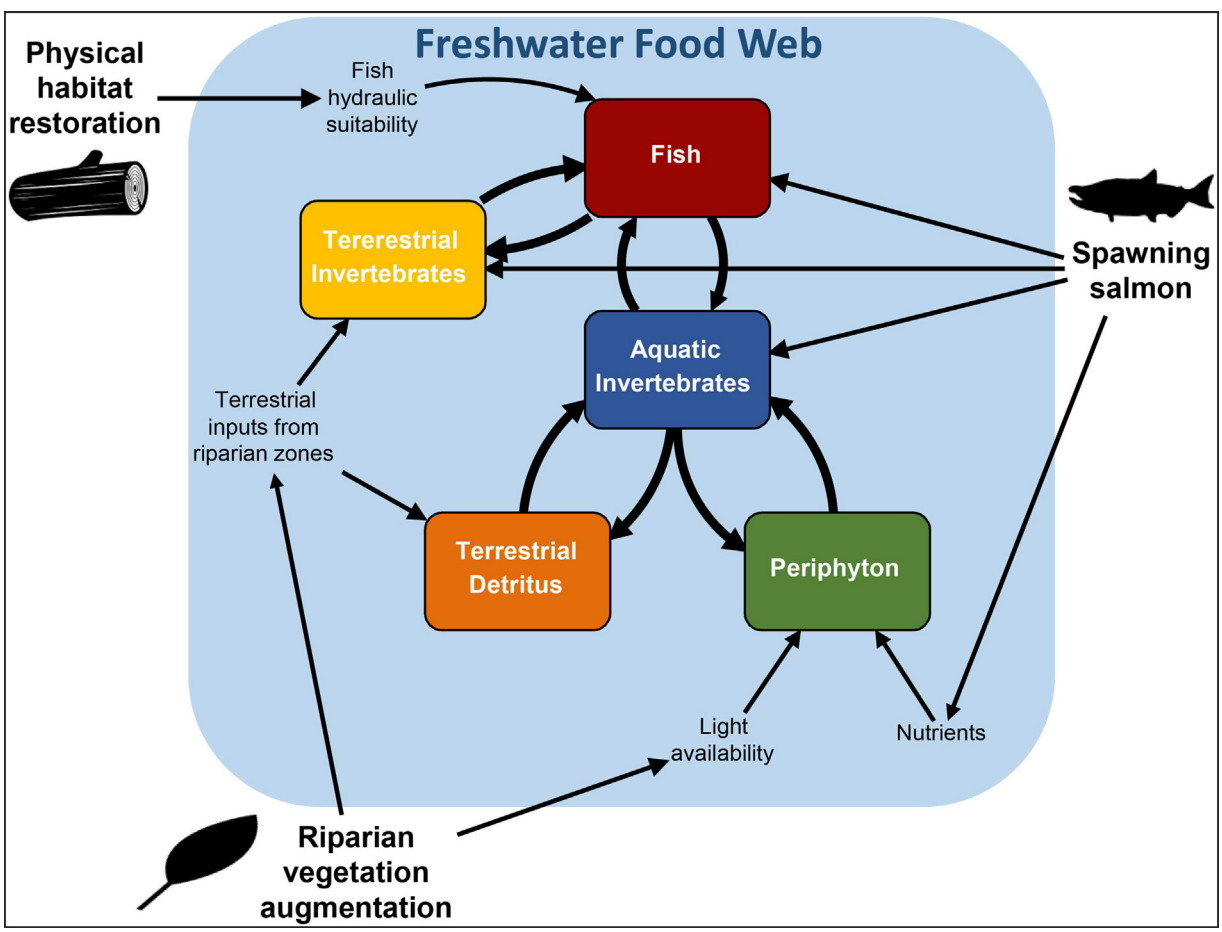

Fig. 2. The Aquatic Trophic Productivity model includes biomass stocks of periphyton, terrestrial detritus, aquatic and terrestrial invertebrates, and fish that are linked together via a series of consumer-resource interactions. The food web is fueled by inputs of light, nutrients, and terrestrial organic matter. Arrows originating outside the shaded region illustrate how alternative river restoration actions mechanistically influence food web dynamics (see Section 2.2 for further explanation).

2016; Whitney et al., 2019). Earlier work has also shown that the ATP model can reproduce fish, invertebrate, and periphyton biomass dynamics for a site in the Methow River watershed (Bellmore et al., 2017). An online interface for the ATP model, which allows users to explore the model structure and run simulations, can be found at https://exchange.iseesystems.com (search by keyword "ATP").

For this analysis, the ATP model was parameterized with environmental data specific to each of the 12 study sites (Table 1; Appendix A), which included: average daily discharge for the calendar year; graphical relationships between discharge and channel hydraulics (width, depth, and the proportion of reach wetted area hydraulically suitable to juvenile salmonids; commonly known as "habitat suitability indices," HSI, (Raleigh et al., 1986)); channel slope; benthic substrate size distribution; the proportion of the stream covered by riparian vegetation (split into coniferous and deciduous cover) and proportion of the stream shaded; average daily water temperature for the calendar year; average monthly water turbidity, dissolved inorganic nitrogen concentration (DIN), and soluble reactive phosphorus concentration (SRP); and a returning adult salmon density of 0.001 salmon/m^2. Hydraulic relationships that describe how site-averaged depth, width, and HSI change with discharge were assembled by summarizing information from previously constructed two-dimensional (2D) hydraulic models (Bureau of Reclamation, 2012, 2015). HSI values were calculated from these hydraulic models by comparing 2D model outputs to depth and velocity suitability indices for juvenile Chinook salmon (Raleigh et al., 1986), which account for the depth and velocity preferences for this species. In turn, HSI values were used to estimate the proportion (0–1) of the total stream wetted area with suitable depths and velocities that fish can occupy. A detailed example of how this was done can be found in Whitney et al. (2019, pp. 49–50). Temporally dynamic model inputs for each site (e.g., daily discharge and temperature time series) are presented graphically in Appendix A.

2.3. Restoration simulations

At each site, we modeled how the biomass of juvenile salmonids responded to three restoration strategies: (1) physical habitat modification, (2) nutrient supplementation via salmon carcass addition, and (3) increased riparian vegetation cover. For physical habitat modification, we focused on a common goal of salmon habitat restoration: an increase in the proportion of the habitat hydraulically suitable for juvenile salmonids, HSI. Increases in fish habitat suitability could result from restoration actions like large woody debris placements that are designed to improve the quantity and quality of habitat available to fish (Roni et al., 2015). In the model, expanding the proportion of hydraulically suitable area provides more habitat for fish to occupy, which reduces fish densities and associated intraspecific competition for food. This can increase fish population size by alleviating density-dependent constraints on foraging (assuming adequate food is available to facilitate larger populations, Bohlin et al., 1994; Grant and Kramer, 1990). To implement this restoration strategy, we increased the proportion of the wetted area that was hydraulically suitable at each site by 0.5, such that 50% of the previously unsuitable wetted area was made suitable for fish. This restoration strategy focused on reducing density-dependent constraints on fish but does not address behavioral changes in fish due to predation risk at higher or lower densities.

To examine the responsiveness of different sites to nutrient supplementation, we added salmon carcasses to each modeled site. Carcass addition is frequently employed in Pacific Northwest streams where a decline in returning adult salmon has led to a decrease in marine-derived nutrients (Kohler et al., 2012; Stockner, 2003). The hypothesis behind these efforts is that increasing salmon subsidies (e.g., though placing salmon carcasses from hatchery operations in streams) will enhance aquatic productivity and salmon population growth (Benjamin et al., 2020). In the ATP model, carcasses can increase aquatic productivity via numerous pathways: carcasses leach nutrients (nitrogen and phosphorus) that can stimulate periphyton production; carcasses contribute organic matter that is directly consumed by aquatic invertebrates and fish (Claeson et al., 2006); and carcasses stimulate an increase in terrestrial invertebrate inputs to the stream (Collins et al., 2016). We simulated the addition of salmon carcasses to the stream each autumn (September 21) at a level consistent with historical salmon spawning abundance (Mullen et al., 1992), which we estimate to be 20× current average spawner densities of 0.001 salmon/m^2 (Snow & Frady, 2013). This equated to adding from 20 to 432 salmon carcasses (5 kg wet mass/carcass), depending on the wetted area of the site.

For riparian vegetation, we doubled the proportion of the stream covered by vegetation. Increasing riparian vegetation could result from active riparian planting and protecting riparian zones that have been disturbed (e.g., by cattle grazing). This type of restoration has been implemented in areas where past land-use practices have reduced levels of riparian vegetation (Beschta, 1997; Platts, 1991). In the model, increased vegetation cover enhances leaf litter and terrestrial invertebrate inputs to the stream from overhanging vegetation, but also reduces light inputs through increased shading. These changes affect the amount of periphyton and terrestrial detritus available to aquatic invertebrates. We assumed that changes in vegetation cover occurred instantaneously, i.e., we do not account for the delay time between riparian planting and vegetation maturation, and that the composition of the vegetation remained the same (same proportion of deciduous and coniferous coverage). Furthermore, the model does not account for changes to stream temperature, instream physical habitat (e.g., bank stability, fish cover), or aquatic macroinvertebrate assemblages that can also result from riparian manipulations (Moore et al., 2005).

To explore how the biomass of juvenile salmon responds to each of these treatments, we ran the ATP model for 10 years (3650 days, starting January 1). The environmental conditions used to parameterize the model were repeated each year. For example, water temperature and flow regimes were held the same from one year to the next. The 10-year model run allowed the model time to equilibrate to the environmental conditions at each of the 12 sites. We report modeled outcomes for the final year of the 10-year simulation after fish biomass values had equilibrated to site conditions. Unless otherwise noted, fish biomass refers to the modeled juvenile salmon biomass and is presented in units of grams of juvenile salmonid AFDM per square meter (g AFDM/m^2), which was calculated by dividing juvenile fish biomass by the average wetted area of the reach. The magnitude of fish response to each restoration scenario was calculated by subtracting background (no-treatment) fish biomass from treatment fish biomass.

To examine which environmental factors most strongly influenced modeled fish biomass and restoration responses across the 12 sites, we conducted a site homogenization experiment, whereby we replaced the unique environmental conditions found at each site, with conditions averaged across the 12 sites. For instance, we replaced the unique water temperature regimes at each site with an average water temperature regime, calculated by taking the average of the 12 unique regimes. We then re-ran the model with this average water temperature regime and evaluated how variation in both background (no-treatment) fish biomass and restoration responses changed, with the expectation that homogenizing highly influential environmental conditions would reduce the magnitude of modeled differences among the 12 sites. This was calculated as a change in the coefficient of variation (ΔCOV). We conducted this homogenization procedure using a one-factor-at-a-time approach for each of the following environmental parameters (or sets of parameters): (1) water temperature, (2) water turbidity, (3) nutrient concentrations (both DIN and SRP), (4) proportion of riparian vegetation cover and stream shading, (5) channel morphology and hydraulics (substrate size distribution, channel slope, hydraulic relationships between discharge and channel width/depth), and (6) fish habitat suitability or the proportion of wetted area that was hydraulically suitable for juvenile salmonids (HSI). We then calculated ΔCOV

when each of these conditions was homogenized. We normalized values by dividing each of the six ΔCOV values by the sum of the total, resulting in a percentage that reflects the importance of each parameter in driving modeled differences among sites.

2.4. Food web structure scenarios

To explore how variation in the structure of food webs might mediate restoration responses, we ran each of the three restoration scenarios with different modeled food web structures. Because we did not have empirical information on how the structure of food webs varied among our 12 sites, we created a set of heuristic food web structures that can—and likely do—occur in the Methow River and other river networks where juvenile salmonids reside. We examined modeled responses to four food structures:

1. *Basic food web:* this scenario represents the food web configuration shown in Fig. 2, where there is a single stock of fish representing juvenile salmonids, and a single stock of aquatic invertebrates representing the entire invertebrate community.
2. *Fish competitors/predators present:* In this scenario, a stock of fish that compete for food with and prey upon the juvenile salmon was added to the model. This second fish stock could be a group of fish that are not the direct target of the restoration but may be affected by restoration actions. For instance, many rivers in the Pacific Northwest include a diverse assemblage of fishes that both compete for food with (e.g., native mountain whitefish and sculpin), and prey upon (e.g., native bull trout and pikeminnow, or nonnative brook trout and smallmouth bass) juvenile salmonids. This scenario explored the potential implications of these non-target fishes, which are often not considered in evaluating restoration outcomes.
3. *Predation-invulnerable invertebrates present:* A stock of predation-resistant aquatic invertebrates was added to the model to represent primary consumers that are less susceptible to predation. Examples of this include armored invertebrates such as cased caddisflies (e.g., *Dicosmoecus* spp.; Limm and Power, 2011) and aquatic grazing snails (e.g., *Juga* spp.; Hawkins and Furnish, 1987), which can be numerically abundant in some locations (and at certain times). This predation "invulnerable" stock competed with the stock of vulnerable aquatic invertebrates for shared periphyton and terrestrial detritus food resources. We assumed that only 25% of the invulnerable invertebrate stock biomass was available to fish predators, relative to 100% for the main aquatic invertebrate stock (*sensu* Atlas and Palen, 2014).
4. *Fish competitors/predators and predation-invulnerable invertebrates present*: In this scenario both the fish competitor/predator and the invulnerable invertebrate stocks were present, generating the most complex of the modeled food webs.

For each of these food web configurations, we calculated the magnitude of juvenile fish response to each restoration scenario by subtracting the background (no-treatment) fish biomass from treatment fish biomass.

3. Results

Background modeled fish biomass varied by several orders of magnitude across the 12 sites in the Methow River (Fig. 3), from a high of 0.69 g AFDM/m^2 at site 1 to essentially 0 at site 4 (3.3×10^{-8} g AFDM/m^2). The river reaches in the upper Methow River (sites 2–4) and Twisp Rivers (sites 7, 8, 10) generally had the lowest modeled fish biomass, whereas sites lower in the watershed (sites 1, 12) and the Chewuch River (sites 5, 6, 9, 11) generally had higher modeled fish biomass. Although empirical fish abundance information is not available for all these sites, model results correspond to observed differences in productivity at different locations in the Methow River (Mejia et al., 2019; Snow & Frady, 2013). Variation in modeled fish biomass across sites was strongly controlled by variation in ambient nutrient availability, followed by riparian vegetation cover and shading, and water temperature (Fig. 3). The four sites with the highest modeled fish biomass (sites 1, 9, 11, 12) had SRP concentrations that were between 87% to 483% higher than the eight other sites (Table 1). The sites with the lowest fish biomass (sites 3, 4, 7, 8, 10) were generally sites that had cold water temperatures, high vegetation cover and shading, and low ambient nutrient availability.

Modeled fish biomass responses to the three restoration strategies were also highly variable across space. Some sites exhibited relatively large fish biomass responses to restoration, whereas other sites were almost entirely unresponsive (Fig. 4, Appendix A). Sites with the largest response varied among the three restoration strategies. The three sites with the greatest response for each strategy included: sites 1, 11, and 12 for increased fish habitat suitability (HSI); sites 5, 8, and 9 for carcass addition; and sites 6, 7, and 8 for increased riparian vegetation cover. By contrast, two sites were relatively unresponsive to all three restoration

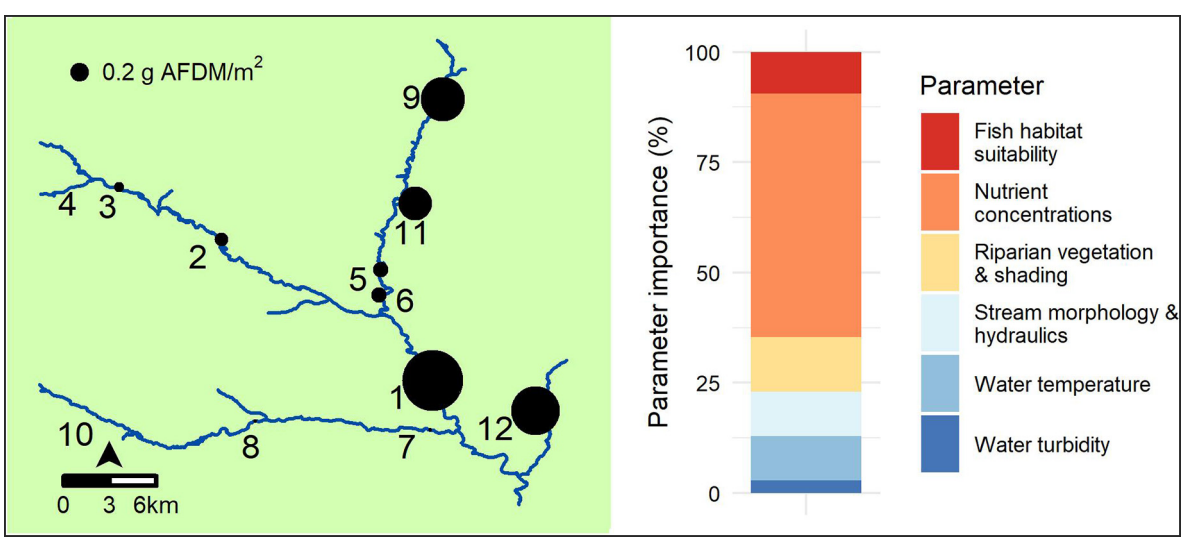

Fig. 3. Left: Modeled fish biomass for each site in grams of ash-free dry mass per square meter (g AFDM/m^2). Circle size is scaled to the fish biomass at each site. Right: Percent contribution of different environmental parameters to modeled variation in fish biomass across sites. Higher percentages indicate a greater influence of those environmental parameters on modeled dynamics.

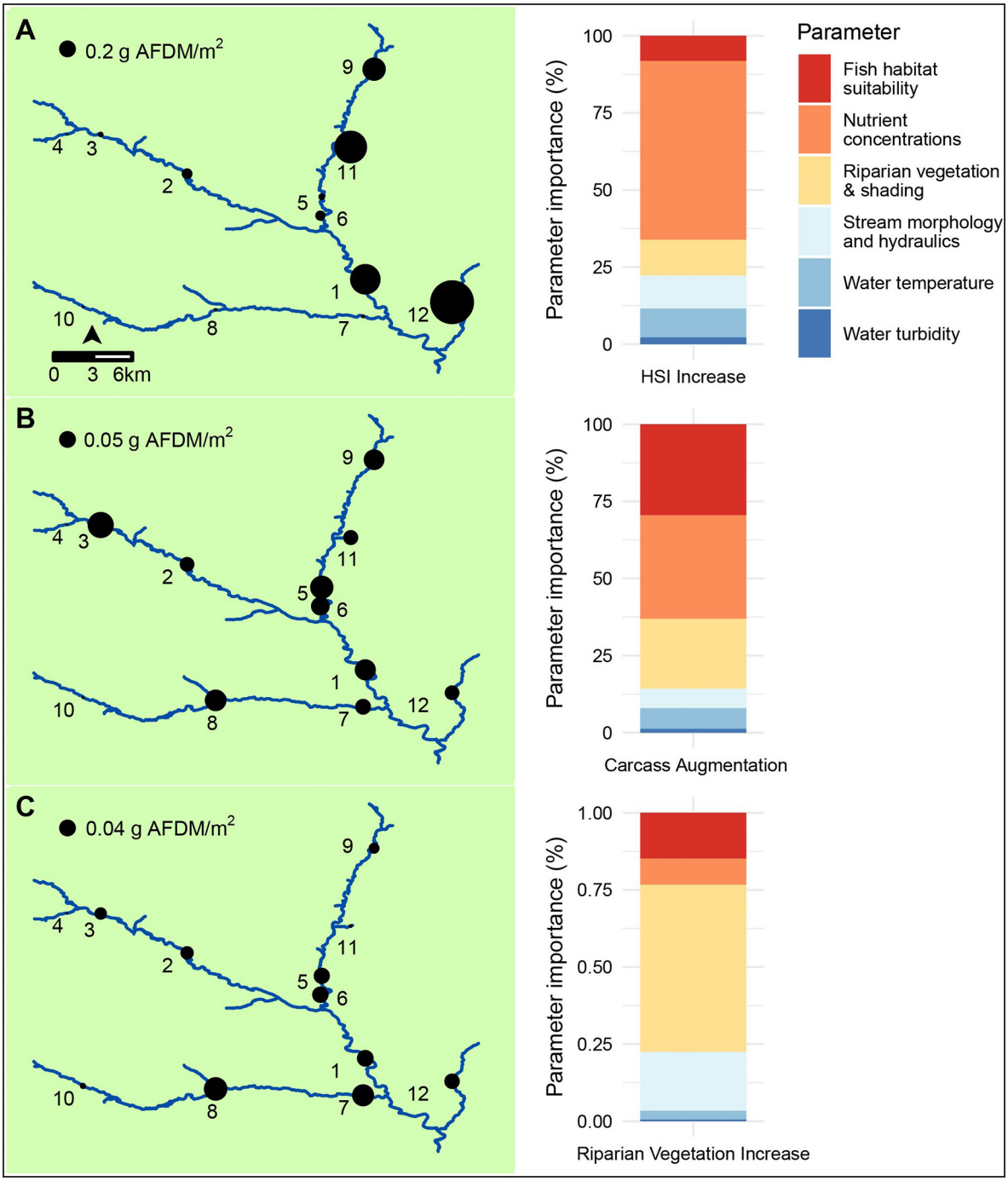

Fig. 4. Left: Modeled change in fish biomass in grams of ash-free dry mass per square meter (g AFDM/m^2) for the following restoration strategies: A) 50% increase in the proportion of the habitat that is hydraulically suitable for fish (HSI), B) salmon carcass augmentation at 20× current salmon spawner density, C) 100% increase in riparian vegetation cover. Circle size is scaled to the change in fish biomass at each site. Right: Percent contribution of different environmental parameters to modeled variation in the fish biomass response to restoration across sites. Higher percentages indicate a greater influence of those environmental parameters on modeled dynamics.

actions (sites 4 and 10); these two sites had the lowest average annual water temperature of all 12 sites (approximately 5 °C, Table 1). On average, the largest positive responses to restoration occurred with increases in HSI, followed by carcass addition, and lowest for riparian vegetation restoration (Fig. 4).

Spatial variation in the magnitude of fish biomass responses to restoration was due to variability in environmental conditions (Fig. 4). However, the primary environmental factors that controlled responses were different for each of the three restoration strategies. Spatial variation in response to increases in HSI was strongly, and somewhat unexpectedly, controlled by differences in nutrient concentrations across the 12 sites (rather than differences in background habitat suitability). Sites that exhibited the largest fish biomass responses were those with the highest SRP concentrations (sites 1, 9, 11, 12). In contrast, variation in the response to carcass addition was strongly influenced by a variety of environmental factors: nutrient concentrations, stream shading, and HSI. Sites with the largest fish biomass response to carcass addition had one or more of the following conditions: low nutrient concentrations (site 8), high levels of stream shading (site 11), and/or high proportions of hydraulically suitable habitat (HSI) for juvenile salmonid rearing

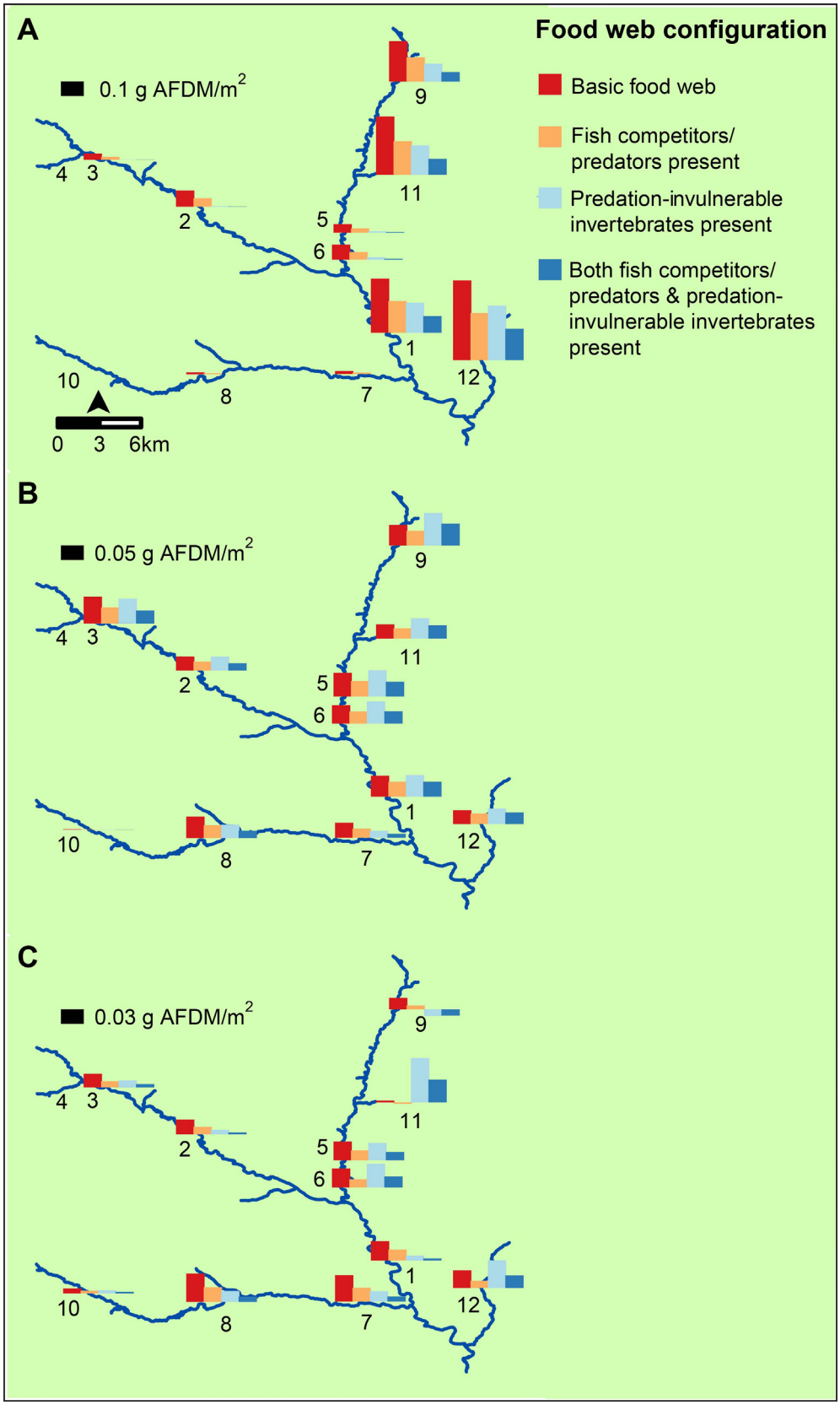

Fig. 5. Modeled change in juvenile fish biomass by restoration strategy and food web structure. Bar height is scaled to the change in fish biomass at each site. A) Increase in proportion of the habitat suitable for fish (HSI), B) salmon carcass augmentation, C) increase in riparian vegetation. Colored bars at each site represent responses to the four different food web configurations (see Section 2.2 for further details).

(sites 3 and 5). Variation in the fish biomass response to increased riparian vegetation cover was most strongly influenced by pre-treatment levels of vegetation cover and stream shading, stream morphology and hydraulics, and HSI. Sites with the largest responses to increases in vegetation cover had hydraulic conditions (low channel gradient and wide channels) that corresponded with lower export rates of organic matter (sites 7 and 8), relatively low vegetation cover and stream shading (sites 1, 5, 6), and/or had high proportions of habitat that was hydraulically suitable for juvenile salmonid rearing (sites 1, 5, 8). It is important to note that the two sites that had extremely low absolute changes in fish biomass in response to carcass addition and riparian vegetation restoration (sites 4 and10), had among the highest percent increases in fish biomass. For example, fish biomass at sites 4 and 10 increased by 10,923% and 458% in response to the carcass addition treatment. However, because these sites had almost non-existent fish populations to begin with ($<3.5 \times 10^{-5}$ g AFDM/m^2) even large percentage increases in fish biomass resulted in relatively small population responses on an absolute scale.

Food web structure strongly mediated the fish biomass response to restoration across all sites. When fish predators/competitors or invulnerable primary consumers were present at a site, the modeled fish biomass response to restoration was generally lower than when these functional groups were absent (Fig. 5). In general, fish biomass responses to restoration were highest under the basic food web scenario, lower when fish predators/competitors or invulnerable primary consumers were present in the food web, and lowest when both fish predators/competitors and invulnerable primary consumers were present together. These different food web structures mediated restoration responses by re-routing energy flows through the food web (Fig. 6). When fish competitors/predators were present, they directly consumed juvenile salmon and usurped a substantial portion of their primary aquatic invertebrate prey. The presence of invulnerable primary consumers rerouted basal periphyton away from predation vulnerable aquatic invertebrates, which increased food limitation for fish.

The effects of different food web structures varied across the three restoration strategies. Specifically, the fish biomass response to carcass addition and riparian vegetation restoration was frequently larger when predation-invulnerable invertebrates were present (Fig. 5). This seemly paradoxical response resulted from greater food limitation for fish when predation-invulnerable invertebrates were present, such that actions that alleviated this limitation (e.g., additions of carcasses and terrestrial subsidies) resulted in greater fish responses to restoration. For carcass addition, larger or equal fish biomass responses in the presence of predation-invulnerable invertebrates compared to responses under the basic food web occurred at all but the least productive sites, such as those in the Twisp River (sites 7, 8, 10), where the presence of predation-invulnerable consumers resulted in fish biomasses near zero. In these cases, carcass addition still increased fish biomass, but because populations were so small, the effect size (in terms of increased fish biomass) was low. For increased riparian vegetation, sites 11 and 12 exhibited much larger increases in fish biomass when predation-invulnerable invertebrates were present. Sites 11 and 12 are the smallest (narrowest) streams with the highest levels of vegetation cover. Thus, these sites experienced substantially more leaf litter and terrestrial invertebrate inputs with a doubling of vegetation cover, enough to alleviate food limitation caused by the presence of predation-invulnerable invertebrates.

4. Discussion

Ecologists have long recognized that outcomes of river restoration are dependent, in part, on the geomorphic conditions of rivers and floodplains (Montgomery and Bolton, 2003; Reeves et al., 1995; Roni et al., 2002). More recently, non-geomorphic abiotic conditions, such as nutrient availability and water temperature (Palmer et al., 2010), and biotic conditions, such as the structure and dynamics of food webs (Naiman et al., 2012), have been identified as important. The modeling framework used in this study merges these three fundamental characteristics of river segments and suggests that variation in these environmental conditions across watersheds can strongly mediate restoration outcomes. Three important findings emerged from our analyses in the Methow River, which likely apply to most watersheds where restoration is conducted. First, variability in the magnitude of fish responses to restoration across the river network was substantial. Second, different locations were more responsive to certain restoration actions than others, depending on factors limiting local fish populations. Third, the structure of the food web strongly influenced the magnitude of fish responses to river restoration. These findings emphasize the context-dependence of restoration outcomes and suggest that river restoration can benefit from assessments that go beyond geomorphic conditions to account for other abiotic conditions, such as water temperature, nutrient availability, and riparian vegetation cover, as well as biotic conditions such as the structure of food webs.

Although the spatial and temporal heterogeneity of river networks regulate the dynamics of stream ecosystems (Power and Dietrich, 2002; Winemiller et al., 2010), the consequences of such heterogeneity for restoration are often unclear (Hobbs, 2007). Our study demonstrated that some locations may experience relatively large increases in fish biomass with restoration, whereas other locations may be almost entirely unresponsive. Locations that did respond to restoration generally had conditions that were more conducive to aquatic productivity (e.g., sites where aquatic productivity was not strongly limited by nutrients or low water temperatures). This was particularly the case for physical habitat restoration. Sites with the largest response to increased HSI tended to have characteristics that supported high aquatic productivity (e.g., high nutrient concentrations, low shading, warm water temperatures), but were restrictive in the amount of hydraulic habitat suitable for fish occupancy (i.e., HSI). In other words, sites with the largest positive responses to physical habitat restoration were those that already had relatively high fish biomasses to begin with (Fig. 4).

By contrast, the sites that were more responsive to the salmon carcass and riparian vegetation additions generally had adequate physical habitat suitability (HSI), but this habitat was not fully utilized due to factors, such as low nutrient concentrations and high stream shading, that limited aquatic productivity and food availability for fish. Thus, supplementing these sites with additional organic matter and nutrients (i.e., salmon carcasses and terrestrial subsidies) increased food resource availability, resulting in greater fish biomass. We also found that there may be locations within river networks that are entirely unresponsive to almost all restoration actions. In our analysis, these intrinsically unproductive sites were constrained by low water temperatures that limited aquatic productivity and fish growth. If true, this finding would question the validity of approaches that prioritize restoration at locations in river networks that are the least productive and emphasizes the need for assessments that can identify the factors that limit local productivity (Roni and Beechie, 2012) and the types of restoration strategies—if any—that may result in the greatest positive response for target organisms.

Equally important as predicting site-specific restoration potential is understanding the mechanistic pathways by which restoration actions affect fish. The three restoration strategies examined in this study influenced fish via different direct and indirect mechanistic pathways, which in turn, mediated the magnitude of the response. Increased HSI had a direct effect on fish in the model by creating more suitable habitat that reduced fish density dependence, resulting in greater juvenile salmonid biomass (Gonzalez et al., 2017). Salmon carcass additions affected fish via both direct and indirect pathways; directly via fish consuming carcasses, and indirectly via nutrient uptake by periphyton and consumption of carcass material by invertebrates. By contrast, increased riparian vegetation cover influenced fish primarily via indirect pathways by

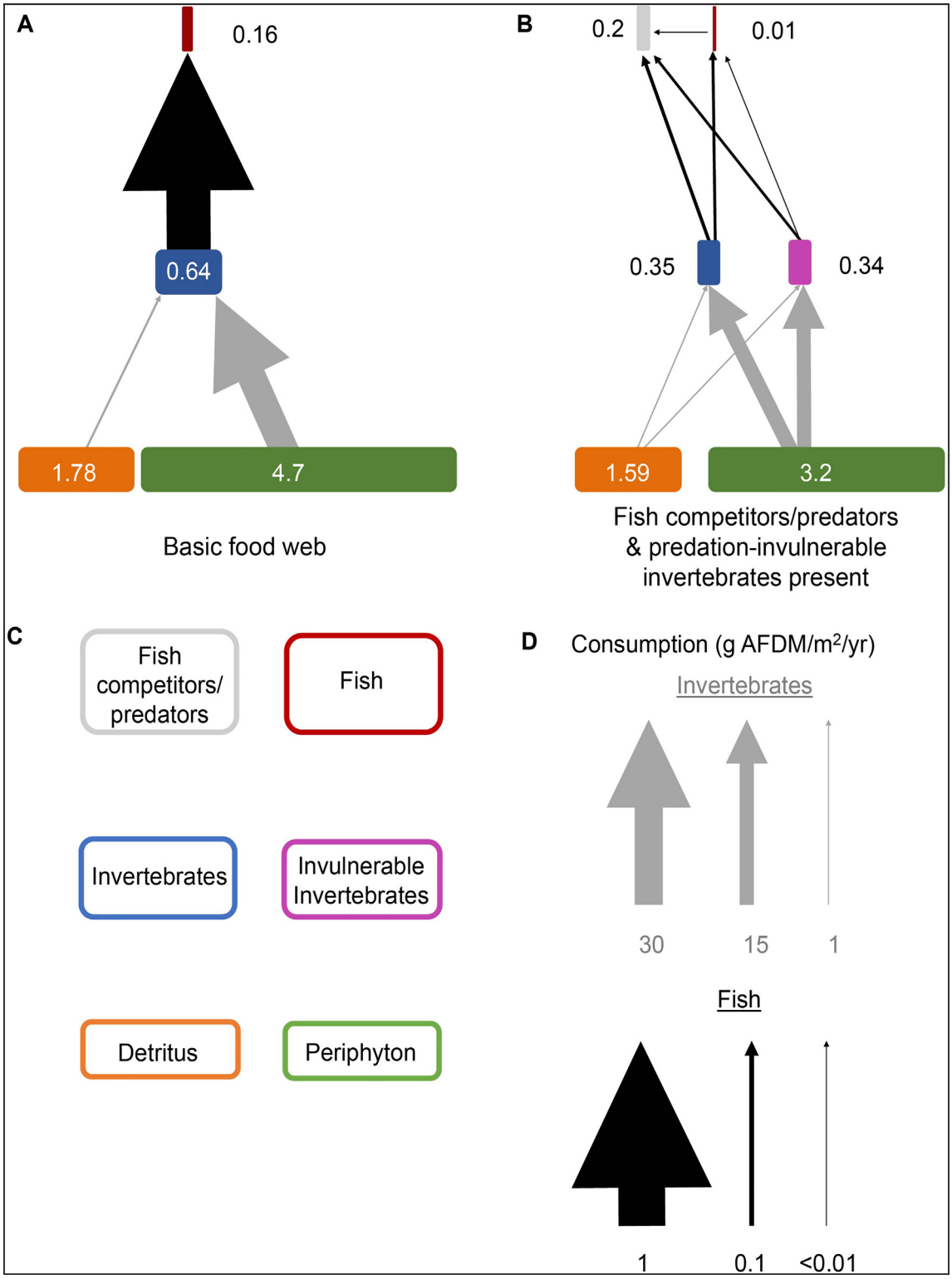

Fig. 6. Food webs diagrams illustrating the annual organic matter flows between consumers and resources (arrow width) and the biomass of the different food web members (relative box widths) for two configurations at site 5: A) basic food web and B) when both fish competitors/predators and predation-invulnerable invertebrates are present. Values adjacent to and within rectangular boxes represent the average annual biomass (in g AFDM/m^2) for that food web member. The legend in C) shows the color and position of the different food web members and D) shows consumptive values for different arrow widths.

modifying the availability of periphyton and detritus at the base of the food web (but also directly via inputs of terrestrial invertebrates). Although restoring riparian vegetation can result in more detrital inputs to streams (two times more in our simulations), significant amounts of this energy can be lost during trophic transfer. A common assumption is that only 10% of production at the lower trophic level is transferred to higher trophic levels due to physiological and ecological inefficiencies (McGarvey and Johnston, 2011). Using this rule-of-thumb, a 100% increase in leaf litter inputs to streams would increase invertebrate production by 10% and fish

production by only 1%. Further affecting the flow of energy to fish is the increase in stream shading as a result of increased vegetation (proportionately higher in narrower streams), which can reduce the sunlight available to fuel periphyton growth. As a result, increased riparian vegetation cover generally had a much lower impact on modeled fish biomass relative to the HSI and carcass addition treatments, which had more direct effects on fish in our model analysis.

Food web structure can drive responses following disturbance (Menge et al., 2003; Wootton et al., 1996), nutrient addition (Davis et al., 2010), and changes to riparian conditions (Baxter et al., 2004). Our simulations add to these by suggesting food web structure can influence the magnitude and direction of ecological responses to restoration. In general, the presence of non-target fishes and predation-invulnerable invertebrates reduced the magnitude of fish biomass responses to restoration. This is an important finding because most river networks contain complex multi-species food webs (Bellmore et al., 2012; Naiman et al., 2012; Preston et al., 2019). In the Pacific Northwest, for instance, salmon and trout-bearing rivers often support diverse fish assemblages. Even relatively species-poor headwater streams can support large populations of non-salmonid species, such as salamanders that share common food resources with and prey upon juvenile salmon and trout (Hawkins et al., 1983; Rundio and Olson, 2003). Although these non-target species are frequently overlooked, they often play significant ecological roles. For example, Bellmore et al. (2013) found that mountain whitefish (*Prosopium williamsoni*) and sculpin (*Cottus* spp.) consumed up to 95% of invertebrate prey resources that support juvenile salmonids in lower reaches of the Methow River. Invertebrate consumers, such as snails and cased caddisflies that are relatively invulnerable to fish predation, are also a common component of many river food webs. For example, the presence of large predation-invulnerable cased caddisflies (*Dicosmoecus* spp.) has been shown to reduce the number of trophic levels in river food webs (Limm and Power, 2011; Wootton et al., 1996). Invasive species are also rewiring river food webs around the globe (Havel et al., 2015) and this restructuring may strongly mediate the potential for restoration to achieve desired outcomes. Our findings should not be interpreted as suggesting that "simpler" food webs (e.g., those that lack species that compete and prey upon target organisms) are better than more diverse and complex food webs; in fact, more complex food webs have been shown contribute to ecological resilience and stability (Bellmore et al., 2015; McCann, 2000; Naiman et al., 2012; Vander Zanden et al., 2016). Rather, our findings suggest that the structure of food webs, in combination with local environmental conditions (e.g., vegetation cover, nutrient availability, flow/temperature regimes), dictate how energy is routed to target organisms, and thus need to be considered when assessing potential outcomes of river restoration.

Although the ATP model allowed us to explore fish responses to river restoration it is worth highlighting a few simplifications and assumptions that could influence modeled outcomes. Physical habitat was modified as an average across the river segment and does not account for the spatial juxtaposition of microhabitats and refuges for juvenile salmonids, as has been implemented in other models for stream-living salmonids (Grossman, 2014; Railsback et al., 2009). Changes to hydraulic habitat heterogeneity not only influence juvenile salmonids but all other vertebrate and invertebrate community members (Lake et al., 2007), which was not accounted for in the model. Carcass addition treatments were assumed to be added annually in perpetuity, which is unlikely given the limited resources available to managers. Research suggests that when carcass additions cease, the benefits they provide likely cease as well (Benjamin et al., 2020). The riparian vegetation addition scenario did not include any influences of vegetation on hydrology, water temperature, channel morphology, or aquatic invertebrate species composition, all of which deserve consideration outside of the model and scenarios considered herein (Naiman et al., 2005; Parkyn et al., 2003). Regardless of these limitations, the inferences drawn from the ATP model simulations provide important and novel insights into the variability of restoration responses across river networks.

Another area for future investigation includes complex spatial processes that involve fish movement and how they use different river segments (Fausch et al., 2002; Schlosser, 1995). In developing a prioritization strategy for restoration, Roni et al. (2002) identified reconnecting high-quality, off-channel floodplain habitats as being of primary importance. These habitats may provide much-needed food resources or refuge for juvenile salmon (Bellmore et al., 2013; Falke et al., 2012) when conditions in main channel habitats are unsuitable. At larger spatial scales, connectivity of entire river networks can also be important for supporting life histories and behaviors of many fish species (Benjamin et al., 2014; Dunham and Rieman, 1999; Young, 2011). Within this broader context, there is an urgent need to understand how reach-scale restoration influences populations of mobile organisms that may live day-to-day within a given reach but rely on the broader river network for their subsistence (Roni, 2018). Future work could merge the ATP model with more continuous watershed models (e.g., Wheaton et al., 2018) to examine how the movement of fishes among different locations mediates responses to local restoration. With the merging of these approaches, a greater understanding of how responses to restoration may ripple throughout the watershed can be achieved. Moreover, multiple independent restoration actions under different abiotic and biotic templates may reveal synergistic (or antagonistic) effects.

We show that expected outcomes from river restoration are context-dependent and that this context involves both the abiotic and biotic conditions of rivers. This means that restoration that is successful at recovering ecological conditions at one location in a river network may not be successful at other locations. We argue that more inclusive approaches are needed that integrate knowledge and approaches from the fields of fluvial geomorphology and stream ecology to better represent the multiple factors that mediate ecological responses to river restoration. In particular, our findings emphasize the need to incorporate information on the structure and dynamics of food webs into restoration planning and management decisions (Naiman et al., 2002; Palmer et al., 2010), which has long been done in the context of lake ecosystems but has generally been overlooked in rivers (Vander Zanden et al., 2016). Dynamic food web models, such as the ATP model, which mechanistically link food webs dynamics and the resultant performance of different web members to the physical and ecological conditions of rivers, can be readily applied to address this need.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Graphs of temporally dynamic environmental inputs for each site (see Table 1 in the main text for data sources)

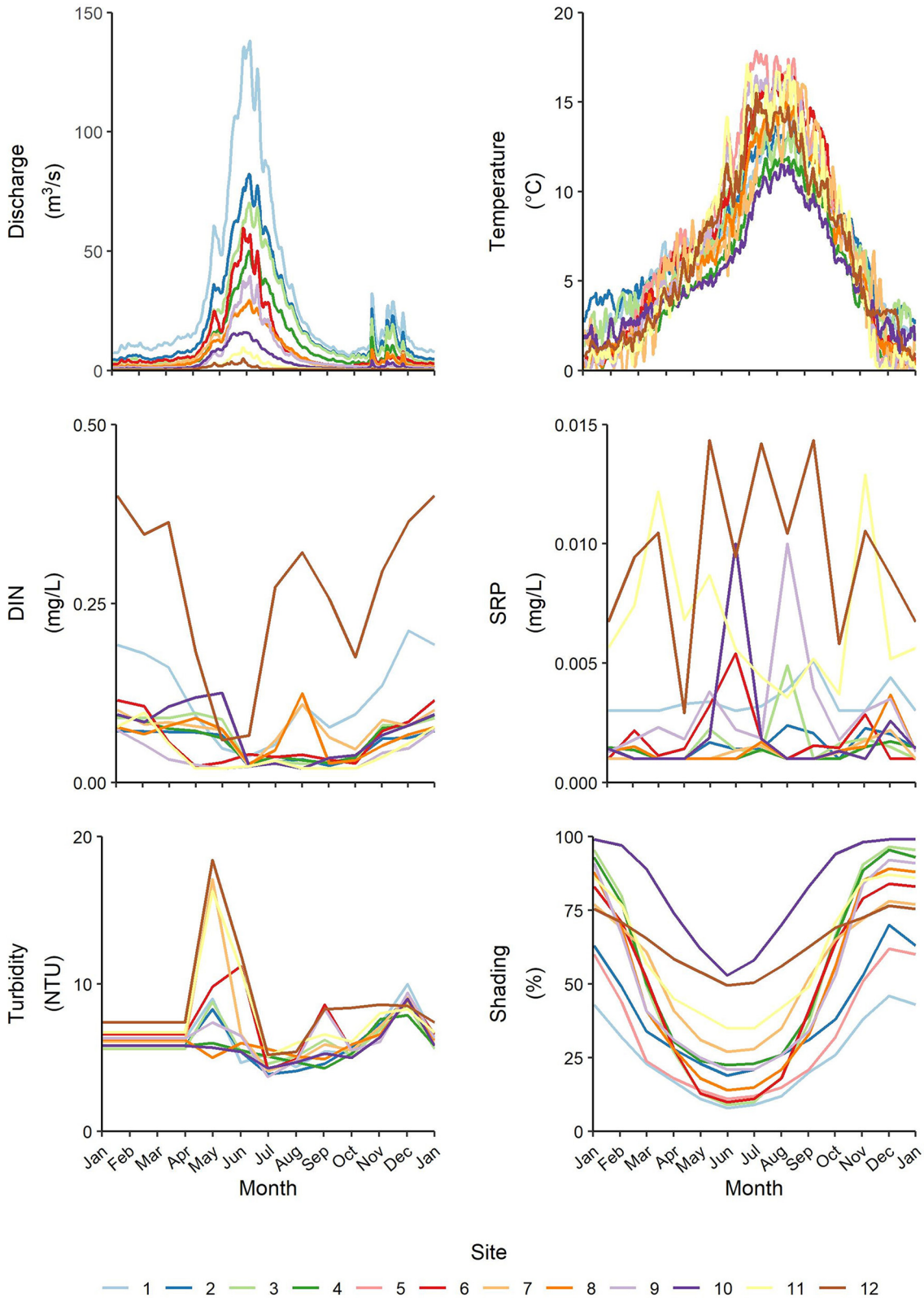

Fig. A.1. Temporally dynamic discharge, water temperature, DIN (dissolved inorganic nitrogen); SRP (soluble reactive phosphorus); turbidity (NTU = nephelometric turbidity unit); shading (percentage of the reach shaded).

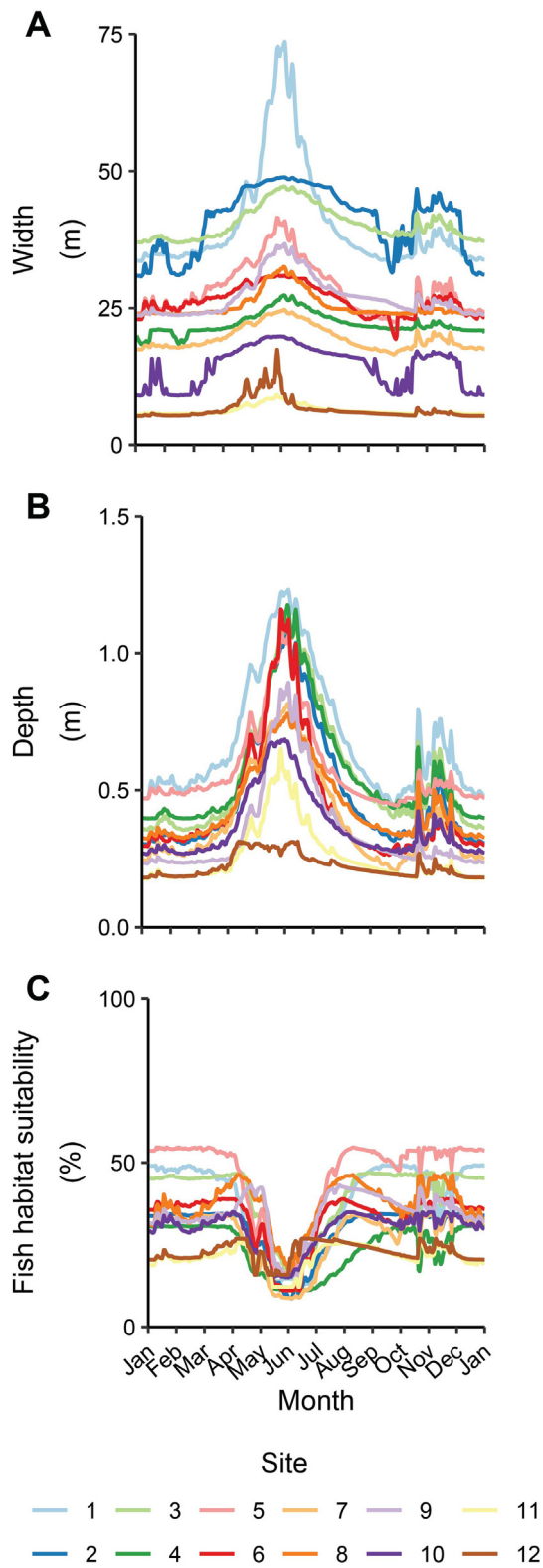

Fig. A.2. Temporally dynamic hydraulic inputs for each site.

Table B.1
Background modeled fish biomass for each site, and change in fish biomass in grams of ash-free dry mass per square meter (g AFDM/m^2) for each food web structure and restoration strategy combination.

Food web structure	Restoration strategy	Site 1	2	3	4	5	6	7	8	9	10	11	12
Basic	Background	0.695	0.139	0.0997	3.28×10^{-8}	0.162	0.162	0.0251	0.0287	0.499	3.49E-05	0.377	0.551
Basic	HSI increase	0.392	0.117	0.0445	2.23×10^{-8}	0.0603	0.108	0.0211	0.0145	0.291	0.000015	0.422	0.577
Basic	Carcass augmentation	0.0649	0.043	0.0827	7.18×10^{-6}	0.0728	0.0565	0.0467	0.0669	0.0638	0.0015	0.044	0.043
Basic	Riparian vegetation increase	0.0401	0.0307	0.028	5.47×10^{-6}	0.0385	0.039	0.0546	0.0588	0.0238	0.0104	0.00377	0.0364
Fish competitors & predators	Background	0.397	0.074	0.0499	1.62×10^{-8}	0.0836	0.0821	0.0131	0.0144	0.286	1.92×10^{-5}	0.203	0.302
Fish competitors & predators	HSI increase	0.23	0.0604	0.0212	1.05×10^{-8}	0.0305	0.056	0.0102	0.00676	0.174	7.22×10^{-6}	0.242	0.341
Fish competitors & predators	Carcass augmentation	0.0461	0.0275	0.0501	3.75×10^{-6}	0.0474	0.0372	0.0285	0.0399	0.0454	0.00085	0.0321	0.0328
Fish competitors & predators	Riparian vegetation increase	0.0225	0.0152	0.0126	2.59×10^{-6}	0.0205	0.0169	0.0286	0.0302	0.00785	0.00558	−0.00286	0.0145
Predation invulnerable invertebrates	Background	0.37	0.00638	0.00189	1.31×10^{-8}	0.0277	0.0312	0.000155	0.000144	0.235	4.46×10^{-6}	0.212	0.376
Predation invulnerable invertebrates	HSI increase	0.218	0.00402	0.000475	6.24×10^{-9}	0.00958	0.0182	8.37×10^{-5}	4.06×10^{-5}	0.129	1.53×10^{-6}	0.213	0.395
Predation invulnerable invertebrates	Carcass augmentation	0.0666	0.0427	0.0768	5.56×10^{-6}	0.0813	0.069	0.0219	0.042	0.101	0.000899	0.0631	0.0482
Predation invulnerable invertebrates	Riparian vegetation increase	0.0101	0.00918	0.0145	4.15×10^{-6}	0.0358	0.0487	0.0217	0.0229	−0.0137	0.00655	0.0921	0.0571
Both additional stocks	Background	0.205	0.00324	0.00104	6.26×10^{-9}	0.0127	0.0135	7.86×10^{-5}	7.42×10^{-5}	0.124	2.52×10^{-6}	0.105	0.202
Both additional stocks	HSI increase	0.12	0.00161	0.000208	2.79×10^{-9}	0.00386	0.00761	3.47×10^{-5}	1.71×10^{-5}	0.0692	7.41×10^{-7}	0.115	0.228
Both additional stocks	Carcass augmentation	0.0459	0.0221	0.0403	2.92×10^{-6}	0.0458	0.0381	0.0123	0.0231	0.0674	0.000519	0.0414	0.0357
Both additional stocks	Riparian vegetation increase	0.00426	0.00411	0.00672	1.95×10^{-6}	0.0172	0.0225	0.0106	0.011	−0.0128	0.00348	0.0469	0.0259

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