

Incorporating food web dynamics into ecological restoration: a modeling approach for river ecosystems

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Abstract. Restoration is frequently aimed at the recovery of target species, but also influences the larger food web in which these species participate. Effects of restoration on this broader network of organisms can influence target species both directly and indirectly via changes in energy flow through food webs. To help incorporate these complexities into river restoration planning, we constructed a model that links river food web dynamics to in-stream physical habitat and riparian vegetation conditions. We present an application of the model to the Methow River, Washington, USA, a location of on-going restoration aimed at recovering salmon. Three restoration strategies were simulated: riparian vegetation restoration, nutrient augmentation via salmon carcass addition, and side channel reconnection. We also added populations of nonnative aquatic snails and fish to the modeled food web to explore how changes in food web structure mediate responses to restoration. Simulations suggest that side channel reconnection may be a better strategy than carcass addition and vegetation planting for improving conditions for salmon in this river segment. However, modeled responses were strongly sensitive to changes in the structure of the food web. The addition of nonnative snails and fish modified pathways of energy through the food web, which negated restoration improvements. This finding illustrates that forecasting responses to restoration may require accounting for the structure of food webs, and that changes in this structure, as might be expected with the spread of invasive species, could compromise restoration outcomes. Unlike habitat-based approaches to restoration assessment that focus on the direct effects of physical habitat conditions on single species of interest, our approach dynamically links the success of target organisms to the success of competitors, predators, and prey. By elucidating the direct and indirect pathways by which restoration affects target species, dynamic food web models can improve restoration planning by fostering a deeper understanding of system connectedness and dynamics.

Key words: *ecological modeling; food webs; invasive species; Pacific salmon; river restoration; species recovery.*

INTRODUCTION

Recovery of imperiled species is one of the most common factors motivating ecosystem restoration (Clewell and Aronson 2013). Although pre-restoration assessments are critical for evaluating potential outcomes (Palmer et al. 2005, Roni and Beechie 2013), these assessments are commonly focused on direct effects of restoration on species of interest, with little consideration of how the larger ecosystem or food web may respond (Vander Zanden et al. 2006, Naiman et al. 2012, Travis et al. 2014). It has long been appreciated, however, that the success of any particular population is linked to the success of other populations in the ecosystem and the ecological interactions that connect them (Forbes 1925, Elton 1927). Although the

target of restoration may be a particular species, restoration efforts will undoubtedly influence the larger network in which these species participate, with effects that can ripple through the food web in complex, nonlinear, and indirect ways (Wootton 1994, Scheffer 2009). Not considering these complexities can result in well-intentioned manipulations having unintended or even undesirable outcomes (Suding et al. 2004). Thus, predicting how species of interest respond to restoration requires holistic approaches that explicitly account for these webs of interactions (Vander Zanden et al. 2006).

River ecosystems are a good example of the need for broader systems approaches to restoration assessment. In rivers, a common restoration goal is the recovery of threatened or endangered fishes. Assessing potential responses to river restoration, however, has traditionally centered on the direct effects of physical habitat on target fish populations (Neill 1998), a focus driven by a long-standing assumption that physical habitat structure is the

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primary regulator of fish populations in rivers (Wipfli and Baxter 2010). That said, numerous studies have illustrated that riverine fishes are also strongly influenced by food web interactions, such as food availability (e.g., Richardson 1993, Kiffney et al. 2014), competition for shared food resources (e.g., Davey et al. 2006, Bellmore et al. 2013), and predation by organisms that occupy higher trophic positions (e.g., White and Harvey 2001, Yard et al. 2011). Moreover, many river restoration actions, such as nonnative species removal, hatchery supplementation, and nutrient augmentation (e.g., salmon carcass addition), are direct food web manipulations that cannot be adequately evaluated with habitat-focused approaches.

Here we argue that dynamic food web models, even relatively simple ones, can be valuable tools for exploring responses to river restoration. Although food web models have rarely been applied to rivers (but see McIntire and Colby 1978, Power et al. 1995), they have a long history in the field of ecology (Gotelli 2001, Pimm 2002), and there have been ongoing calls for their incorporation into riverine fisheries management (Naiman et al. 2012). One of the strengths of this approach is that, unlike many statistical and habitat-based fisheries models, dynamic food web models are rooted in, and constrained by, the fundamental laws of thermodynamics (i.e., conservation of energy). The production of a population cannot exceed the availability of that population's prey and the efficiency at which consumed prey is converted into biomass (Lindeman 1942). Moreover, these models can easily be adapted to different environmental contexts by adding or subtracting different species from the food web, and by linking physiological rates of web members (e.g., consumption and respiration rates) to local environmental conditions, such as water temperature and channel hydraulics (Power et al. 1995, Doyle 2006). Alternative management actions can then be explored by modifying these environmental conditions to represent potential changes wrought by restoration.

Here we outline the structure of a dynamic river web model termed the Aquatic Trophic Productivity (ATP) model, which was constructed to explore how restoration actions affect river food webs and fish populations. In this paper we present an example application of the model to a river-floodplain segment of the Methow River, Washington, USA, a location of ongoing river restoration aimed at the recovery of Pacific salmon and steelhead. Three restoration strategies were simulated: (1) riparian vegetation restoration, (2) nutrient augmentation via salmon carcass addition, and (3) side channel reconnection. We also added populations of nonnative snails and fish to the model to explore how changes in the structure of the food web influence restoration outcomes.

METHODS

The ATP model is a dynamic food web simulation model, whereby the capacity of river ecosystems to

sustain fish is explicitly tied to transfers of organic matter between different components of a simplified river food web (Fig. 1). This model mechanistically links the dynamics of the food web, and the resultant performance of different web members, to (1) the physical and hydraulic conditions of the stream, (2) the structure and composition of the adjacent riparian zone, and (3) marine nutrient subsidies delivered by adult salmon. 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 wrought by restoration, or changes to the structure of the food web itself (e.g., species invasion), might affect the overall dynamics of the food web and the performance of specific web members.

General model structure

We took an ecosystem-based approach to structuring the model (Lindeman 1942, Odum and Barrett 2005), whereby the different biotic players were aggregated into stocks of biomass that represent the generalized trophic structure of river ecosystems (Fig. 1). The backbone of the model contained four biomass stocks or state variables: (1) in-stream primary producers (periphyton, P), (2) terrestrially derived organic matter (leaf litter, D), (3) aquatic invertebrates (I), and (4) fish (F). In the model, periphyton and terrestrial detritus were consumed by aquatic invertebrates, and aquatic invertebrates were consumed by fish. As with all ecosystems, the modeled food web was an open system, in that energy and materials enter the system from external locations. These external inputs represented the raw ingredients that fuel aquatic productivity, and included (1) light and nutrients, which provide energy and materials needed for periphyton production; (2) lateral inputs from the riparian zone, which provide terrestrial detritus (leaf litter) and direct food resources for fish (terrestrial invertebrates); and (3) returning adult salmon, which represent a source of marine carbon and nutrients (marine-derived nutrients, MDN) that were incorporated into the food web via nutrient uptake by periphyton and direct consumption of carcass material by fish and invertebrates.

The dynamics of each biomass stock in the model were governed by a series of simple mass balance equations (Table 1). Biomass increases if the processes that contribute to biomass gains (e.g., consumption and energy assimilation, upstream/lateral inputs, production) outweigh the processes that contribute to biomass losses (e.g., predation, downstream export, respiration). For example, periphyton biomass (P) increases via the processes of growth and upstream inputs, and decreases via consumption by invertebrates, microbial decay, and downstream export. In the sections that follow, we describe the functional form of these processes, and illustrate how each was linked to environmental conditions of the river and the adjacent riparian zone (Table 2, Fig. 2). The

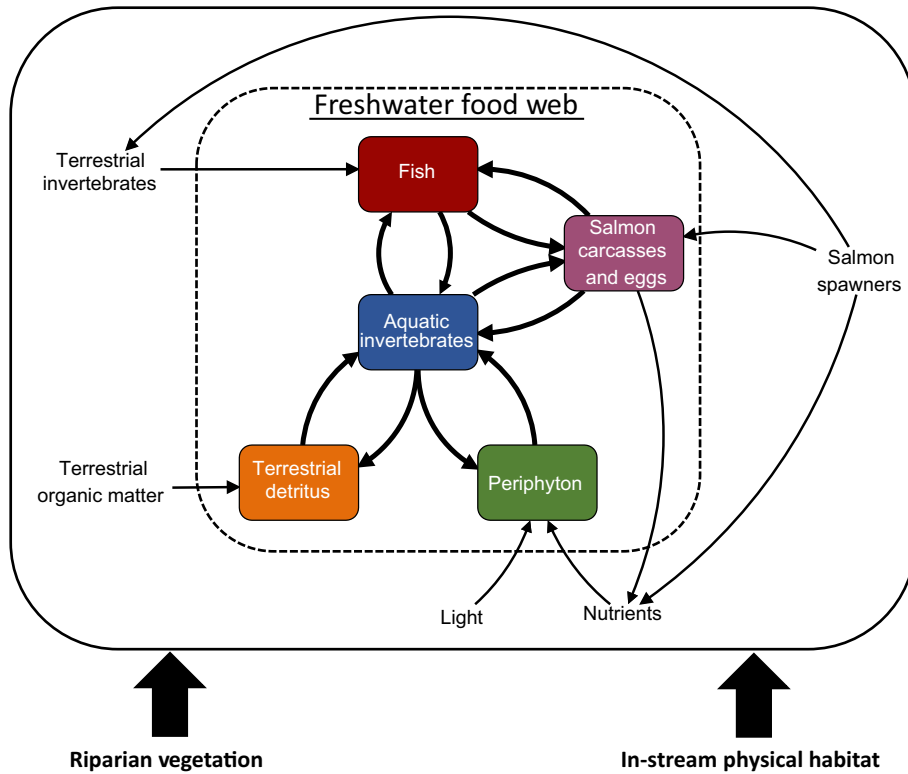


FIG. 1. Conceptual diagram of the Aquatic Trophic Productivity Model, illustrating (1) biomass stocks of organisms and organic matter (rectangular boxes), (2) consumer–resource interactions that link biomass stocks, (3) inputs of energy, nutrients, and organic matter from outside the system (salmon spawners, light, nutrients, terrestrial organic matter and terrestrial invertebrates), and (4) the reliance of these interactions on in-stream physical habitat and riparian vegetation conditions. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1. Biomass mass-balance equations for the state variables in the Aquatic Trophic Productivity (ATP) model, where α_{XY} is the proportion of prey type X consumed by predator Y that is assimilated. See *Food Web Structure Manipulations* section below for description of nonnative fish and snails.

State variable	Mass balance equation
Fish, F	$\frac{dF}{dt} = \text{Consumption}_{IF}\alpha_{IF} + \text{Consumption}_{TF}\alpha_{TF} + \text{Consumption}_{CF}\alpha_{CF} + \text{Consumption}_{EF}\alpha_{EF} + \text{Consumption}_{LF}\alpha_{LF} - \text{Consumption}_{FF} - \text{Respiration}_F - \text{Mortality}_F$
Invertebrates, I	$\frac{dI}{dt} = \text{Consumption}_{PI}\alpha_{PI} + \text{Consumption}_{DI}\alpha_{DI} + \text{Consumption}_{CI}\alpha_{CI} + \text{Upstream}_I - \text{Consumption}_{IF} - \text{Consumption}_{IH} - \text{Respiration}_I - \text{Mortality}_I - \text{Export}_I$
Periphyton, P	$\frac{dP}{dt} = \text{Production}_P + \text{Upstream}_P - \text{Consumption}_{PI} - \text{Consumption}_{PL} - \text{Decay}_P - \text{Export}_P$
Terrestrial detritus, D	$\frac{dD}{dt} = \text{Lateral}_D + \text{Upstream}_D - \text{Consumption}_{DI} - \text{Decay}_D - \text{Export}_D$
Salmon carcass, C	$\frac{dS}{dt} = \text{Marine}_C + \text{Upstream}_C - \text{Consumption}_{CF} - \text{Consumption}_{CI} - \text{Consumption}_{CH} - \text{Decay}_C - \text{Export}_C$
Nonnative Fish, H	$\frac{dH}{dt} = \text{Consumption}_{IH}\alpha_{IH} + \text{Consumption}_{TH}\alpha_{TH} + \text{Consumption}_{CH}\alpha_{CH} + \text{Consumption}_{EH}\alpha_{EH} + \text{Consumption}_{LH}\alpha_{LH} + \text{Consumption}_{FH}\alpha_{FH} - \text{Respiration}_F - \text{Mortality}_F$
Nonnative Snail, L	$\frac{dL}{dt} = \text{Consumption}_{PL}\alpha_{PL} + \text{Upstream}_L - \text{Consumption}_{LF} - \text{Consumption}_{LH} - \text{Respiration}_L - \text{Mortality}_L - \text{Export}_L$

Note: Subscript definitions: C, salmon carcass; D, detritus; E, salmon eggs; F, fish; H, nonnative fish; I, aquatic invertebrates; L, nonnative snail; P, periphyton; and T, terrestrial invertebrates.

TABLE 2. Values and sources of environmental input data from the Methow River, Washington, USA, used to parameterize the ATP model.

Environmental input	Units	Variable type	Used values	Source
Discharge	m ³ /s	temporally dynamic	see Fig. 2	National Water Information System, USGS 12448500 Methow River at Winthrop, Washington
Water temperature (<i>T</i>)	°C	temporally dynamic	see Fig. 2	<i>unpublished data</i>
Air temperature	°C	temporally dynamic	see Fig. 2	National Oceanic and Atmospheric Administration, Winthrop 1 WSW, Washington USA
Nephelometric turbidity (NT)	NTU	temporally dynamic	see Fig. 2	Washington Department of Ecology, 48A140 Methow River at Twisp, Washington
Nitrogen (DIN)	mg/L	temporally dynamic	see Fig. 2	Washington Department of Ecology, 48A140 Methow River at Twisp, Washington
Soluble reactive phosphorus (SRP)	mg/L	temporally dynamic	see Fig. 2	Washington Department of Ecology, 48A140 Methow River at Twisp, Washington
Leaf litter input (Lateral _D)	g AFDM/m ²	temporally dynamic	see Fig. 2	Reach Assessment, Bureau of Reclamation (2010); tree foliage biomass regressions (Jenkins et al. 2004)
Invertebrate drop from riparian vegetation (<i>B</i> _{drop})	g AFDM/m ²	temporally dynamic	see Fig. 2	Bellmore et al. (2013)
Shading (<i>p</i> _{shade})		temporally dynamic	see Fig. 2	field data collected for this study
Photosynthetically active radiation (PAR _{can})	mol·m ⁻² ·d ⁻¹	temporally dynamic	see Fig. 2	USDA, UV-B Monitoring and Research Program, Pullman, Washington
Relationship between discharge and wetted width		graphical function	see Appendix S1	two-dimensional hydraulic model, Bureau of Reclamation (2012)
Relationship between discharge and water depth		graphical function	see Appendix S1	two-dimensional hydraulic model, Bureau of Reclamation (2012)
Reach length	m	constant	16000	Reach Assessment, Bureau of Reclamation (2010)
Channel slope (<i>S</i>)	m/m	constant	0.005	Reach Assessment, Bureau of Reclamation (2010)
Proportion of stream covered by vegetation (<i>p</i> _{veg})	–	constant	0.05	Reach Assessment, Bureau of Reclamation (2010)
Number of returning salmon	number	constant	200	Hillman et al. (2014)
Substrate size distribution	m	cumulative distribution	0.11†	field data collected for this study

† Median substrate size (D50) of distribution.

model was constructed in STELLA 10.1 (ISEE Systems, Lebanon, New Hampshire, USA) and was run on a daily time step with units of grams of ash-free dry mass (AFDM).

Prey consumption and assimilation

Consumption represents the amount of prey biomass ingested by a predator. For a given predator *Y*, the consumption of prey *X* was modeled as

$$\text{Consumption}_{XY} = B_Y (\text{cons}_{\text{max},Y} f_1(\text{Temp}) f_2(\text{PreyAvailability, SelfLimit}) \cdot \text{selection}_{XY}) \quad (1)$$

where $\text{cons}_{\text{max},Y}$ is the maximum rate of consumption for predator *Y* when temperature conditions are optimum, predator biomass *B_Y* is low (no density dependence) and prey resources are not limiting; *f*₁ and *f*₂ are functions that range from 0 to 1 and describe the limiting effects of water

temperature (Temp, °C), prey availability, and predator self-limitation; and selection_{XY} is the proportion of predator *Y*'s consumption that is directed at prey type *X*. The amount of consumed prey that was available for predator growth was calculated by multiplying consumption by a prey-specific assimilation efficiency (α_{XY} , the proportion of prey *X* biomass consumed by predator *Y* that is assimilated).

The temperature limitation function *f*₁(Temp) was represented by an asymmetrical Gaussian distribution (Rutherford et al. 2000) and has the form

$$f_1 = \exp \left(- \left(\frac{\text{Temp} - \text{Temp}_{\text{opt}}}{\text{Temp}_{\text{opt}} - \text{Temp}_{\text{min}} / \sqrt{\ln(100)}} \right)^2 \right), \quad \text{if Temp} < \text{Temp}_{\text{opt}}$$

$$f_1 = \exp \left(- \left(\frac{\text{Temp} - \text{Temp}_{\text{opt}}}{\text{Temp}_{\text{max}} - \text{Temp}_{\text{opt}} / \sqrt{\ln(100)}} \right)^2 \right), \quad \text{if Temp} \geq \text{Temp}_{\text{opt}} \quad (2)$$

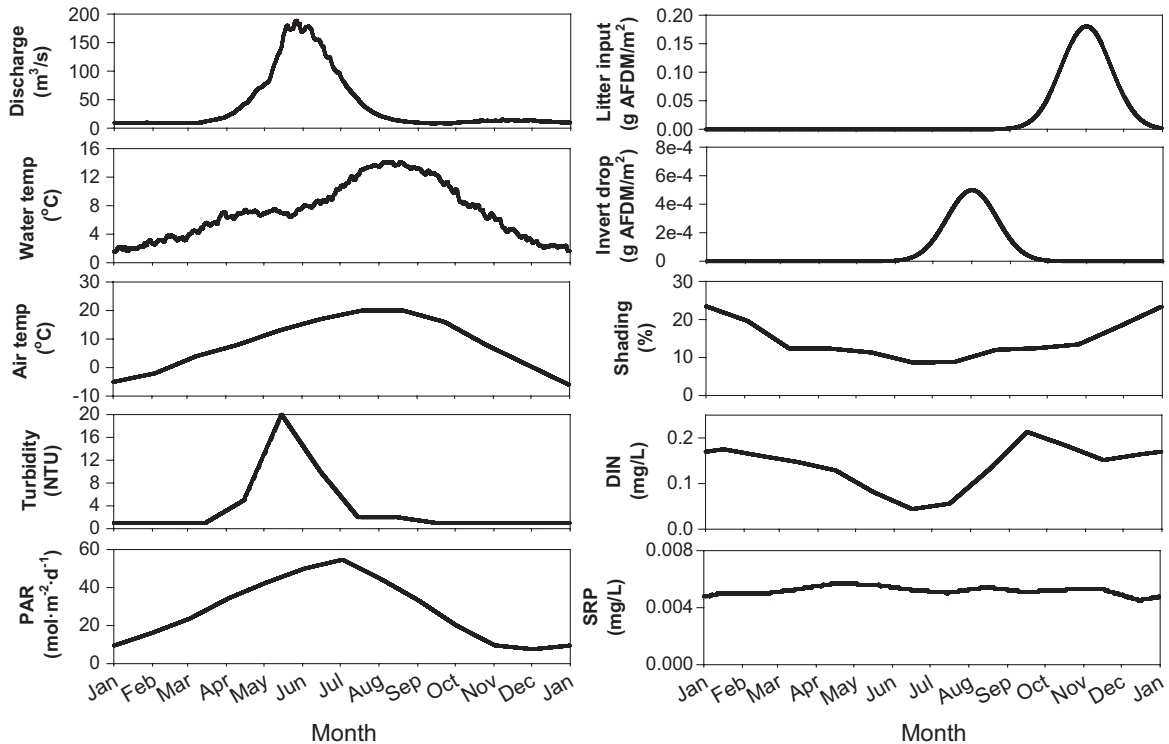


FIG. 2. Temporally dynamic environmental inputs used to parameterize the Aquatic Trophic Productivity model to a floodplain segment of the Methow River, Washington, USA. Temp, temperature; litter input, lateral input of leaves from riparian vegetation (L_{in}); invert drop, the aerial input of terrestrial invertebrates from overhanging riparian vegetation (B_{drop}); DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; and PAR, photosynthetically active radiation.

where $Temp_{opt}$ is the optimum temperature for consumption, and $Temp_{max}$ and $Temp_{min}$ are the maximum and minimum threshold temperatures, respectively, where consumption is 1% of what can be achieved at the optimum temperature. Using this formulation, consumption rate declines as water temperatures rise above or fall below the temperature optimum.

A type II functional response was used to describe the limiting effect of prey availability and predator density (f_2) as follows (Gotelli 2001)

$$f_2 = \frac{\sum_i^n B_i - B_i^*}{\sum_i^n (B_i - B_i^*) + (k_Y + \gamma_Y B_Y)} \quad (3)$$

where B_i is the biomass of prey type i in the environment, B_i^* is the biomass of prey type i that is unavailable to consumers (i.e., refuge biomass), n is the total number of prey types available to predator Y , k_Y is the density-independent prey biomass half-saturation level, and γ_Y is a dimensionless self-interaction parameter ($\gamma_Y > 0$ for interference, $\gamma_Y < 0$ for facilitation) that adjusts consumption rates for consumer biomass density (B_Y).

In the model, consumers adjust foraging to maximize their energy intake by preferentially selecting prey items that are highly abundant and/or of high quality. The proportion of predator Y 's consumption directed at prey X was calculated as follows:

$$selection_{XY} = \alpha_{XY} (B_X - B_X^*) / \left(\sum_i^n \alpha_{iY} (B_i - B_i^*) \right) \quad (4)$$

In this formulation, the consumption rate of prey X by predator Y is a product of the quantity (available biomass) and quality (assimilation efficiency; α_{XY}) of prey type X , relative to the summation of the quantity and quality of each prey type i available to predator Y . This predator switching mechanism releases prey from strong predation when their densities become low (sensu Holling Type III function response; Gotelli 2001).

Respiration, decay, and mortality

Respiration is the process by which biomass is lost to satisfy metabolic requirements of aquatic invertebrates and fish, whereas decay represents loss of periphyton, terrestrial detritus, and carcass biomass to microbial decomposition. Both respiration and decay were assumed to increase exponentially with water temperature (T) as follows (Rutherford et al. 2000):

$$\begin{aligned} \text{Respiration}_i &= B_i r_{ref,i} \theta_i^{T-T_{ref}} \\ \text{Decay}_i &= B_i d_{ref,i} \theta_i^{T-T_{ref}} \end{aligned} \quad (5)$$

where $r_{ref,i}$ and $d_{ref,i}$ are respiration and decay rates, respectively, for biomass stock i at the reference

temperature T_{ref} ($T_{\text{ref}} = 20^\circ\text{C}$), and θ_i is a dimensionless temperature coefficient. Mortality is an additional loss term for fish and invertebrate biomass, which was controlled by a constant mortality rate (m_i).

Export

Export represents the detachment/mobilization and subsequent downstream transport of benthic organisms (periphyton and aquatic invertebrates) and organic matter (terrestrial detritus and salmon carcass material). This includes downstream export due to both (1) loss of biomass when benthic substrates are mobilized by scouring flows and (2) losses of biomass on stable substrates due to water friction on the stream bed. The export of stock i was represented by

$$\text{Export}_i = (B_i - B_i^*) \times (e_{\text{shear},i} (1 - r_{\text{scour}}) + r_{\text{scour}}) \quad (6)$$

where B_i^* is a refuge biomass that is not susceptible to mobilization (e.g., hyporheic invertebrates), and r_{scour} and $e_{\text{shear},i}$ represent the rates of biomass loss to benthic substrate mobilization and shear velocity on the stream bed, respectively. Export due to scouring of the stream bed is the amount of bed that is newly mobilized by high flows at each time step (Bellmore et al. 2014) and was calculated as

$$r_{\text{scour}} = \left\{ \begin{array}{l} \frac{(1 - p_{\text{scour},t-1}) - (1 - p_{\text{scour},t})}{(1 - p_{\text{scour},t-1})} \text{ if } p_{\text{scour},t} > p_{\text{scour},t-1} \\ \text{else } 0 \end{array} \right\} \quad (7)$$

where $p_{\text{scour},t}$ is the proportion of bed that is mobilized at a given time step. This formulation allows for the rate of scour to be positive only when the proportion of the bed being scoured increases from one time step to the next. Once the proportion of bed scour stabilizes (or decreases), no additional biomass is removed from the system due to scour. For those portions of the bed that are not being mobilized, export increases due to friction velocity on the stream bed (u_* , m/s) following a sigmoid function

$$e_{\text{shear},i} = \left(\frac{0.01 e^{a_i u_*}}{0.01 e^{a_i u_*} + 0.99} - 0.01 \right) \quad (8)$$

where a_i is a parameter that determines the sharpness at which the sigmoid curve approaches its maximum of 0.99 (i.e., 99% biomass export). See *Physical controls* for a description of how friction velocity and proportion of bed scour were calculated.

Periphyton production

Production represents the process by which primary producer biomass (termed “periphyton”) is accrued on the stream bed. Here we used a periphyton production formulation adapted from Bellmore et al. (2014)

$$\text{Production}_P = B_P g_{\text{max}} f_1 (\text{Temp}) f_3 (\text{Density}) f_4 (\text{Light}) f_5 (\text{Nutrients}) f_6 (\text{Velocity}) \quad (9)$$

where g_{max} is the maximum rate (1/d) of periphyton growth when biomass (B_P) is very low (no density dependence), resources are not limiting, and environmental conditions are ideal. This maximum rate was multiplied by five dimensionless functions that range from 0 to 1, and account for the limiting effects of water temperature (f_1 ; see Eq. 2 above), periphyton density (f_3), light (f_4), nutrients (f_5), and water velocity (f_6). All limiting factors except temperature were represented by Michaelis-Menton functions, where the effect of each factor on periphyton growth follows a type II functional response. The density function has the form

$$f_3 = 1 - \frac{B_P}{B_P + (1 - p_{\text{scour}}) k_P} \quad (10)$$

where k_P is the biomass level (B_P) where periphyton growth rate is half its maximum, and accounts for self-limitation within the periphyton community; i.e., as the algal mat grows there is increased competition for nutrients and light (Hill and Harvey 1990). The half-saturation value for biomass (k_P) was adjusted at each time step to account for the proportion of the bed currently being scoured (p_{scour}). Scoured surfaces were assumed unsuitable for periphyton growth during the scouring event. The limiting effect of light took the form

$$f_4 = \frac{\text{PAR}_{\text{bed}}}{\text{PAR}_{\text{bed}} + k_{\text{par}}} \quad (11)$$

where PAR_{bed} is the amount of photosynthetically active radiation (PAR; $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) reaching the stream bed at each time step, and k_{par} is the half-saturation level for PAR. The amount of light reaching the bed of the stream was determined from empirical estimates of above-canopy PAR (PAR_{can}) following Julian et al. (2008):

$$\text{PAR}_{\text{bed}} = (\text{PAR}_{\text{can}} \cdot (1 - p_{\text{shade}}) \cdot p_{\text{reflect}}) e^{-0.17 \cdot \text{NT} \cdot z} \quad (12)$$

where p_{shade} is the proportion of light lost to shading, p_{reflect} is the proportion of PAR that enters the water after reflection, NT is nephelometric turbidity, and z is average water depth in meters.

The nutrient function calculates the effect of a single limiting nutrient on periphyton growth, either dissolved inorganic nitrogen (DIN; $\text{NO}_2 + \text{NO}_3 + \text{NH}_4$) or soluble reactive phosphorus (SRP), as follows:

$$f_5 = \text{MIN} \left(\frac{[\text{DIN}]}{[\text{DIN}] + k_{\text{DIN}}}, \frac{[\text{SRP}]}{[\text{SRP}] + k_{\text{SRP}}} \right) \quad (13)$$

where [DIN] and [SRP] are the concentration (mg/L) of nitrogen and SRP in the water column, and k_{DIN} and k_{SRP} are the half-saturation levels for these two nutrients. At any given time, only the nutrient that is most limiting affects periphyton growth. The final limitation function calculates the limiting effect of water velocity (v ; m/s) on periphyton growth (McIntire 1973), as follows:

$$f_6 = \text{MIN} \left(1, 0.2 + \frac{v}{v + k_v} \right) \quad (14)$$

where k_v is half-saturation level for water velocity. This function assumes that low velocities can limit nutrient uptake.

Lateral and upstream inputs

Lateral inputs (Lateral_D) of leaf litter from the riparian zone directly contribute to the in-stream stock of terrestrial detritus (D). This process is an exogenous input to the model, and therefore no equation is provided. However, the magnitude and timing of this input (see Fig. 2) can be calculated by considering the density, composition, and aerial coverage of riparian vegetation (Minshall and Rugenski 2006).

Lateral inputs of terrestrial invertebrates are directly consumed by fish. Unlike leaf litter, however, we assumed that terrestrial invertebrates were either immediately consumed by fish or exported downstream. The availability of this subsidy at a given time step was modeled as

$$\text{Input}_{\text{Terr Inverts}} = (p_{\text{veg}} B_{\text{drop}}) + (B_{\text{winged}} \times \text{CarcassStrandingMultiplier}) \quad (15)$$

where p_{veg} is the proportion of the stream covered by riparian vegetation, B_{drop} is the daily biomass (g AFDM/d) of invertebrates dropping from vegetation, B_{winged} is the daily biomass input of winged invertebrates calculated from an empirical relationship with air temperature (Edwards and Huryn 1995), and the CarcassStrandingMultiplier is a multiplier that adjusts inputs of winged insects for the quantity of salmon carcasses stranded in terrestrial habitats (e.g., gravel bars). The CarcassStrandingMultiplier was calculated as follows:

$$\text{CarcassStrandingMultiplier} = \frac{(\text{MAX}_{\text{stranding}} - 1) B_{\text{S, stranded}}}{B_{\text{S, stranded}} + k_{\text{S, stranded}}} + 1 \quad (16)$$

where $\text{MAX}_{\text{stranding}}$ is the maximum possible effect of salmon on terrestrial invertebrate inputs, $k_{\text{S, stranded}}$ is the carcass biomass value where the response is one-half of the maximum, and $B_{\text{S, stranded}}$ is the biomass of stranded carcasses.

Upstream inputs (Upstream_i) represent organic matter (leaf litter and periphyton) and organisms (aquatic invertebrates) transported into the modeled river segment from upstream river segments. For the purposes of the simulations presented here, we made the simplifying assumption that upstream inputs (Upstream_i) to the modeled river segment equal downstream exports (see Eq. 6). When multiple river sections are linked end-on-end, upstream inputs to downstream reaches can be directly modeled (i.e., upstream inputs equal downstream export from the segment immediately upstream).

Effects of salmon on the food web

The magnitude of nutrients and organic matter from marine inputs are proportional to the number of adult salmon that return to the system, or, in the case of carcass addition, the number of carcasses added. Contributions of nitrogen and phosphorus from salmon were calculated using mass-specific excretion/leaching rates. During salmon spawning, salmon eggs become available for fish consumption via redd superimposition. In addition, scouring of the stream bed during redd construction detached benthic organisms and organic matter. Details on how these processes were modeled have been previously documented (see Bellmore et al. 2014). Once dead, salmon carcasses were available for invertebrate and fish consumption (Marine_S).

Physical controls

Channel discharge was converted to average wetted width and water depth (z) using graphic relationships between total discharge and width/depth (Appendix S1). Water velocity (v) was then solved for using the continuity equation (Gordon et al. 2004). Friction velocity u_* was calculated from channel slope (S), hydraulic radius (R), and acceleration due to gravity (g)

$$u_* = \sqrt{gSR}. \quad (17)$$

The proportion of the stream bed actively scoured at a given time step (p_{scour}) was determined by calculating the diameter of substrate at the threshold of motion (critical substrate size, D_{crit}) for a given water depth and slope (Gordon et al. 2004)

$$D_{\text{crit}} = \frac{d \cdot S}{(\rho_s - 1) \cdot \tau^*} \quad (18)$$

where ρ_s is substrate density (2.65 kg/m³) and τ^* is the Shields number (0.045) following Henderson (1966, p. 415). At each time step, critical substrate size (D_{crit}) was compared against a cumulative substrate size distribution to calculate the proportion of the stream bed containing substrates smaller than the critical size; this represents the portion of the stream bed scoured (p_{scour}) by hydraulic forces (see Bellmore et al. 2014).

Model parameterization

We parameterized the model for a 16-km river-floodplain segment of the Methow River, a fifth-order tributary of the Columbia River in north-central Washington, USA. We chose this segment because (1) it has been the site of ongoing river restoration efforts; (2) environmental data necessary to parameterize the model were readily available (Table 2); and (3) empirical food web data existed to compare with model simulations (Bellmore et al. 2013, Zuckerman 2015). The majority of precipitation falls in the winter as snow, and the hydrograph is typical of snow-melt systems, with peak flows in May and June (Fig. 2). The Methow River once supported large runs of spring Chinook

salmon (*Oncorhynchus tshawytscha*) and summer steelhead (*O. mykiss*; Mullen et al. 1992), but these populations are significantly depressed from historic levels, and both are listed under the Endangered Species Act. In an effort to recover these fishes, the Methow River has been the focus of numerous river restoration actions, including habitat restoration (especially side channel reconnections), riparian vegetation planting, and nutrient augmentation via additions of salmon carcasses.

The sources and values of environmental inputs used to parameterize the model for this river segment are presented in Table 2 and Fig. 2. Graphical relationships used to convert discharge into reach-averaged wetted width and water depth are shown in Appendix S1, and were developed by summarizing information from a previously constructed two-dimensional hydraulic model (Bureau of Reclamation 2012). Riparian vegetation cover and composition was converted into leaf-litter inputs using published relationships between tree diameter and foliage biomass (Jenkins et al. 2004).

We used previously published values for most of the model parameters; such as half-saturation values, respiration and consumption rates, and assimilation efficiencies (Appendix S2). In cases where no literature values existed, we adjusted parameter values to produce model runs that were stable (i.e., biomass stocks maintained positive values) and that matched reasonably well with empirical fish, invertebrate, and periphyton biomass (Bellmore et al. 2013, Zuckerman 2015).

For fish, bioenergetic parameter values (e.g., consumption/respiration rates) for juvenile Chinook salmon were used because recovery of this endangered species is one of the main goals of restoration in the Methow River. That said, we interpret simulated fish biomass as the capacity to sustain all of the numerically dominant native fishes found in the modeled river segment, which also includes: westslope cutthroat trout (*O. clarkii lewisii*), rainbow trout (*O. mykiss*), mountain whitefish (*Prosopium williamsoni*), longnose dace (*Rhinichthys cataractae*), and sculpin (*Cottus* spp.). Because these species can have different bioenergetic rates than Chinook salmon, our selection of parameter values has the potential to influence model outcomes. We account for this parameter uncertainty by including fish bioenergetics parameters into our model sensitivity analysis (see *Global sensitivity analysis*). By lumping all the fish species into a single “native fish biomass” stock, we also assumed that actions that increase (or decrease) the capacity to sustain all these native fishes will similarly improve (or degrade) conditions for the target anadromous species (Chinook salmon and steelhead). We think this is a valid assumption, given that all of the dominant native fishes are primarily invertivores (Bellmore et al. 2013). However, the dynamics of any one of these fish species could also depend on complex inter- and intra-specific interactions with other fishes, and species-specific habitat preferences. A much more complex model would be needed to represent these interactions, which was outside the scope of this manuscript.

Global sensitivity analysis

A global sensitivity analysis (GSA) was conducted to explore how uncertainty in model input parameters influenced modeled fish, aquatic invertebrate, periphyton, and terrestrial detritus biomass, and to determine which of these parameters the model was most sensitive to. In GSAs, the value of all uncertain parameters are adjusted simultaneously. Thirty model parameters were selected for this analysis, including assimilation efficiencies (α_{XY}), self-interaction parameters (γ_i), half-saturation values (k), maximum consumption and growth rates ($\text{cons}_{\text{max}, Y}$, g_{max}), respiration and decay rates ($r_{\text{ref}, i}$, $d_{\text{ref}, i}$), mortality rates (m_i), and shape parameters for export (a_i). The range of “uncertainty bounds” surrounding the value of each parameter (reported in Appendix S2) were adjusted to account for perceived uncertainty in the value of the parameter: $\pm 25\%$ for literature-derived values, and $\pm 50\%$ for parameter values that were assumed (ranges shown in Appendix S2). Sensitivity analyses were then conducted using a Latin hypercube sampling (LHS) design (McKay et al. 1979). In LHS, the uncertainty range for each parameter is divided into N strata of equal width (where $N =$ the number of simulations conducted), and a random parameter values is selected within each strata. From the N possibilities for each parameter, LHS randomly selects one of these values (without replacement) for use in each run. Thus, LHS ensures adequate sampling across the entire range of each parameter.

We conducted a 10000 simulation sensitivity analysis using this approach to produce 10000 separate estimates of fish, aquatic invertebrate, periphyton, and terrestrial detritus biomass. These outputs were used to calculate confidence intervals around background biomass estimates. In addition, to determine how sensitive the model was to each uncertain variable we employed the R package Random Forest (Random Forest 4.6-2; The R Foundation, Vienna, Austria; Breiman and Cutler 2011), which is an accepted approach for ranking parameter importance in complex ecological models (Harper et al. 2011, Bellmore et al. 2014). Using the matrix of input and output parameter values across the 10000 simulations, Random Forest calculated the importance for each parameter, including its interaction with all other parameters in determining modeled fish, aquatic invertebrate, periphyton and terrestrial detritus biomass. Briefly, importance values represent the change in prediction error of the regression tree when the value of a given parameter is changed while values for all other parameters remain the same (for a details on this approach, see Harper et al. 2011). Importance values for each parameter were normalized by the sum of importance values for all parameters.

Restoration simulations

We explored the response of the modeled river segment to three river restoration alternatives: (1) riparian

vegetation restoration, (2) nutrient augmentation via salmon carcass addition, and (3) reconnection of side channel habitats. We adjusted the magnitude of each treatment to represent the restoration potential of the reach based on geomorphic and vegetation assessments as well as historic conditions (Mullen et al. 1992, Bureau of Reclamation 2010). To represent the effects of riparian vegetation restoration, we instantaneously increased the aerial coverage of vegetation (composed of black cottonwood; *Populus trichocarpa*) by 50% (from 5% aerial coverage of the channel to 7.5% cover). We also increased shading by 50% above background. Although riparian restoration can also influence bank stability, in-stream cover for fish, water temperature, and nutrients, this simulation was solely focused on the effects of riparian restoration on inputs of organic matter and light.

For nutrient augmentation, we evaluated the effect of adding salmon carcasses to the channel at a magnitude similar to estimated historic salmon spawning abundance (20× greater than the current number of spawners; Mullen et al. 1992). This equated to an addition of 4000 salmon carcasses to the modeled river segment, which were added each year of the 10-year model simulation. Each carcass weighed 5 kg, and all carcasses were added to the channel as a single pulse on 21 September (after spring Chinook salmon spawning).

To simulate effects of side channel reconnection, we added a side channel parallel to the main channel. The environmental conditions of this channel were parameterized to match those of a side channel that was recently reconnected within the modeled river-floodplain segment (Bureau of Reclamation 2012). Environmental conditions that were modified from those of the main channel were discharge, channel hydraulics (width/depth/velocity), riparian vegetation cover, and shading. Once connected, a portion of the total discharge (ranging from 2% during low flow to 23% at bankfull flows) was routed into the side channel. The side channel had narrower wetted width and shallower depth than the main channel, as well as a greater proportion of vegetation coverage (due to the narrower channel). Similar to the main channel, the relationship between discharge and water depth/width for the side channel was determined by summarizing output from a two-dimensional hydraulic model (Appendix S1; Bureau of Reclamation 2012).

All simulations were run for 3650 d (10 yr), starting on 1 January. Results are reported for the final 365 d of the model simulation, after the model equilibrated to initial conditions. Results are presented in grams of AFDM per meter of river length. Uncertainty in predicted responses was determined by running a separate sensitivity analyses using the same LHS design described above. A smaller set of 1000 simulations was deemed adequate for this analysis; simulated biomass and variance produced with 1000 simulations was not significantly different than with 10000 simulations (F test for variances, $P > 0.05$; t test for means, $P > 0.05$). This analysis produced 1000

separate estimates of fish, aquatic invertebrate, periphyton, and terrestrial detritus biomass for the background condition and each restoration treatment. For each simulation, we subtracted background biomass from treatment biomass to produce 1000 response magnitude estimates. Response magnitudes are summarized with box-and-whisker plots that illustrate the 25th and 75th, 10th and 90th, and 5th and 95th percentiles around the median response.

Food web structure manipulations

To evaluate how changes in food web structure influence model simulations, we modified the basic model structure (Fig. 1) to include a nonnative grazing snail (L) and a nonnative stock of piscivorous fish (H). Nonnatives were coded using the same mass balance approach used for the others biomass stocks (see equations in Table 1). The equations for biomass gains and losses (consumption, respiration, mortality, import/export rates) were also the same as used previously (Eqs. 1–8), but with modified parameter values (see Appendix S2). The main difference between the nonnatives and their native counterparts was their trophic relationship to the other stocks. Snail diets were restricted to grazing of periphyton (they did not consume terrestrial detritus), and nonnative fishes not only consumed invertebrates and salmon carcasses, but were also allowed to directly prey upon native fish. The snail was coded to represent nonnative New Zealand mudsnails (*Potamopyrgus antipodarum*), which can dominate invertebrate biomass and energy flow in invaded streams (Hall et al. 2003). Although mudsnails are consumed by fish, they have little nutritional value and can cause weight loss if consumed in large numbers (Vinson and Baker 2008), which we accounted for by reducing the assimilation efficiency for fishes consuming mudsnails ($\alpha_{LH} = 0.09$). We did not code the nonnative fish stock for a specific nonnative species, however we adjusted the bioenergetics rates for this stock to represent a larger piscivorous species, several of which could invade this river segment in the future (e.g., smallmouth bass). We added each of these stocks to the model independently, first nonnative snails then nonnative fish, and then in combination, resulting in four food web configurations: (1) nonnatives absent, (2) snails present, (3) nonnative fish present, and (4) nonnative snails and fish present. We ran the river restoration scenarios described above with each food web configuration to explore how changes in web structure mediate restoration responses.

RESULTS

Model corroboration and sensitivity analysis

Model runs conducted with the basic food web structure (nonnative snails and fish absent) produced estimates of fish, aquatic invertebrate, and periphyton

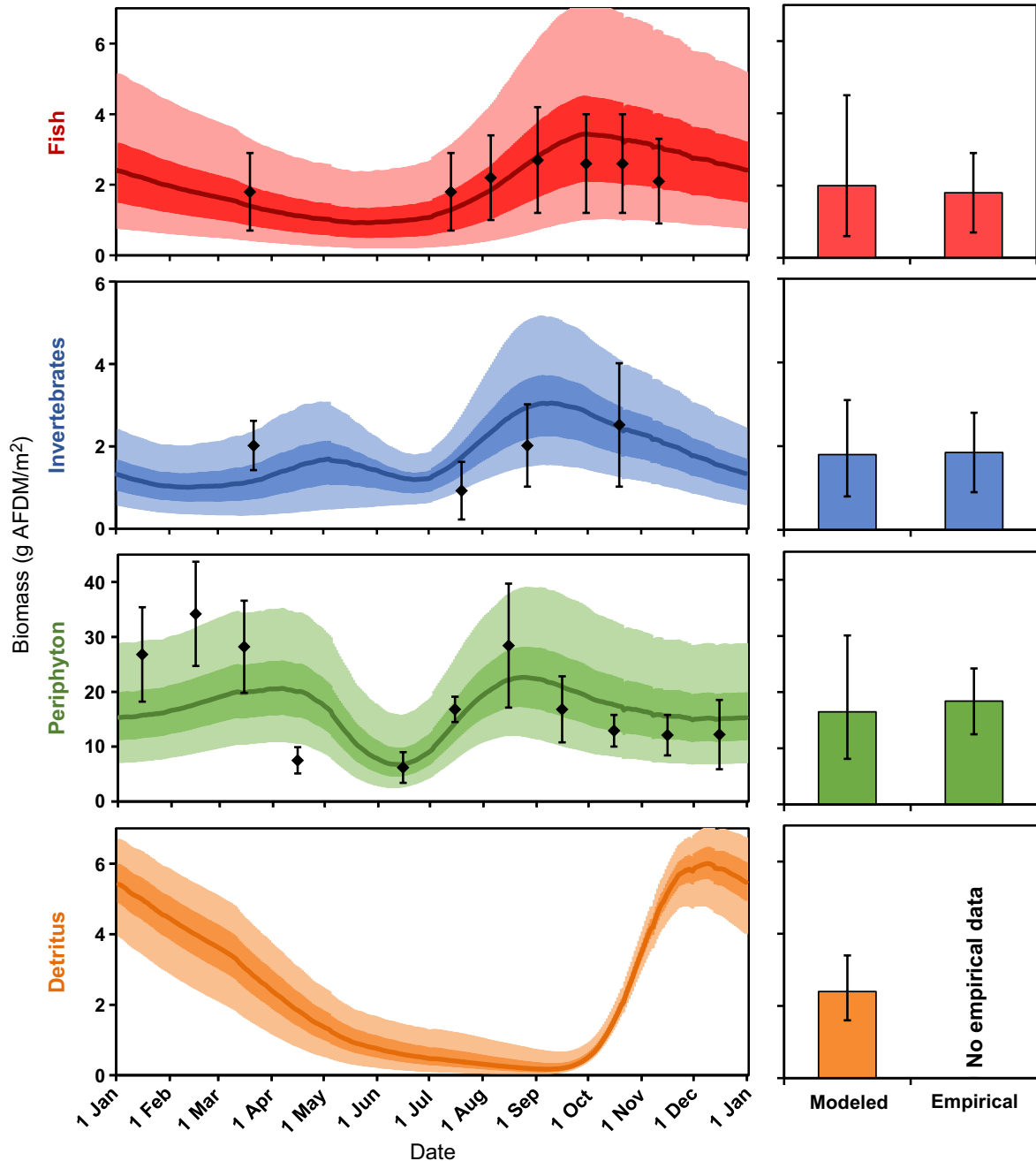


FIG. 3. Sensitivity of biomass stocks to uncertainty in model parameter values, and comparison of model outcomes to available empirical data. Panels on the left shows modeled daily biomass dynamics for native fish, aquatic invertebrates, periphyton, and terrestrial detritus with 25th and 75th (dark shaded area), and 5th and 95th (light shaded area) percentile bounds around model outcomes calculated from a 10000 run sensitivity analysis. Empirical biomass estimates ($\pm 95\%$ confidence intervals) are superimposed on top of model results. Panels on the right compare modeled and empirical estimates of average annual biomass ($\pm 95\%$ confidence intervals). [Color figure can be viewed at wileyonlinelibrary.com]

biomass that were similar to those measured empirically (Fig. 3; Bellmore et al. 2013, Zuckerman 2015). Model simulations fell within the 95% confidence intervals of empirical data in most cases (Fig. 3). Seasonal patterns of modeled biomass were also consistent with what might be expected given the physical and riparian conditions of the

modeled river segment. Terrestrial detritus biomass (for which we did not have empirical estimates) increased with leaf abscission in the autumn, and then declined throughout the winter and spring as this material was decomposed, consumed by invertebrates, and exported downstream. Periphyton biomass was lower in winter,

increased in the spring with warmer water temperatures and greater light availability, declined in late-spring with high flows (when turbidity and bed scour were high; Fig. 2), and then peaked in late summer, a pattern frequently observed in snow-melt-dominated systems such as the Methow River (Minshall et al. 1992). On an annual basis, the biomass of periphyton was over $20\times$ greater than the biomass of terrestrial detritus, as might be expected given the width of the channel (40 m wide at base flow). The peak in aquatic invertebrate biomass lagged slightly behind the peak in periphyton biomass, and the peak in fish biomass lagged slightly behind that of invertebrates.

Modeled fish, aquatic invertebrate, periphyton, and terrestrial detritus biomass were sensitive to uncertainty in model parameters included in the global sensitivity analysis (Fig. 3). The width of percentile bounds surrounding average annual biomass estimates, for instance, ranged from an average of $\pm 38\%$ for terrestrial detritus to $\pm 97\%$ for fish. Modeled fish and invertebrate biomass was found to be highly sensitivity to parameters that influenced basal periphyton production (maximum periphyton growth rate, $g_{\max,P}$; periphyton half saturation for density, k_D), as well as the efficiency at which this organic matter is assimilated by invertebrates and fish (α_{PI} ; α_{IF}) (Fig. 4). Periphyton biomass was also sensitive to parameters that influence periphyton production ($g_{\max,P}$; k_D), as well as invertebrate consumption and

mortality rates ($\text{cons}_{\max,I}$; m_I). Terrestrial detritus biomass was most sensitive to invertebrate consumption and mortality ($\text{cons}_{\max,I}$; m_I).

Responses to restoration

Modeled response to restoration with the basic food web structure varied among the three treatment actions, across the four biomass stocks, and through time (Fig. 5). Riparian vegetation restoration increased the availability of in-stream terrestrial detritus, particularly during and shortly following leaf abscission. However, this increase in detritus did not propagate up the food web. Instead, fish and invertebrate biomass decreased, almost imperceptibly, because of a slight reduction in periphyton biomass due to additional riparian shading.

In contrast to the vegetation treatment response, salmon carcass addition did increase fish biomass. Fish biomass increased sharply following carcass addition and remained above background most of the year. Aquatic invertebrates also increased following carcass addition, but returned to background by January. Periphyton, however, did not respond to carcass addition.

The biomass of terrestrial detritus, periphyton, aquatic invertebrates, and fish all increased in response to adding a side channel adjacent to the main channel. The magnitude of this increase was greater than that simulated for either carcass addition or riparian vegetation restoration

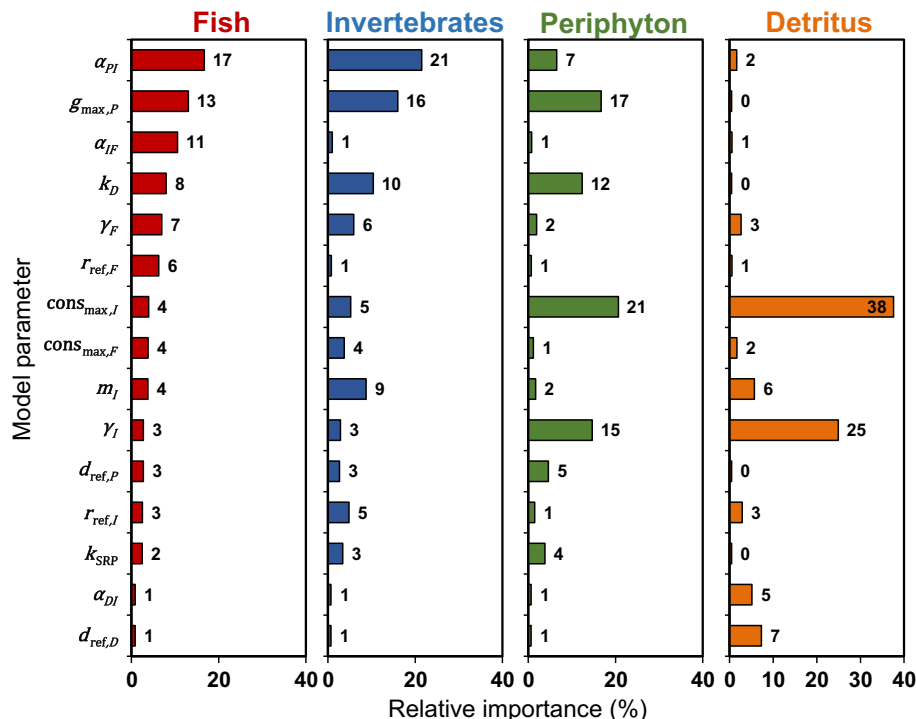


FIG. 4. Relative importance of different model parameters in determining the average annual biomass of native fish, aquatic invertebrates, periphyton, and terrestrial detritus determined from Random Forest analysis. The figure shows the top 15 most important parameters in determining modeled outcomes, ranked according to those most important in explaining fish biomass. See *Methods* or Appendix S2 for descriptions of each parameter. [Color figure can be viewed at wileyonlinelibrary.com]

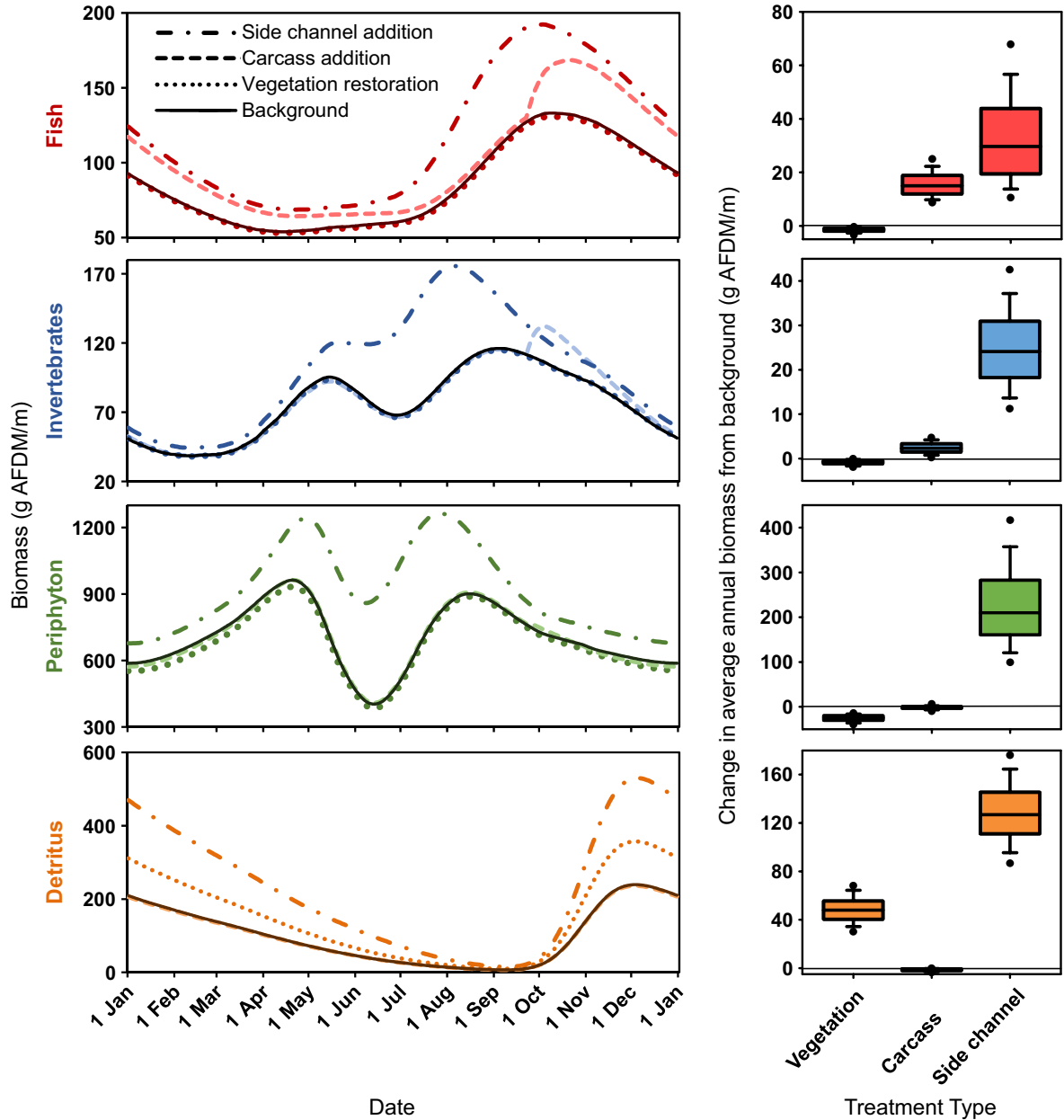


Fig. 5. Modeled responses to riparian vegetation restoration, salmon carcass addition, and side channel addition. Panels on the left show modeled intra-annual biomass dynamics for the background (no treatment) condition and each restoration action. Panels on the right show the change in average annual biomass for each restoration action from the background condition. Percent changes from background are represented with box-and-whisker plots that show the sensitivity of modeled outcomes to uncertainty in model parameter values, where the line within each box is the median outcome, box boundaries are 25th and 75th percentiles, whiskers are 10th and 90th percentiles, and dots are 5th and 95th percentiles. [Color figure can be viewed at wileyonlinelibrary.com]

(Fig. 5). Ranked from lowest to highest, the magnitude of the fish biomass response to each restoration action was vegetation restoration (2% decrease in average annual biomass), carcass supplementation (18% increase), and side channel addition (31% increase). Importantly, the relative magnitude and ranking of these responses was insensitive to uncertainty in the value of model parameters (Fig. 5). Relative to the other treatment types, side channel addition had the greatest positive impact on

fish biomass 91% of the time (910 of 1000 runs; 9% for carcass addition).

Food web manipulations

The capacity of the system to support native fish biomass was highly sensitive to changes in the structure of the food web. The presence of either nonnative snails or fish decreased the biomass of native fish by 35% (5th

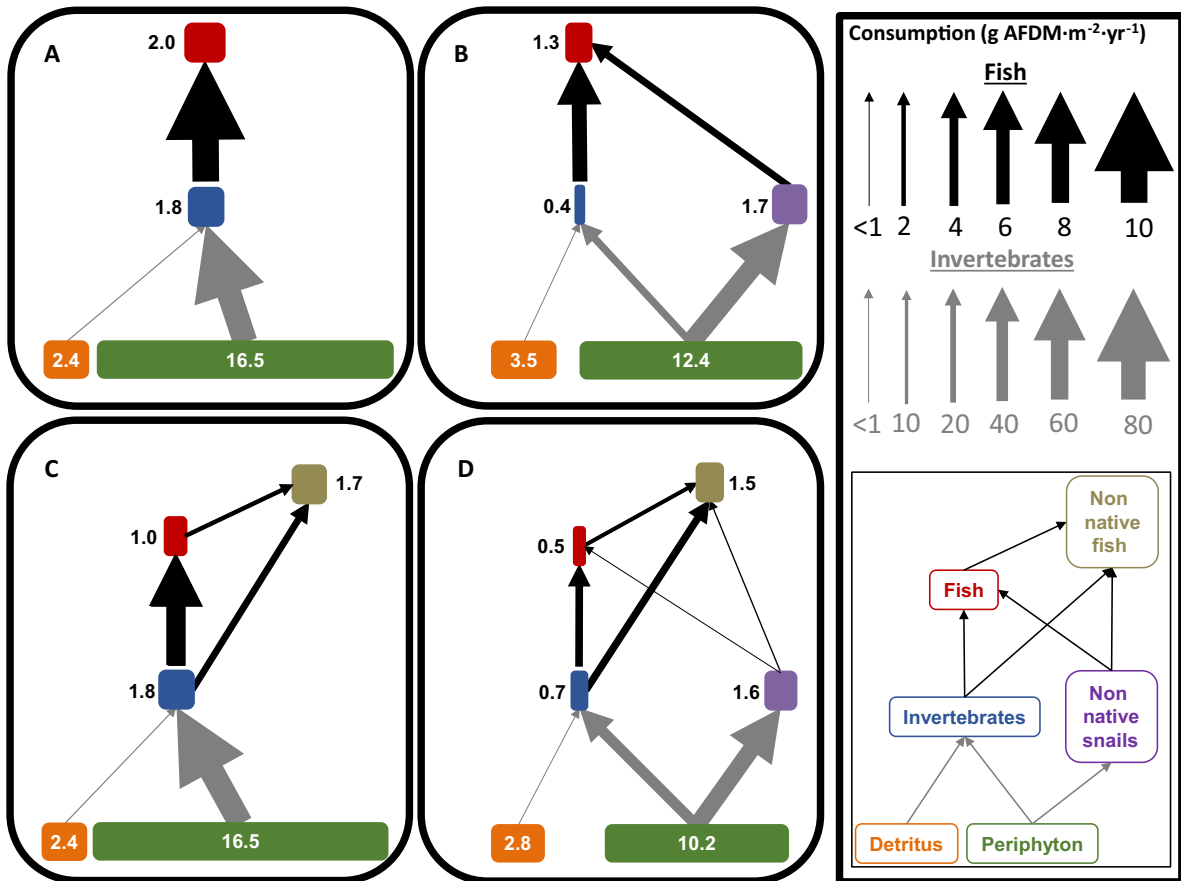


FIG. 6. Food web maps depicting the annual organic matter flow between consumers and resources (relative arrow width) and the size of different biomass stocks (relative bar widths) for four different food web configurations: (A) basic food web, (B) nonnative snails added to web, (C) nonnative fish added to web, and (D) nonnative snails and fish added to web. Values next to biomass stocks represent the average annual biomass ($\text{g AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). The legend on the right shows consumptive values for different arrow widths (top), and a key to the different food web members (bottom). [Color figure can be viewed at wileyonlinelibrary.com]

and 95th confidence bounds, 7–71% decrease) and 50% (40–67%), respectively (Fig. 6). When both nonnative snails and nonnative fish were present, native fish biomass was reduced by 75% (60–99%).

Reductions in native fish biomass were a result of changes in the pathways and magnitudes of organic matter flow through the food web (Fig. 6). With the basic food web structure (Fig. 6A), organic matter flowed in a chain of strong interactions from periphyton to invertebrates and from invertebrates to fish. When snails were added (Fig. 6B), much of the organic-matter flow from periphyton was rerouted to snails, reducing periphyton biomass, and strongly reducing native aquatic invertebrate biomass, which led to a subsequent reduction in native fish. Although fish did consume some snails, because fish only assimilate a small portion of snail biomass (only 9%), snail consumption could not offset the loss of the fishes' preferred native aquatic invertebrate prey.

When nonnative fish were added to the food web (Fig. 6C), native fish biomass decreased due to direct predation by nonnatives, and also competition for shared

aquatic invertebrate prey. Last, the presence of both nonnative snails and nonnative fish resulted in the greatest decline in native fish biomass because of the combined effects of basal energy rerouting, top-down predation, and competition for shared food resources (Fig. 6D).

Restoration and food web manipulation interaction

The native fish response to carcass and side channel addition was highly sensitive to the presence/absence of nonnative snails and fish (Fig. 7). When nonnatives were absent salmon carcass addition increased fish biomass by 15 $\text{g AFDM}/\text{m}$ relative to background conditions. This response was actually greater when nonnative snails were present in the food web (19 $\text{g AFDM}/\text{m}$), and much lower in the presence of nonnative fish or when nonnative fish occurred with snails (8 $\text{g AFDM}/\text{m}$). For side channel addition, the native fish response was highest when both nonnatives were absent (29 $\text{g AFDM}/\text{m}$). The magnitude of this increase was slightly lower when snails were present (16 $\text{g AFDM}/\text{m}$), and significantly lower when

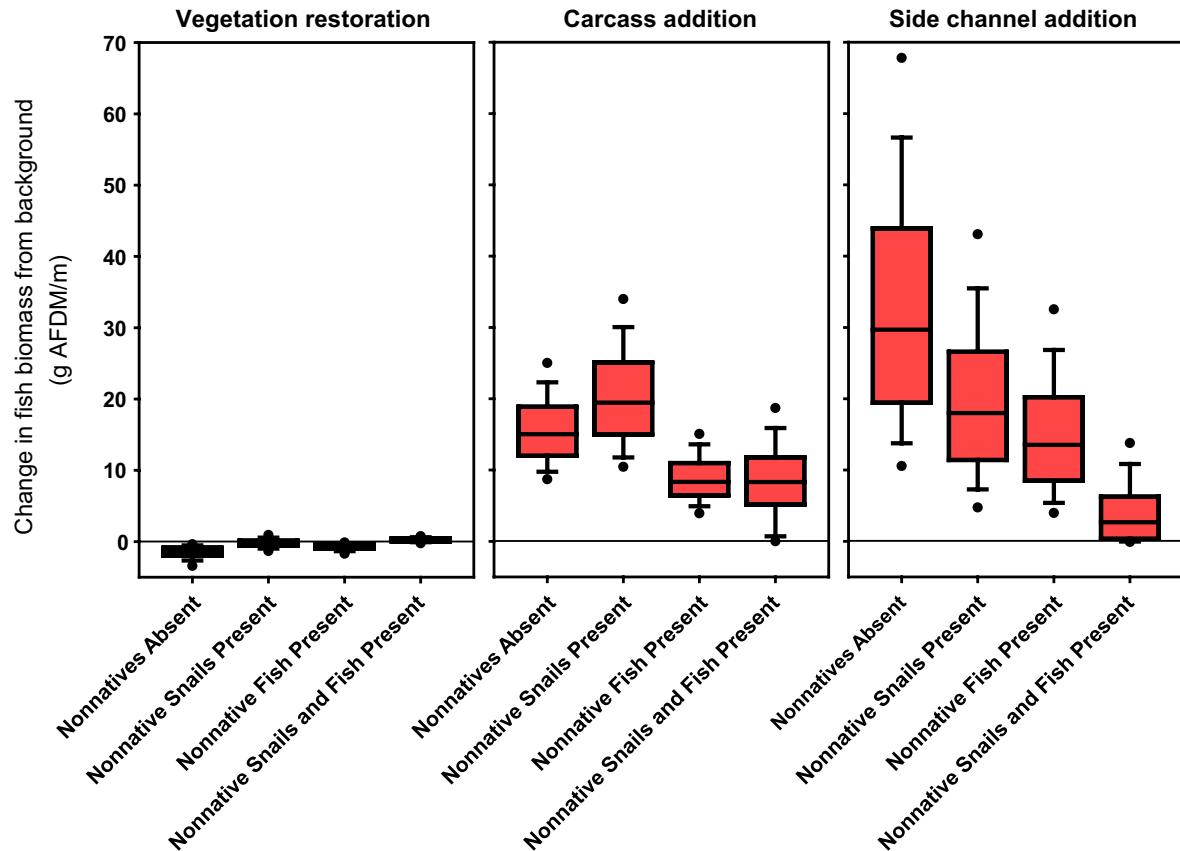


FIG. 7. Native fish response to modeled restoration actions when nonnative snails and fish are present/absent. The zero line represents the background (no treatment) condition for each food web configuration. Changes from background are represented with box-and-whisker plots that show the sensitivity of modeled outcomes to uncertainty in model parameter values, where the line within each box is the median outcome, box boundaries are 25th and 75th percentiles, whiskers are 10th and 90th percentiles, and dots are 5th and 95th percentiles. [Color figure can be viewed at wileyonlinelibrary.com]

nonnative fish were present (13 g AFDM/m). When both nonnative snails and fish were present in the food web, side channel restoration produced little positive native fish response (3 g AFDM/m), and the lower 10th percentile of model runs overlapped with the 0 response line.

DISCUSSION

We constructed a model that explicitly linked river food web dynamics to instream physical habitat and riparian conditions. Although our model was a simplification from that of real river food webs, it was able to produce realistic dynamics that were similar to those measured empirically. Our simulations illustrate that food web models can be used to explore responses to a variety of river restoration actions, from those that represent direct manipulations of the food web (e.g., salmon carcass addition), to those that are focused on modifying the physical template upon which these webs of interaction emerge (e.g., side channel reconnection). Unlike habitat-based approaches that model the direct effects of habitat on single species of interest, our approach dynamically linked the success of target organisms to the success

of competitors, predators, and prey, via flows of energy through the food web. Our results emphasize that restoration actions can influence stream ecosystems via multiple pathways. Perhaps the most important finding was that the structure of the food web strongly mediated restoration responses; the occurrence of nonnative snails and fish modified pathways of energy flow through the modeled food web, which strongly influenced the magnitude of the desired native fish response. This model experiment illustrates that forecasting responses to restoration may require accounting for the structure of food webs, a finding that provides additional support for on-going calls to incorporate food web interactions into restoration planning (Vander Zanden et al. 2006, Wipfli and Baxter 2010, Naiman et al. 2012).

Responses to restoration

In the river-floodplain segment of the Methow River evaluated here, our simulations suggested that some actions may be more likely than others to produce desired increases in fish productivity. For instance, adding a side channel adjacent to the main channel had the greatest

effect on fish (and all other trophic levels), indicating that efforts to enhance river-floodplain connectivity may be beneficial (Bellmore et al. 2013, Martens and Connolly 2014). Our simulations also suggest that adding high-quality organic matter and nutrients, in the form of salmon carcasses, could produce positive fish responses. Increasing riparian forest cover, however, had minimal effects on modeled fish biomass, showing that, from the perspective of changes in leaf-litter inputs and light associated with additional vegetation, this strategy may not significantly influence fish populations in this particular river segment. Importantly, we found that the direction and relative magnitude of modeled responses to these alternative restoration actions were generally robust to parameter uncertainty. This finding indicates that the ATP model may be valuable for ranking alternative actions even if the value of important model parameters is unknown. That said, the model was highly sensitive to parameters that control basal periphyton production and the efficiency of consumers to assimilate this basal energy, suggesting that obtaining better estimates for these processes could improve prediction.

One of the benefits of food web modeling, and simulation modeling in general, is the ability to provide insight into the mechanisms and pathways by which management actions propagate through the food web to influence specific populations or trophic levels (McIntire and Colby 1978, Power et al. 1995, Doyle 2006). Adding a side channel adjacent to the main channel, for example, increased fish biomass for the following reasons. First, routing some of the flow from the main channel into a lower-energy (i.e., lower stream power) side channel increased the capacity of the modeled river segment to retain basal organic matter (periphyton and terrestrial detritus). This resulted in more organic matter being assimilated in situ instead of being transported downstream. Second, the additional ribbon of riparian vegetation associated with the side channel doubled the input of terrestrial leaf litter and invertebrates to the modeled river segment. Finally, the most important mechanism was that side channel addition increased the wetted area of the segment (by an average of 23%), and therefore, there was simply more habitat to support biological production.

The observed increase in fish biomass with carcass addition was primarily due to the direct consumption of labile carcass material by fishes and invertebrates. Fish preferentially selected for and foraged upon carcass material in our model simulations because of the high quality of salmon carcass tissue relative to invertebrate prey (Gende et al. 2002), as has been empirically illustrated in carcass addition experiments (e.g., Collins et al. 2016). Carcass material was also directly consumed by aquatic invertebrates, which increased their biomass and provided further prey resources for fish. We did not, however, observe an increase in periphyton biomass with carcass addition. The lack of a measurable periphyton response was due to the large size of the river relative to

the quantity of nutrients contributed by carcasses. In other words, the river was too large for the nutrients leached out of the carcasses to increase nutrient concentrations enough to stimulate periphyton production. In a separate empirical study, however, we did find that live salmon spawners, even at low densities, can increase primary production (Benjamin et al. 2016). Overall, these model findings corroborate the results of field experiments and other model analyses that highlight the importance of direct consumptive pathways over indirect “bottom-up” pathways for incorporation of marine carbon into freshwater food webs (Kiernan et al. 2010, Bellmore et al. 2014).

Riparian restoration had little effect on food web dynamics or fish biomass, which was surprising given the prevalence of riparian restoration efforts (Bernhardt et al. 2005), and the general belief that more forest cover equates to better habitat for fish (but see Wilzbach et al. 2005, Wootton 2012). In our model simulations, the lack of an effect was due to the large size of the river (40 m wetted width at base flow) relative to the size of the treatment. Although we increased riparian cover by 50%, this only equated to an increase in aerial coverage from 5% to 7.5%. Moreover, most of the aquatic invertebrate biomass for this particular river segment was not supported by terrestrial derived organic matter, but by in-stream production of periphyton, which was on average 20× more abundant than terrestrial detritus, and a higher quality (more labile) resource. Consequently, although adding riparian vegetation increased the input of terrestrial detritus, this did not translate into greater production at higher trophic levels. This finding is in line with the basic tenants of the river continuum concept (Vannote et al. 1980), which predicts reduced interaction between rivers and riparian zones for larger channels such as the river segment modeled here. That said, riparian vegetation not only contributes leaf litter and invertebrates to rivers, but also labile nutrients (leached from abscised leaves), and large woody debris. Neither of these pathways were included in our analysis, but have been shown to influence river food webs and habitat suitability for fish (Meyer et al. 1998, Gregory et al. 2003).

Effects of food web structure

Model simulations suggested that changes in food web structure associated with species invasions (or extinctions) may strongly change the pathways of energy flow that sustain target populations, a finding that is supported by numerous empirical studies (Baxter et al. 2004, Benjamin et al. 2011, Cross et al. 2011). In our simulations, the presence of nonnative snails rerouted basal energy away from native aquatic invertebrates, which in turn lowered fish biomass by reducing the availability of their preferred (and higher quality) aquatic invertebrate prey. This finding is supported by empirical studies, which show that New Zealand mudsnails can numerically dominate aquatic invertebrate assemblages, and

consume a significant portion of basal primary production (Hall et al. 2003, Krist and Charles 2012). Similar results have also been observed for other nonnative aquatic invertebrates (Johnson et al. 2009).

The presence of a nonnative fish also rerouted energy flow through the food web, with top-down and bottom-up consequences for native fishes. Specifically, nonnatives directly preyed on and competed for food with native fish. The modeled reduction in fish biomass from this competition and predation is similar to empirical observations and experiments, which illustrate that nonnative predatory fishes can have negative consequences for native fish assemblages (Fritts and Pearsons 2004, Kuehne and Olden 2012), as well as other aquatic organisms, such as amphibians (Knapp and Matthews 2000).

When both nonnative snails and fish were present together, we simulated the strongest reduction in native fish biomass owing to a combination of basal energy rerouting, top-down predation, and competition for shared food resources. This finding suggests that multiple invaders can have additive effects on energy flow through food webs (Walsworth et al. 2013), with negative consequences for native species (Johnson et al. 2009). Most importantly, these simulations suggest that river segments with similar physical and environmental conditions, but dissimilar food web structures (regardless of whether species are native or exotic), may strongly differ in their capacities to sustain species of interest. This finding questions the validity of approaches that calculate “carrying capacity” via assessment of physical habitat and channel hydraulics alone (e.g., Bovee 1986), and highlights the importance of empirical studies that aim to decipher the complex array of species interactions in rivers (Power 1990, Cross et al. 2013).

Our simulations suggest that understanding these complex webs of interactions may also be necessary to forecast potential responses to river restoration. Changing the structure of the food web in our model simulations by adding nonnative snails and fish strongly mediated the magnitude of the native fish response to restoration. When nonnative fish were present, adding carcasses to the river subsidized these nonnatives, which led to additional predation and competition with the native fish and a reduction in their biomass. In contrast, when nonnative snails were present (and nonnative fish were absent) native fish were more limited by food because the availability of the fishes’ desired native aquatic invertebrate prey was much lower (See Fig. 6B). As a result, these food-limited fish responded more strongly to salmon carcasses being added to the stream. For side channel addition, the presence of nonnative fish or snails in the side channel rerouted energy similar to that shown in Fig. 6, reducing the benefit of restoration. When both nonnative snails and fish were present, their interactive effects almost entirely negated native fish response to side channel addition. In this case, there was not only less aquatic invertebrate biomass available (due to competition with snails), but reduction in invertebrate availability indirectly reduced native fish

biomass by shifting the nonnative fishes’ foraging preferences toward more piscivory. These findings should be concerning, as they suggest that the on-going spread of invasive species may have the potential to undermine river restoration efforts, particularly in situations where invaders may dramatically shift energy or nutrient flow through food webs (Hall et al. 2003).

The value and application of food web modeling

The basic structure of the ATP model was coded for small and medium sized rivers where most primary production and secondary invertebrate production occurs in the benthos. Although we parameterized the model to a floodplain segment of the Methow, it can easily be parameterized to other river segments by updating the environmental inputs (i.e., discharge and hydraulics, substrate, temperature, nutrients, turbidity, light, and terrestrial and marine inputs). Additional food web complexity could also be added to this model (i.e., by adding different stocks of organisms), and we encourage others to build upon and customize the structure of this model to better represent local conditions and processes of interest. Care should be taken, however, in adding too much additional complexity. Although complex food web models are important for testing and exploring ecological theory (see Pascual and Dunne 2006), they can produce dynamics that may be difficult to interpret, which can decrease their value as heuristic tools.

Regardless of how well food web models are customized to specific contexts, they will always be abstractions of reality. As such, model predictions should not be interpreted as truth, but instead, as defensible hypotheses that can be used to structure decision making. In the Methow River, for example, the food web model presented here is being used to inform restoration planning. Although results from the model may prove to be wrong, information collected by subsequent monitoring of restoration treatments can be used to refine model parameters, the structure of the model, and even the underlying knowledge and assumptions on which the model is based. Moreover, although restoration practitioners will be most interested in the predictions these models produce, food web models can also be used to promote understanding, identifying knowledge gaps, and inform empirical studies.

CONCLUSION

We show that dynamic food web models can be useful for guiding river restoration and management. Although restoration assessments frequently focus on the direct effects of restoration on species of interests, restoration also influences the larger ecological system in which these species participate. Understanding responses to restoration in this context will require accounting for these complexities, and food web modeling provides a means for doing so. Linking these approaches to restoration planning, however, will require that modelers work directly

with managers, restoration practitioners, and other stakeholders to incorporate their local knowledge into the modeling process early and often (Roni and Beechie 2013). It should be clear, however, that the goal of this interaction is not to provide perfect predictions, but to improve restoration planning by fostering a deeper understanding of the dynamics and complexity of the system.

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DATA AVAILABILITY

Data for this paper have been deposited in figshare: <https://doi.org/10.6084/m9.figshare.4287773>