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ARTICLE

Use of an Ecosystem-Based Model to Evaluate Alternative Conservation Strategies for Juvenile Chinook Salmon in a Headwater Stream

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Abstract

Declining abundance of Chinook Salmon *Oncorhynchus tshawytscha* across the Pacific Northwest is an issue of great concern ecologically, culturally, and economically. Growth during the first summer is vitally important for juvenile Chinook Salmon, as it influences not only life history decisions (to smolt or not to smolt) but also subsequent river and ocean survival. Using Ecopath with Ecosim, we developed a food web model for a representative stream in the Salmon River basin, Idaho, to evaluate potential species-specific and food web effects of three management strategies: (1) adding salmon carcasses or carcass analogs to promote primary production and detrital availability that were lost due to declining salmon returns; (2) removal of nonnative Brook Trout *Salvelinus fontinalis*, which are competitors with and predators on juvenile Chinook Salmon; and (3) stocking hatchery Chinook Salmon into streams to supplement wild production. Overall, juvenile Chinook Salmon responded strongly to increases in basal resources. Removal of Brook Trout had little effect on potential production for juvenile Chinook Salmon, but the responses of sculpins *Cottus* spp. were strong, primarily due to the sculpins' high degree of dietary overlap with and predation by Brook Trout. Supplementation with hatchery-origin juveniles depressed the production of wild juvenile Chinook Salmon, especially at the densities commonly applied to streams in this region. Our results suggest that efforts to enhance basal resources are likely to be the most effective in promoting the production of juvenile Chinook Salmon and nearly all food web groups considered in our model system. Removal of nonnative Brook Trout is unlikely to substantially affect salmon but could have a disproportionately large effect on nongame species, which are generally overlooked in single-species management approaches.

The conservation of threatened and endangered populations of Pacific salmon *Oncorhynchus* spp. is a well-established example of federally mandated single-species management for which an increasingly broad ecosystem perspective has been advocated (Naiman et al. 2002; Independent Scientific Advisory Board 2011). This broader ecosystem perspective and the implementation of specific ecosystem management techniques require an understanding of the ecological framework in which a species functions and the complex suite of direct and indirect interactions among organisms (Boersma et al. 2001). Ecosystem modeling has become an important tool in exploring these

connections and in developing and testing alternative management and conservation strategies. Modeling exercises can reveal tradeoffs that improve conditions both for target species and for the whole food web (Christensen et al. 1996). This is particularly relevant for work with threatened and endangered species, where the opportunities to field test multiple alternative management options or ecosystem manipulations are limited.

Wild populations of Chinook Salmon *O. tshawytscha* have declined across the Pacific Northwest, spurring a great deal of interest in the factors that promote (or inhibit) production of juvenile Chinook Salmon in rearing streams (Kareiva et al. 2000).

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The growth and survival of juvenile salmon in freshwater are affected by a number of ecological factors. In the present study, we focused on three areas of particular concern with regard to wild Chinook Salmon survival and production in headwaters of the interior Columbia River basin: (1) declining numbers of returning adults, leading to the loss of nutrient subsidies provided by the decay of spawner carcasses (Stockner 2003); (2) species invasion—specifically the introduction of Brook Trout *Salvelinus fontinalis* (Sanderson et al. 2009a; Macneale et al. 2010); and (3) stocking of hatchery-origin juveniles into systems that contain wild populations, thus impacting resource availability for target and nontarget wild fishes (Levin et al. 2001; Weber and Fausch 2005).

These three factors reflect processes by which the production of juvenile Chinook Salmon can be affected: bottom-up resource availability, top-down predator effects, and direct and indirect competition. First, declines in adult salmon abundance lead to a loss of nutrient and organic matter subsidies in these oligotrophic stream environments, which may result in reduced juvenile salmon production through several pathways that are mediated by the stream food web (Wipfli and Baxter 2010). Carcasses of postspawn adult salmon provide a direct detrital subsidy to invertebrates and fish, and the inorganic nutrients that are released during the decomposition of the carcasses can promote periphyton growth, thereby indirectly increasing secondary production (Bilby et al. 1998; Kiernan et al. 2010). Second, in many of these same systems, invasive piscivores are having profound impacts on native salmonids (Eby et al. 2006; Sanderson et al. 2009a). In headwater streams of western North America, the most pervasive invader is the Brook Trout (Dunham et al. 2002; Peterson et al. 2008), which both preys upon and competes with native salmonids (Dunham et al. 2002; Peterson et al. 2004). Finally, juvenile salmon of hatchery origin are an additional source of resource competition in many nursery streams. Fish that are stocked as parr often remain in or near the area where they were released (Peery and Bjornn 2000), which can lead to direct competition among wild and hatchery-origin fish throughout the critical growth period in summer. A number of studies have documented declines in native salmonid abundance when hatchery-origin fish are stocked into systems with wild populations (Nickelson 2003; Weber and Fausch 2005).

Food web models have become important tools for exploring the effects of management actions aimed at conservation of species that are known to experience important bottom-up, top-down, and competitive relationships (Christensen et al. 1996). In application to streams, food web models have been used to evaluate functional redundancy, bottom-up versus top-down controls, and the impacts of invasive species (McIntyre et al. 2007; Saito et al. 2007). For lake and ocean ecosystems, Ecopath with Ecosim (EwE) software (Christensen and Walters 2004) is a well-established semiquantitative ecosystem/food web modeling program based on a mass-balance framework for energy flow through the system. The EwE program is a particularly valuable tool for evaluating how changes in the abundances of

species or groups of species directly and indirectly affect other groups. For example, EwE models have been used to estimate the extent of bottom-up control in aquatic food webs, effects of top predators on lower trophic levels, communitywide impacts of fishery bycatch, and ecosystem-scale impacts of fishery management practices (reviewed by Christensen and Walters 2011). The EwE program has been applied to streams in only a few cases, but the work by Meyer and Poepperl (2004) clearly demonstrated that balanced and informative Ecopath models can be created for small stream ecosystems and that the common practice of integrating empirical data with parameter borrowing (Christensen and Walters 2004) to fill out models can be applied.

We created an EwE model for a typical tributary of the Snake River, Idaho, in which juvenile Chinook Salmon occur sympatrically with nonnative Brook Trout. We simulated and monitored food web responses to three management actions that were designed to address the three focus areas of concern noted above for juvenile Chinook Salmon:

- (1) Increase basal resources via salmon carcass and carcass analog additions;
- (2) Reduce or remove a nonnative competitor/predator (Brook Trout); and
- (3) Increase competition by stocking hatchery-origin juvenile Chinook Salmon into the stream with the existing population of wild Chinook Salmon.

METHODS

Study Site

The stream from which most of our data are derived, the South Fork of the Salmon River, Idaho, is an important Chinook Salmon spawning and nursery stream that also contains a self-sustaining population of wild Brook Trout in the main stem and associated tributaries (Adams et al. 2002). We created our model by using fish abundance, invertebrate abundance, and diet data from this fourth-order stream in the Snake River basin, with salmon abundances, nonnative trout abundances, and habitat in the middle range of those observed for Chinook Salmon rearing streams in this region (Achord et al. 2007; Sanderson et al. 2009b). Typical Chinook Salmon nursery streams in the region are alluvial, with gradients ranging from about 1% to 5% and with mixed riparian vegetation consisting of grasses, woody shrubs, and conifers. In mid-summer, fish communities are dominated by juvenile Chinook Salmon (Macneale et al. 2010), in particular the evolutionarily significant unit of spring/summer (or “stream-type”) Snake River basin Chinook Salmon. The majority of juvenile salmon rear over the summer and migrate out of the headwaters by mid-October; some overwinter in the system, but their numbers are substantially reduced and the relative dominance of resident fish species increases. Our study focused on food web dynamics during the summer months, when juvenile salmon dominate; this is the period for which we have well-quantified empirical data on fish and invertebrate

abundances as well as fish diets (see Supplement A in the online version of this article). In addition to Chinook Salmon, fishes that were found in our study stream during snorkel surveys included Cutthroat Trout *O. clarkii*, Rainbow Trout/steelhead *O. mykiss*, Brook Trout, sculpins *Cottus* spp., Bull Trout *S. confluentus*, and Mountain Whitefish *Prosopium williamsoni*. The Bull Trout is a threatened species, and as such Bull Trout were not captured or handled during any aspect of this study. Although Bull Trout were identified as present during the snorkel surveys, they were rare—only two individuals were identified. See Supplement A and Macneale et al. (2010) for fish diet and snorkel sampling methods.

Study Design

We first created an Ecopath model for the representative stream system. Ecopath consists of a series of linear equations that describe flows of mass into and out of the biomass pools. For each functional group i ,

$$BA_i = B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i, \quad (1)$$

where BA_i = biomass accumulation of group i ; B_i = biomass of group i ; P/B = the production : biomass ratio (roughly equal to total mortality); EE_i = ecotrophic efficiency, or the proportion of total mortality that is attributable to other model groups (predators and fisheries); the summation term represents losses to all predators j ; B_j = biomass of predator j ; Q/B = the consumption : biomass ratio of j ; DC_{ji} = the proportion of group i in the diet of predator j ; Y_i = fishery yield; and E_i = net emigration (assumed to be equal to 0). A group is at biomass equilibrium when production equals losses and when BA_i is equal to 0.

We used direct empirical data collected in 2004 to determine the B -parameters for fish, invertebrate, and periphyton groups and to determine fish diet composition (Macneale et al. 2010). As is common for Ecopath applications, when direct measurements were unavailable we used parameters from comparable systems to fill out the model (Christensen and Walters 2004). We assumed that P/B and Q/B were similar to literature-reported values from comparable ecosystems (Minshall et al. 1983, 1992; Meyer and Poepperl 2004; see Supplement A). The B -values for all 16 groups of biota as well as for macrophytes and periphyton were derived from summer empirical data; diet data for four fish taxa (Brook Trout, sculpins, Chinook Salmon, and Rainbow Trout/steelhead) were empirically derived. Diet data for the remaining fish were derived from literature values or from empirical data describing similar species in the field (see Supplement A for details). Invertebrate diet data were based on family classification and the functional feeding group designations given by Merritt and Cummins (1996), with diets for each order weighted relative to the abundance of each family in field samples. Periphyton P/B ratios and benthic organic matter con-

centrations were derived from data on comparable streams in the Salmon River basin (Minshall et al. 1983, 1992). Macrophyte P/B was derived from Riis et al. (2009).

Once all of the B , P/B , Q/B , and DC values were entered, we used the mass-balancing algorithm in Ecopath to balance the model; this was done by simultaneously solving the unknown value, EE, in equation (1) for all groups (Christensen and Walters 2004). When all EE values are less than or equal to 1.0, the system is in balance; if one or more EE values are greater than 1.0 (indicating more use of a resource than is available), then the model does not meet thermodynamic requirements, and the parameters must be adjusted (within a given range determined by the data or by convention) in order to balance energy within the system (Christensen and Walters 2004; Essington 2007). In open systems such as streams, where resources are constantly in flux due to moving water, the assumption of balance may not be well supported at all times. In this study, we assumed that nutrient and biomass fluxes into the study area generally equaled fluxes and export out of the study area; this assumption is consistent with other applications of EwE to streams (Meyer and Poepperl 2004). Food web groups and final parameter values are reported in Table 1, and initial diet compositions are provided in Table 2. Details on model balancing, parameter estimation, and diets are provided in Supplement A.

Once the initial Ecopath model was balanced, we ran the Ecosim portion of the model to compare the responses of juvenile Chinook Salmon and other groups in the food web to our three management alternatives. In the Ecosim model, biomasses of all functional groups are dynamic and represented by differential equations such that the trophic linkages between groups will permeate throughout the food web by direct and indirect pathways (Christensen and Walters 2004). The Ecosim equation for each group i is

$$\frac{dB_i}{dt} = g_i \cdot \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i, \quad (2)$$

where g_i = growth efficiency; $\sum_j C_{ji}$ = rate of consumption of all prey j by group i ; $\sum_j C_{ij}$ = rate of consumption of group i by all predators j ; I_i = immigration rate; M_i = mortality not attributable to other model groups; F_i = fishing mortality rate; e_i = emigration rate; and B_i = biomass. In our models, all I_i and e_i are equal to 0. The C terms are density dependent in that consumer diets will vary from their initial values as a function of changing prey densities (Christensen and Walters 2004). Within Ecosim, parameters of individual groups can be perturbed, and such changes will reverberate through the food web via direct and indirect trophic interactions.

For each of the management options explored below, we applied a continuous perturbation to one or more functional groups as outlined below, and then we ran model simulations through for 20 “years” (i.e., annual time steps for 20 model iterations). For example, for a 10% increase in the primary

TABLE 1. Input parameters for the Ecopath model, including the production : biomass ratio (P/B); consumption : biomass ratio (Q/B); ecotrophic efficiency (EE); and production : consumption ratio (P/Q). Fish groups include Brook Trout less than 150 mm (BKT < 150); Brook Trout greater than 150 mm (BKT > 150); Bull Trout less than 150 mm (BLT < 150); Bull Trout greater than 150 mm (BLT > 150); juvenile Chinook Salmon less than 150 mm (CH < 150); Rainbow Trout/steelhead less than 150 mm (RBT < 150); Rainbow Trout/steelhead greater than 150 mm (RBT > 150); Cutthroat Trout (CT; all sizes); sculpins (SCLPN; all sizes); and whitefishes *Prosopium* spp. (WHTFH; all sizes).

Group name	Trophic level	Biomass (g/m ²)	P/B	Q/B	EE	P/Q	Detritus import (g·m ⁻² ·year ⁻¹)
Periphyton	1.00	1.287	83.91		0.09		
Macrophytes	1.00	0.893	7.39		0.24		
Microbes	2.00	8.944	15.48	64.49	0.04	0.24	
Ephemeroptera	2.13	0.272	3.72	46.47	0.86	0.08	
Plecoptera	3.03	0.089	2.99	16.64	0.46	0.18	
Trichoptera	2.13	0.130	2.28	19.00	0.95	0.12	
Chironomidae	2.27	0.100	12.50	96.15	0.98	0.13	
Coleoptera	2.28	0.148	3.50	17.50	0.44	0.20	
Noninsect aquatics	2.69	0.166	3.40	21.26	0.93	0.16	
Other Diptera	2.11	0.221	8.83	73.56	0.71	0.12	
BKT < 150	3.28	0.009	0.86	3.45	0.75	0.25	
BKT > 150	3.96	0.008	0.37	1.84	0.00	0.20	
BLT < 150	3.26	0.002	0.86	3.45	0.00	0.25	
BLT > 150	3.90	0.014	0.37	1.84	0.00	0.20	
CH < 150	3.23	0.109	1.45	5.82	0.05	0.25	
RBT < 150	3.20	0.038	1.26	5.05	0.01	0.25	
RBT > 150	3.20	0.021	0.55	2.75	0.48	0.20	
CT	3.14	0.032	1.26	5.05	0.00	0.25	
SCLPN	3.35	0.010	1.44	5.74	0.80	0.25	
WHTFH	3.33	0.032	0.41	4.14	0.00	0.10	
Detritus	1.00	82.760			0.99		375

production rate, we increased the primary production rate by 10% above the initial Ecopath model level and maintained production at 10% above initial throughout the next 20 iterations of the model. In response to press perturbations, functional groups increased or decreased in biomass, depending on the magnitude of the perturbation and the strength of the direct and indirect food web pathways that linked them to the perturbed group(s). For example, groups (e.g., Ephemeroptera and Coleoptera) that feed to the greatest degree on periphyton should respond strongly to increased periphyton at first; however, as the biomass of these groups increases, their predators should respond positively, thereby tempering their final relative biomass response. The strength of the EwE model is that it accounts not only for these individual predator–prey dynamics but also for how potential increases in predator biomass due to greater food resources in one group (e.g., Ephemeroptera) may influence predation pressure in another group that would not have necessarily benefited to the same degree from increasing periphyton (e.g., non-insect aquatic taxa). Eventually, the model reaches a new equilibrium, reflecting a new balance in the system among all model groups. The model generally reached this new steady state after about 15 annual iterations in our analysis.

Management Scenarios

Increase basal resources (periphyton and detritus).—We used the forcing function option in Ecosim to evaluate five levels of increased periphyton P/B : 2, 5, 10, 25, 50, and 100% increases. The small increases reflect a range of potential changes in production associated with greater nutrient availability after the addition of adult salmon carcasses or carcass analogs. The larger increases were applied to evaluate a broader range of food web responses, but these higher values are clearly possible; Sanderson et al. (2009b) documented order-of-magnitude increases in periphyton standing stocks on nutrient-diffusing substrate with added nitrogen and phosphorus in salmon rearing streams within the Salmon River basin, Idaho.

Salmon carcasses not only provide nutrients that can promote primary production but also detritus that is consumed directly. A simple increase in detrital availability would not necessarily reflect the highly labile nature of this food source, so rather than increase the baseline detrital B , we instead increased the vulnerability (*sensu* Christensen and Walters 2004) of detritus to its consumers by 2, 5, 10, 25, 50, and 100%. This is not a direct proxy for carcass inputs, but it is functionally similar, as it represents greater access to the detritus pool. Many invertebrate species have been shown to feed on salmon

TABLE 2. Diets used in the Ecopath model. Values represent the proportion of the predator's diet that consists of the prey item listed in the first column. Fish groups are defined in Table 1.

Prey/diet item	Predator				
	Microbes	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae
Periphyton	0	0.308	0.02	0.188	0.122
Macrophytes	0	0.011	0.01	0.075	0.039
Microbes	0	0.113	0.09	0.119	0.126
Ephemeroptera	0	0.003	0.27	0.003	0.015
Plecoptera	0	0	0.06	0.001	0.001
Trichoptera	0	0	0.05	0.001	0
Chironomidae	0	0.006	0.22	0.004	0.01
Coleoptera	0	0	0.03	0	0.01
Noninsect aquatics	0	0	0.05	0.001	0.017
Other Diptera	0	0.006	0.05	0.002	0.06
BKT < 150	0	0	0	0	0
BKT > 150	0	0	0	0	0
BLT < 150	0	0	0	0	0
BLT > 150	0	0	0	0	0
CH < 150	0	0	0	0	0
RBT < 150	0	0	0	0	0
RBT > 150	0	0	0	0	0
CT	0	0	0	0	0
SCLPN	0	0	0	0	0
WHTFH	0	0	0	0	0
Detritus	1	0.553	0.15	0.606	0.6
Import	0	0	0	0	0

carcasses, so we ensured that all invertebrate groups had detritus as a component of their diets (Table 2). Microbes consumed 100% detritus; Trichoptera, Chironomidae, and other Diptera were the macroinvertebrate groups that were most heavily reliant on detritus. None of the fish groups consumed detritus directly.

Reduce or remove a nonnative competitor/predator.—The relative influence of Brook Trout was evaluated by altering Brook Trout B . We reduced Brook Trout B (in both size-classes) by applying four different levels of fishing mortality (F ; equation 2): 5, 25, 50, and 100%. These mortality rates represent the degree of instantaneous mortality at the start of each model iteration. As with the increases in basal resources, the larger F -values were included to evaluate potential end-member responses. We calculated the final biomass responses of juvenile Chinook Salmon and other food web groups relative to their initial status and then compared relative responses within and among scenarios.

Increase competition by stocking hatchery-origin juvenile Chinook Salmon.—To assess the impacts of stocking juvenile hatchery-origin Chinook Salmon into this system, we included an additional group (hereafter, “stocked CH0”) in the model. For this analysis, we created a separate model that encompassed all of the original groups and original values from the original bal-

anced model (including EE values) along with the stocked CH0 group. Simulated CH0 stocking densities ranged from 0.02 to 2.0 g dry weight (DW)/m². The summer B of wild juvenile Chinook Salmon in the focal stream from which all biomass data were collected was 0.11 g DW/m². The density of hatchery-origin juvenile Chinook Salmon is rarely quantified per unit area since the fish disperse after release, but the range of stocking values assessed in our analysis encompassed the range of densities occurring after poststocking dispersal, as observed in Snake River tributaries by Peery and Bjornn (2000). Although hatchery-origin fish do not necessarily grow at exactly the same rate or feed on exactly the same diet items as wild fish, for the purposes of this analysis, we assumed that EwE parameters for CH0 were the same as those for wild fish. With inputs that included EE values, the initial Ecopath model accounted for imbalance through biomass accumulation or loss (i.e., the BA term in equation 1). We then ran Ecosim for 20 iterations and evaluated the final responses of juvenile Chinook Salmon and other food web groups to densities of stocked CH0.

Analysis

We focus our present analysis on a comparison of the final relative change in B within and among model scenarios for each taxonomic group at the end of the model runs. We focus only on

TABLE 2. Extended.

Prey/diet item	Predator					
	Coleoptera	Noninsect aquatics	Other Diptera	BKT < 150	BKT > 150	BLT < 150
Periphyton	0.35	0.02	0.199	0	0	0
Macrophytes	0.02	0	0.05	0	0	0
Microbes	0.213	0.199	0.10	0	0	0
Ephemeroptera	0	0.034	0.001	0.09	0.05	0.10
Plecoptera	0	0	0	0.02	0.05	0.05
Trichoptera	0	0	0	0.58	0.15	0.58
Chironomidae	0.05	0.12	0.003	0.06	0.01	0.06
Coleoptera	0	0	0	0.02	0.01	0.02
Noninsect aquatics	0	0.067	0.001	0.03	0.04	0.03
Other Diptera	0	0.168	0.001	0.04	0.01	0.04
BKT < 150	0	0	0	0.01	0.123	0.01
BKT > 150	0	0	0	0	0	0
BLT < 150	0	0	0	0	0	0
BLT > 150	0	0	0	0	0	0
CH < 150	0	0	0	0.01	0.123	0.01
RBT < 150	0	0	0	0	0	0
RBT > 150	0	0	0	0.01	0.104	0.01
CT	0	0	0	0	0	0
SCLPN	0	0	0	0.05	0.25	0.01
WHTFH	0	0	0	0	0	0
Detritus	0.367	0.392	0.645	0	0	0
Import	0	0	0	0.08	0.08	0.08

the relative change to allow for greater internal consistency in comparing the influence of the three management options on the same original Ecopath model. We used a linear regression model to assess the final relative change in B as a function of trophic position for each group under each of the four basic scenarios (increased periphyton, increased detritus, Brook Trout removal, and CH0 stocking at a density equal to the wild population). For these regressions, we used an α value of 0.05 as the criterion for significance.

RESULTS

Increase Basal Resources (Periphyton and Detritus)

Increased primary production and greater access to labile detritus led to increases in relative B for most groups by the end of the model run. Increases in primary production led to the largest increases in relative B of juvenile Chinook Salmon among the individual manipulation scenarios (Figure 1). A 5% increase in periphyton production led to a 6% increase in juvenile Chinook Salmon B in our modeled food web. With a 10% increase in periphyton production, juvenile Chinook Salmon B increased by 12%; with more substantial increases in primary productivity (25% and 50%), juvenile Chinook Salmon B increased linearly by 29% and 60%, respectively (Figure 2).

There were also notable increases in B for nearly all other groups, especially the fish groups (Table SB.1 in Supplement B online).

Increases in detrital vulnerability led to notable increases in juvenile Chinook Salmon B ; however, the responses were not as strong for increased detrital vulnerability as they were for increased periphyton production (Figure 2; Table SB.1). When periphyton production and detrital vulnerability were both increased, final relative changes in B for the food web groups were, as expected, larger than those observed for either scenario alone. For example, a scenario involving a 25% increase in periphyton production and a 5% increase in detrital vulnerability yielded slightly more than a 31% increase in relative B of juvenile Chinook Salmon (Table SB.1).

The relative change in final B caused by increasing basal resources was greater for higher trophic levels. The responses in final relative B to increased periphyton production across groups were significantly related to trophic position ($P = 0.004$, $r^2 = 0.35$; Figure 3A); relative B responses to increased detrital availability were also significantly related to trophic position ($P < 0.001$, $r^2 = 0.75$; Figure 3B). As expected, invertebrate groups with larger periphyton components in their diets, such as Ephemeroptera and Coleoptera, experienced substantial increases in relative B early in the model progression; however, as predator B subsequently increased, the relative B of these grazer

TABLE 2. Extended.

Prey/diet item	Predator						
	BLT > 150	CH < 150	RBT < 150	RBT > 150	CT	SCLPN	WHTFH
Periphyton	0	0	0	0	0	0	0
Macrophytes	0	0	0	0	0	0	0
Microbes	0	0	0	0	0	0	0
Ephemeroptera	0.08	0.076	0.121	0.121	0.182	0.181	0.15
Plecoptera	0.10	0.005	0	0	0	0.09	0.07
Trichoptera	0.161	0.033	0.228	0.228	0.379	0.30	0.15
Chironomidae	0.01	0.083	0.093	0.093	0.003	0.25	0.15
Coleoptera	0.01	0.023	0.178	0.178	0.024	0.037	0.15
Noninsect aquatics	0.04	0.007	0.016	0.016	0.008	0.03	0.14
Other Diptera	0	0.009	0.027	0.027	0.051	0.04	0.13
BKT < 150	0.123	0	0	0	0	0.008	0
BKT > 150	0	0	0	0	0	0	0
BLT < 150	0	0	0	0	0	0	0
BLT > 150	0	0	0	0	0	0	0
CH < 150	0.123	0	0	0	0	0.008	0.01
RBT < 150	0	0	0	0	0	0.008	0
RBT > 150	0.123	0	0	0	0	0.008	0
CT	0	0	0	0	0	0	0
SCLPN	0.15	0	0	0	0	0.04	0
WHTFH	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0
Import	0.08	0.764	0.337	0.337	0.353	0	0.05

taxa and other invertebrate prey groups declined, although the responses still generally remained positive (Figure 3A).

Reduce or Remove a Nonnative Competitor/Predator

Despite some dietary overlap and a predator-prey interaction between Brook Trout and juvenile Chinook Salmon, Brook Trout removal had a limited influence on juvenile Chinook Salmon in our model (Figure 1). The *B* of juvenile Chinook Salmon increased by only 3.4% after the complete removal of Brook Trout. A comparable increase in *B* could be achieved with only about a 3% increase in periphyton production (Figure 2). The majority of the food web groups were minimally affected by 100% Brook Trout removal, and responses were not well associated with trophic position or broad taxonomic groupings (Figures 1, 3).

Although the influence of Brook Trout removal was limited for most invertebrate groups and for juvenile Chinook Salmon in summer, Brook Trout removal did influence sculpins and, to a lesser degree, other trout species. Complete Brook Trout removal led to a 51% increase in the *B* of sculpins, a 22% increase in the *B* of Rainbow Trout/steelhead larger than 150 mm, and a 16% increase in the *B* of Bull Trout larger than 150 mm. In contrast to the limited amount of primary production that was needed to attain a juvenile Chinook Salmon response equivalent to that from Brook Trout removal, the model comparison suggested that an appreciable increase in periphyton produc-

tion (65%) was required to generate an increase in sculpin *B* comparable to the response obtained via Brook Trout removal (Figure 2). Unlike responses to increased basal resources, the responses of sculpins to decreases in Brook Trout *B* were non-linear. Slight reductions in Brook Trout *B* led to relatively substantial increases in sculpin *B* (Figure 2C).

Increase Competition by Stocking Hatchery-Origin Juvenile Chinook Salmon

The addition of hatchery-origin juvenile Chinook Salmon in this model yielded declines in wild juvenile Chinook Salmon abundance. When CH0 stocking density was equal to resident wild population abundance during summer (~0.11 g DW/m²), the relative *B* of wild Chinook Salmon declined by about 7% (Figure 2D). However, densities of stocked fish are generally much higher than this, especially immediately after the stocking event (Peery and Bjornn 2000). At higher stocking densities, the impacts of CH0 on wild Chinook Salmon and on other native fishes were more severe. For example, at a CH0 stocking density of 0.5 g DW/m² (nearly five times the density of wild juvenile Chinook Salmon in this study), juvenile Chinook Salmon *B* declined by 34% and Cutthroat Trout *B* declined by 40% (Figure 2D). The degree of impacts from stocked CH0 was also significantly related to trophic position, with higher trophic levels generally declining the most ($P < 0.001$, $r^2 = 0.60$; Figure 3D).

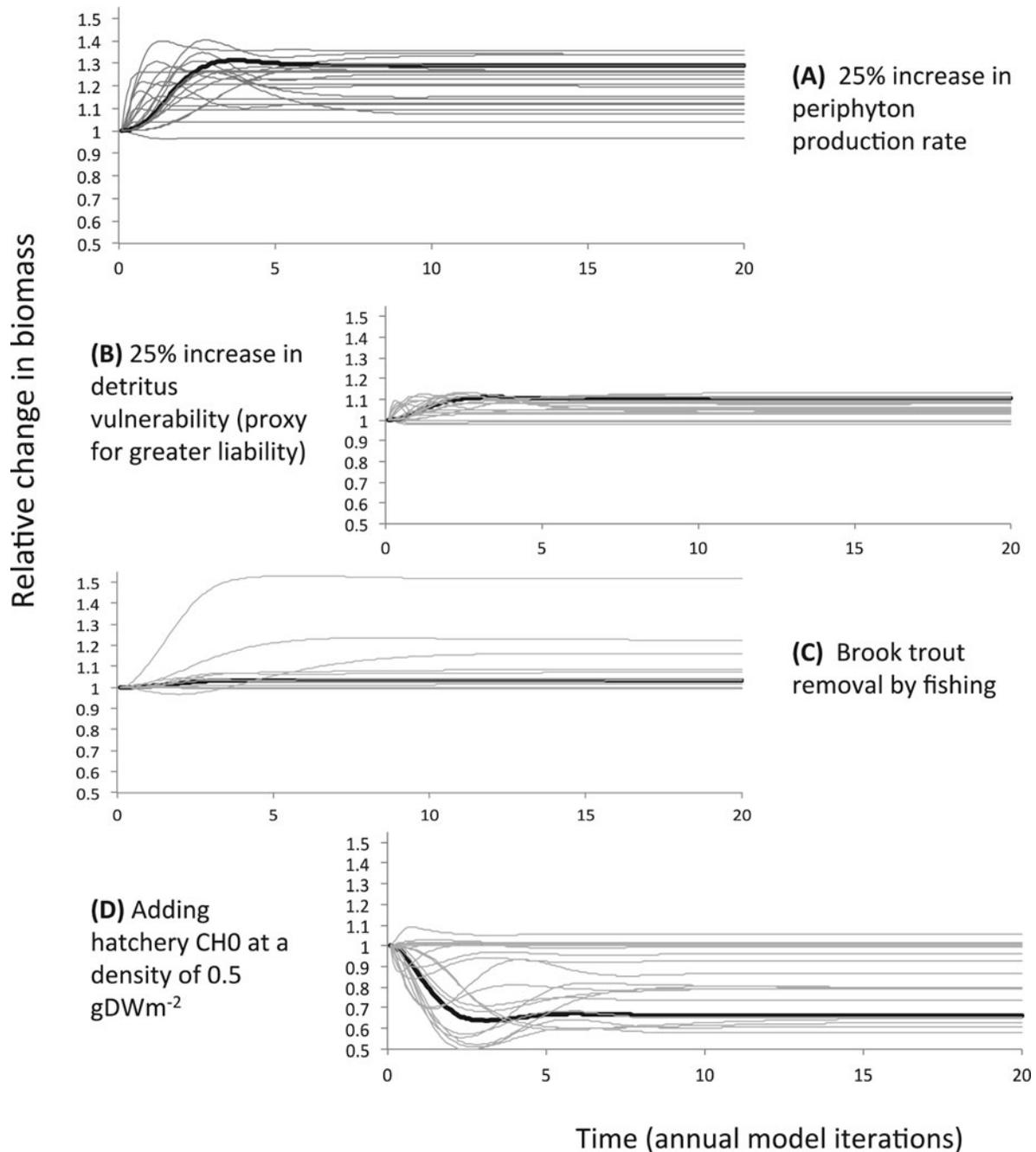


FIGURE 1. Model output of the food web responses to four scenarios, with the juvenile Chinook Salmon response highlighted in bold: **(A)** 25% increase in periphyton primary production; **(B)** 25% increase in detrital vulnerability, reflecting anticipated increases in labile carbon in detritus with the addition of salmon carcasses; **(C)** 100% removal of Brook Trout from the study reach; and **(D)** stocking of hatchery-origin juvenile Chinook Salmon (CHO) at a density of $0.5 \text{ g dry weight (DW)/m}^2$.

DISCUSSION

Our model indicates that basal resource availability has a much stronger influence on juvenile Chinook Salmon production potential than Brook Trout presence or CHO stocking in typical nursery streams in the Salmon River basin. This supports the contention that even minor declines in primary pro-

duction and detritus associated with decreasing salmon populations and postspawn carcass inputs could influence summer production of juvenile Chinook Salmon in this region (Naiman et al. 2002; Stockner 2003). Brook Trout removal had a substantial influence on native sculpins in the model, but otherwise the overall food web impacts appeared to be limited relative to the

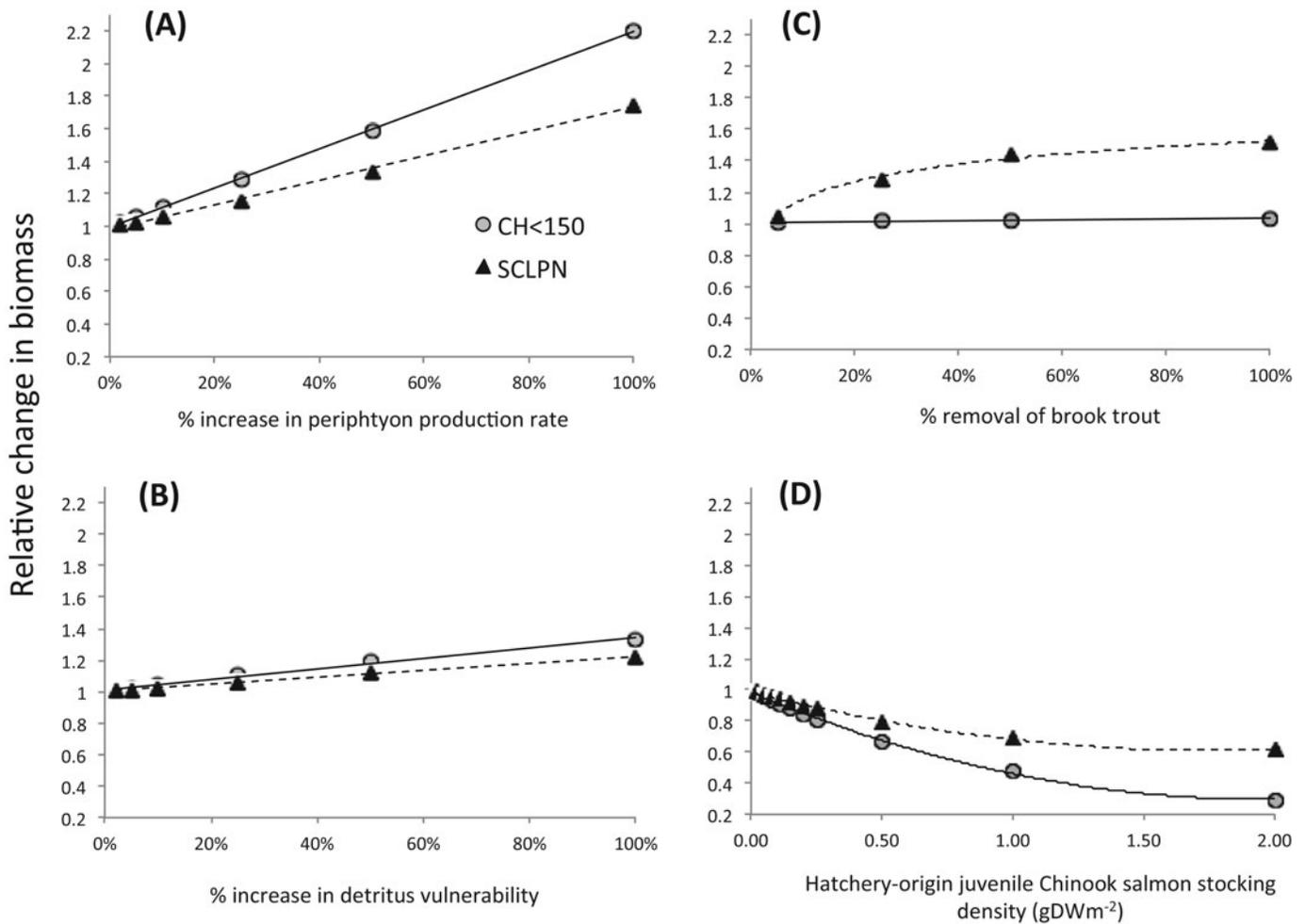


FIGURE 2. Final model results (after 20 iterations) for the relative change in biomass of juvenile Chinook Salmon in response to varying degrees of (A) increase in periphyton production rates, (B) increase in detrital vulnerability, (C) decrease in Brook Trout abundance (i.e., increase in Brook Trout removal), and (D) hatchery-origin juvenile Chinook Salmon stocking (g dry weight [DW]/m²). Circles represent the final responses of wild juvenile Chinook Salmon smaller than 150 mm (CH<150); triangles represent the final responses of sculpins (SCLPN). A relative change of 1.0 indicates no response to the change in predator abundance or resource availability. A relative change of 1.5 indicates a 50% increase in biomass at the end of the model run relative to the initial biomass.

impacts exerted by changes in basal resource availability and juvenile Chinook Salmon densities in summer. Stocking of CH0 diminished the capacity of the system to support wild juvenile Chinook Salmon, particularly at higher densities.

Responses to Increased Basal Resources

Results from our model suggest strong bottom-up controls on secondary production in this stream. In particular, increased periphyton production yielded much larger increases in secondary production than did increases in detritus availability for consumers. Although streams are a well-established example of allochthonously subsidized ecosystems (Fisher and Likens 1972; Wallace et al. 1997), studies from forested streams have demonstrated that processes which increase primary production, such as increased light due to forest management, lead to substantial increases in secondary production above and beyond levels

associated with pretreatment conditions, when allochthonous material input dominated the base of the food web (Kiffney et al. 2003). The relatively limited response to increased detritus vulnerability is likely due in part to limitations in the model and our inability to account for carbon lability. We increased detritus vulnerability to detrital consumers, but it is unclear how much an increase in carcasses affects the entire detrital pool. We addressed this in the current study by presenting a range of potential changes. The specific magnitude of the response remains uncertain and clearly warrants further research.

The magnitude of salmon carcass inputs or other anthropogenic nutrient inputs (intended or unintended) that is required to yield a measurable increase in primary productivity will depend upon the underlying conditions of the system and how nutrients (and carcasses, specifically) are added (Janetski et al. 2009). Overall, though, our results suggest that efforts to

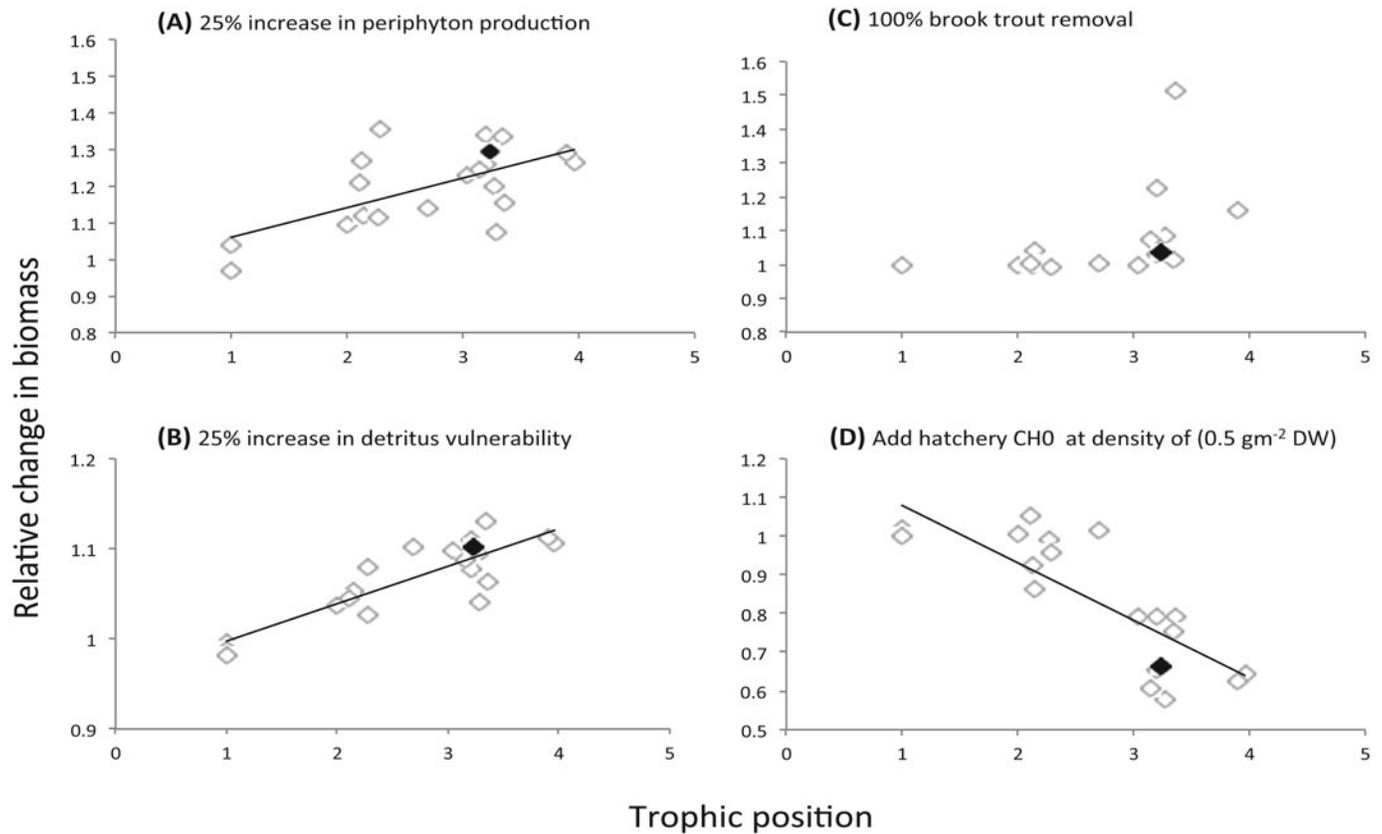


FIGURE 3. Final relative change in biomass from the model output (after 20 annual iterations) relative to trophic position for each food web group under four scenarios: (A) a 25% increase in periphyton production, (B) a 25% increase in detrital vulnerability, (C) 100% removal of Brook Trout, and (D) stocking of hatchery juvenile Chinook Salmon (CH0) at a density of 0.5 g dry weight (DW)/m². The best-fit lines indicate significant relationships for the periphyton ($P = 0.004$), detritus ($P < 0.001$), and stocked CH0 ($P < 0.001$) scenarios. The black-shaded symbol represents the change in biomass of juvenile Chinook Salmon.

mitigate cultural oligotrophication are warranted, assuming that salmon carcass or carcass analog additions are large enough to actually promote periphyton production. If greater carcass abundances occur naturally through increased spawner densities, the periphyton response may depend upon substrate mobility. Some studies have found clear positive associations between spawning salmon and stream periphyton (e.g., Johnston et al. 2004; Chaloner et al. 2007), whereas other studies have found that spawning activities that disrupt substrates across a large area can lead to decreases in periphyton standing stocks (Verspoor et al. 2010) or have indicated that food itself is not likely to be limiting salmon abundance (Bellmore et al. 2012). The presence of actively spawning salmon also substantially increases direct carbon subsidies above and beyond carcass additions alone through dislodged eggs, a factor that is not accounted for in our model. The addition of salmon carcasses or carcass analogs alone—without associated substrate modification from spawning—often yields increases in primary production and secondary production (Wipfli et al. 2004), but a positive response is not guaranteed (Ambrose et al. 2004; Harvey and Wilzbach 2010). Ultimately, increasing periphyton production

can be effective, but background conditions of the system will influence the effectiveness of these additions (Ambrose et al. 2004; Bellmore et al. 2012); furthermore, it should be noted that other factors (e.g., disease introduction) warrant consideration before additions are unilaterally applied (Compton et al. 2006).

The Impacts of Brook Trout Invasion

Our analysis suggested that the impacts of Brook Trout invasion in these systems are confined to relatively few species. This was surprising given that the impacts of nonnative species in other systems have been shown to be widespread, with direct effects on competitors and prey species and indirect effects that radiate through the food web (Pringle et al. 2007). In aquatic environments, fish invasions have been particularly striking in their direct and cascading influences on the invaded ecosystems (Vander Zanden et al. 1999; Baxter et al. 2004). The invasion of a novel predator into aquatic ecosystems has been shown to dramatically impact native prey species and can produce shifts in the diet and behavior of native predators (Vander Zanden et al. 1999; Lepak et al. 2006). Invasion by a nonnative trout species

can affect not only native salmonids but also native invertebrate communities, with implications for terrestrial biota that feed on insects emerging from the stream (Baxter et al. 2004). We observed a clear impact of Brook Trout on a few native fish species in our analysis, but the overall food web impacts within the stream appeared to be relatively limited.

The limited responses to Brook Trout removal were somewhat unexpected, but competitive interaction, degrees of predation, and diet overlap among salmonids can also vary regionally and with the size and complexity of the fish and invertebrate communities (Sanderson et al. 2009a). For example, Dunham et al. (2000) found substantial diet overlap between Brook Trout and Lahontan Cutthroat Trout *O. clarkii henshawi* in southeastern Oregon and northern Nevada, but similar studies in other regions found limited diet overlap and instead attributed Brook Trout invasion success to differential recruitment (McGrath and Lewis 2007). In most cases, predation is not thought to be the dominant factor leading to Brook Trout displacement of native salmonids (Dunham et al. 2002); however, it has been noted as a probable impact in some cases (McHugh et al. 2008). We did include juvenile Chinook Salmon in the diet of Brook Trout for our model, but (in mid-summer at least) the *B* of predatory Brook Trout and the levels of predation were insufficient to severely impact juvenile Chinook Salmon *B*. We acknowledge that a focus on summer processes could underestimate Brook Trout predation on young-of-the-year salmon in spring. Given the lack of a strong whole-food-web effect of Brook Trout removal during summer in the current model analysis as well as the limited diet overlap documented by Macneale et al. (2010), we hypothesize that for the summer period, Brook Trout impacts on native salmonids are likely to be a result of larger Brook Trout excluding other fish from preferred habitats rather than a result of direct predation or competition for food resources. This would be consistent with work by McGrath and Lewis (2007) in the interior western USA; those authors found that competition for space at bottlenecks in life history strategies between Brook Trout and native Greenback Cutthroat Trout *O. clarkii stomias* had the greatest impact on the native species. The stream evaluated here is somewhat larger than those assessed by McGrath and Lewis (2007), but habitat availability and competition for habitat are clearly key considerations. Competition for space is difficult to simulate in Ecosim; one way of doing so is the use of “mediation functions” (Espinosa-Romero et al. 2011), wherein the ability of a group (e.g., juvenile Chinook Salmon) to forage on prey (e.g., invertebrates in preferred stream habitat) is made to be functionally dependent upon the abundance of a mediating group (in this case, Brook Trout). The challenge in using mediation functions is identifying reasonable functional shapes (e.g., linear, hyperbolic, or sigmoid) and response magnitudes, which must be determined through careful experimentation. We did not apply such functions here because they would have been largely speculative in the absence of experimental data.

Hatchery/Stocking Influence

As expected, the stocking of CH0 at high densities significantly impacted all fish groups and most invertebrate groups in the system. For the period shortly after stocking, when densities are particularly high, impacts on the local food web are likely to be especially strong. As the CH0 disperse, their densities do decline, but the densities remain elevated for the duration of the summer, at least within 5 km of the stocking areas (Peery and Bjornn 2000). Our model results suggest that the presence of stocked CH0 even at low densities has the potential to influence wild Chinook Salmon populations. To avoid this competition, CH0 are often held until the smolt life stage so that they emigrate early, thereby reducing their influence on local wild populations.

When fish are stocked into a stream, their realized densities can be difficult to calculate; we therefore evaluated a range of potential CH0 densities in our analysis. This range of densities encompassed those estimated in an experiment quantifying the densities of stocked hatchery-origin juvenile (parr) Chinook Salmon in four Snake River tributaries over the course of a summer (Peery and Bjornn 2000). In that study, fish were stocked at a single period in time but under two different regimes: single-point stocking versus stocking at multiple points along 5–6-km reaches. At 12 weeks poststocking, estimated parr biomass densities in the study reaches proximate to the initial stocking sites declined from early maxima of as much as 1.14 g DW/m² but remained between 2.0 and 4.5 times the 0.11-g DW/m² biomass density of wild Chinook Salmon in our study stream (0.22 g DW/m² for the dispersed stocking and 0.48 g DW/m² for the single-point stocking). Actual fish additions ranged from 12,000 juvenile Chinook Salmon parr in a 7-m-wide stream to 80,000 parr in a 12-m-wide stream; the biomass density (g DW/m²) estimates are based on a mean parr mass of 5 g and DW equal to 20% of wet weight (Trudel et al. 2005). The range of stocking values assessed in our analysis covered the likely range of potential realized densities of stocked CH0, depending upon how far the area of interest is from a specific stocking location.

Management for salmon systems like the Salmon River and the Snake River rarely includes a single action. Although stocking is widespread in many Snake River basin streams, salmon carcass or carcass analog additions are also widespread, and these management options can occur concurrently. The importance of the interactions among management options is highlighted in Pearsons' (2008) paper, stressing the need to consider multiple interacting factors in salmon management—specifically the stocking of hatchery fish into systems that support wild populations. While the scenario comparisons described here suggest that salmon carcass additions have the potential to mitigate the negative impacts of stocking CH0 into a stream with wild juvenile Chinook Salmon in summer, we stress that this sort of speculation based on the results presented here should be considered with great caution. Given the limitations of our data, our results are a reasonable first step in hypothesis generation for future research on such interacting effects, but

greater empirical data on year-round diet and biomass will be needed to more effectively flesh out concurrent management options.

Mixed Trophic Impacts and Model Caveats

We used the mixed trophic impact output (Table SB.2) from the Ecosim analysis to conduct a preliminary exploration of model sensitivity. This output is a matrix of each group's impact on each of the other groups. The mixed trophic impact analysis is similar to an "ordinary sensitivity analysis" (Majkowski 1982; Libralato et al. 2006). Overall, the mixed trophic impact output suggested a fairly balanced food web, with no single group having a disproportionate influence across all other groups. In our model, the strongest positive effect of one group on another was for Bull Trout and Trichoptera. This is somewhat counterintuitive since trichopterans are part of the Bull Trout's diet, but Bull Trout also prey upon and compete with a number of other fish species that also eat trichopterans. Therefore, in this analysis, once all food web interactions were accounted for, Bull Trout provided a net benefit for Trichoptera. The strongest negative relationship between two groups was the impact of juvenile Rainbow Trout/steelhead on sculpins (value = -0.771). For juvenile Chinook Salmon, all values in the mixed trophic impact analysis were between -0.2 and $+0.3$, indicating that no single group had disproportionate leverage on the juvenile Chinook Salmon responses evaluated here.

Because the literature on Brook Trout interactions with native salmonids suggests that predation can vary widely (Dunham et al. 2000, 2002), we also conducted a preliminary exploration of Brook Trout diet effects—specifically, the influence of changes in the amount of Brook Trout predation on juvenile Chinook Salmon in the balanced model and with Brook Trout removal. For larger Brook Trout, switching the diet proportion consisting of sculpins (0.25) with the diet proportion consisting of juvenile Chinook Salmon (0.123) yielded a balanced model, and there did not appear to be a strong response to the dietary shift. In the Ecosim model with Brook Trout removal, sculpins still responded much more strongly than juvenile Chinook Salmon. We then elevated the proportion of juvenile Chinook Salmon in the diets of larger Brook Trout to 0.4 and decreased the other diet components proportionally. When Brook Trout were then removed, juvenile Chinook Salmon responses were more pronounced, but in the end the impacts of Brook Trout removal were still more pronounced for sculpins than for juvenile Chinook Salmon (see Tables SB.3 and SB.4 for model run results on juvenile Chinook Salmon under the initial and modified Brook Trout diets).

An additional caveat in the interpretation of the present results is the seasonal nature of the empirical data used (including *B* estimates and diet data). By focusing only on the summer diet, the model can miss key periods when consumers exhibit highly specialized diets. As noted above, while Ecosim allows for shifts in the proportion of existing prey, predators cannot exploit a novel food resource in the model. For example, sculpins are

important salmon egg predators when adult salmon are spawning, and Brook Trout may also eat salmon eggs (Levin et al. 2002). Omission of these relationships (if they are important) eliminates potential pathways and feedbacks from the model.

Overall, we remained internally consistent in this analysis and focused on a comparison of relative responses to various management options within the same model framework. In thinking beyond the specific scenario comparisons, our results do provide the foundation for hypothesis development and future experimental work on the interaction among biota in the systems. The influence of nonnative Brook Trout on native sculpins was particularly striking in this respect. Sulpins are often overlooked in salmon carcass studies since they are not target species for fish management and since they are difficult to capture and efficiently deplete in multiple-pass electrofishing surveys. Because sculpins are hard to see, are hard to quantify, and carry no recreational value, they have received limited consideration in studies evaluating the impacts of nonnative Brook Trout and the loss of anadromous salmon. We hypothesize that some of the most severe impacts of Brook Trout invasion may be on native sculpin populations rather than on native salmonids.

Limitations in our ability to account for labile carbon from salmon carcasses and eggs likely weighted our results more heavily toward autotrophic pathways in a hypothetical carcass addition scenario. Although changing carbon susceptibility worked in a general sense to address the addition of labile carbon, future development of this model will include greater accountability for potentially labile allochthonous carbon from carcasses and eggs. In regard to autotrophic responses, the characteristics of a specific stream are a key consideration in evaluating autotrophic responses to nutrient supplementation from salmon carcass analogs or direct addition (Janetski et al. 2009). For this reason, we evaluated the food web responses in our model across a wide range of changes in primary production.

Conclusions

The model applied here suggests that juvenile Chinook Salmon production in a low-gradient, mid-order stream of central Idaho is dominated by bottom-up food web processes relative to the influences of a nonnative competitor/predator or stocked conspecifics (Figure SB.1 in Supplement B). Responses to increases in the availability of basal resources in summer were widespread and were significantly related to trophic position. In contrast, Brook Trout trophic effects in the model were confined largely to sculpins, which filled comparable niches in the food web. Our results suggest that conservation efforts focusing only on juvenile Chinook Salmon should direct efforts toward projects that increase labile carbon and promote primary production, especially if those systems receive a high density of stocked CH0 in addition to the wild population. If, however, one takes a whole-ecosystem perspective that incorporates impacts on other fish species (especially native sculpins) and the invertebrate community or if behavioral interactions (e.g., space competition with native salmonids) prove significant, then

Brook Trout removal should be considered in addition to efforts that increase basal resources.

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