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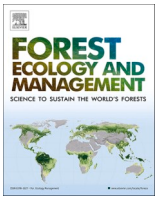

Pathways of productivity and influences on top consumers in forested streams

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ABSTRACT

Forested stream ecosystems involve complex physical and biotic pathways that can influence fish in numerous ways. Consequently, the responses of fish communities to disturbance can be difficult to understand. In this study, we employed a food web model that links biotic (e.g., physiology, predator–prey interactions) and abiotic (e.g., temperature, sunlight) attributes to address fish responses to changes in stream-riparian ecosystems. We modeled responses to food web dynamics in four streams, using scenarios that included responses to riparian disturbance, climate change, and shifts in top consumers. The two consumers we focused on were coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and sculpin (*Cottus* spp., collectively treated as a functional group). We found the responses to environmental changes varied by fish species and among streams, and that responses were not independent due to exploitative interspecific competition. Simulations based on long-term data indicated that coastal cutthroat trout were responsive to changes in allochthonous resources including terrestrial detritus and invertebrates, whereas sculpin were more responsive to changes to autochthonous resources that included, periphyton and aquatic invertebrates. These results may be, in part, a consequence of species-specific foraging behavior. Trout have a higher propensity to drift feed and therefore receive a substantial subsidy from terrestrial invertebrates, whereas sculpin feed mostly on aquatic insects on the streambed. Simulations of changes in summer temperature and stream discharge suggest decreased biomass of both fish species because of physiological constraints on invertebrate prey which reduce fish foraging opportunities. Exploitative competition also may be important in fish responses: when one fish taxon was removed, the other showed increased biomass. Although the pattern of simulation results was consistent across the four streams, the magnitude of change varied among streams. Streams with food webs fueled by multiple energy sources may be more resilient to changes to riparian forests and climate. Through application of a systems model, we gained insights into pathways of productivity for fish in forested stream ecosystems that provide understanding of processes that influence fish and streams, as well as implications for management of both.

1. Introduction

Knowledge of food web dynamics is fundamental to understanding ecosystem dynamics. For example, basal resources and top consumers can affect pathways of energy flow, resulting in shifting patterns of energy transfer and productivity (Polis and Winemiller, 1996). Moreover, the pathways through which energy transfers to top consumers can vary across space and time (Kawatsu et al., 2021). Stream-riparian ecosystems provide an excellent example of the importance of spatial and temporal variability in food web dynamics. In forested stream

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ecosystems, inputs of energy and organic matter include two fundamental pathways: energy derived from terrestrial sources (often referred to as allochthonous production or terrestrial subsidies) and that produced within the aquatic environment (i.e., autochthonous production; Vannote et al., 1980). Interactions between these two pathways can be complex, with terrestrial and aquatic systems sharing multiple reciprocal subsidies (Baxter et al., 2005). Additional complexity emerges as transfers of energy and organic matter occur through aquatic food webs, with dozens of potential interactions (Bellmore et al., 2013; Marcarelli et al., 2020). The challenge of untangling this complexity is arguably one of the central issues in stream ecology today.

Many assessments of stream ecosystems focus on top consumers, such as fish (Reeves et al., 2018), incompletely accounting for the interactions that take place within lower trophic levels of riverine food webs (Richardson and Danehy, 2007; Davis et al., 2013). Typically, empirical studies examine only a limited range of abiotic or biotic conditions (Fausch et al., 2010) and do not address the full range of direct and indirect pathways that can influence top consumers (Baxter et al., 2005). Further, when such detailed work is conducted, it is often limited to a small number of locations and does not evaluate temporal or spatial stability of ecosystem dynamics (Penaluna et al., 2015a; Marcarelli et al., 2020). Studies explicitly linking abiotic (e.g., geomorphic, water chemistry, temperature) to biotic (e.g., community structure, trophic pathways) conditions are critical to understand how ecosystems respond to natural and anthropogenic disturbance and climate variability.

Process-based food web models offer an opportunity to address gaps and limitations characteristic of empirical studies. Additionally, these types of models can contribute to understanding the function of ecosystems, aid in management decisions, and clarify observed mechanisms (Cuddington et al. 2013; Bellmore et al. 2017). A range of process-based modeling approaches have emerged to address ecological complexity in riverine ecosystems (Robson et al., 2017; Osakpolor et al. 2021). Here, we employ a dynamic food web simulation model, the Aquatic Trophic Productivity model (ATP; Bellmore et al., 2017, Whitney et al., 2019), to examine how adjacent riparian forest or climate change disturbances influence various pathways of organic matter in streams, and to contrast the implications of changes in energy sources through food webs. The ATP model simplifies the food webs into main energy channels linking producers to top consumers to describe differential responses along alternative pathways. This approach is much more tractable than complex, full-scale food web descriptions. In addition to following pathways of energy within food webs, the impacts of environmental conditions (e.g., temperature, hydraulics, riparian vegetation) on consumer/resource interactions can be quantified. To understand the function of forested stream ecosystems and pathways of energy to top consumers, we assembled empirical data (Table 1) from a long-term (10-yr) study of forested streams in northwestern Oregon. This study measured responses that included major physical and biological drivers.

Two fish species common in headwater streams in the Pacific Northwest are coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and sculpins (*Cottus*, spp.; Olson and Weaver, 2007; Penaluna et al., 2021a). These fishes can vary in their capacity to use resources and disturbances to resource availability may influence how they respond. Generally, trout are opportunistic and forage both within the water column and from the water surface on terrestrial prey, with occasional benthic foraging (Keeley and Grant, 2001; Romero et al., 2005). In contrast, sculpins are generally smaller in size, have subterminal mouths, are closely associated with benthic environments, and forage primarily on prey living in the stream bed (Falke et al., 2020). Relative to the two major sources of organic matter to stream ecosystems, trout should be expected to be more responsive to changes in terrestrial inputs, whereas sculpins should be more sensitive to changes to in-stream productivity of benthic insects. Further, differences in species' physiological traits could be important (Lefevre et al., 2021) and influence the way these fish might respond to alterations in available resources.

Table 1
Summary of empirical data used, years collected and source to inform the Aquatic Trophic Productivity model. No data were collected in 2012. Unpublished data are available upon request at https://traskstudy.forestry.oregonstate.edu/ for turbidity and substrate or https://lemma.forestry.oregonstate.edu/data for riparian vegetation composition.

Data	Years	Source
Proportion of stream shaded from July-Sept	2008, 2013	Johnson and Ashkenas, 2022a
Photosynthetically active radiation (PAR)	2007–2016	Johnson and Ashkenas, 2022a
Proportion of stream covered by vegetation	2008, 2013	Johnson and Ashkenas, 2022a
Riparian vegetation composition	2008, 2013	Unpublished
Terrestrial invertebrate inputs	2001–2002	Romero et al., 2005
Nutrients (DIN; SRP)	2007–2011, 2013–2016	Johnson and Ashkenas, 2022b
Turbidity	2007–2016	Unpublished
Hydrology	2007–2016	Johnson et al., 2022a
Substrate	2008, 2013	Unpublished
Temperature	2007–2016	Johnson et al., 2022b
Periphyton	2007–2011, 2013–2016	Johnson and Ashkenas, 2022c
Macroinvertebrates	2009–2011, 2013–2016	Li et al., 2022
Fish diets	2008	Raggon, 2010
Fish	2007–2010, 2013–2016	Jensen, 2017

The overall goal in this work was to evaluate how forest conditions influenced aquatic consumers in small streams with contrasting trophic and physiological characteristics. We focused on responses of fish consumers in the systems, coastal cutthroat trout and sculpin (Raggon, 2010; Jensen, 2017). Specifically, our objectives were to (1) parameterize the ATP model to corroborate biomass of food web members observed across four neighboring streams; (2) conduct sensitivity analysis of environmental variables (e.g., dissolved nutrients, water temperature, riparian conditions) to evaluate their relative influences on trout and sculpin in four streams; and (3) evaluate how food web responses among streams vary under different hypothetical scenarios, such as changes to canopy cover, climate, or fish occurrence, that may affect trophic dynamics or physiological traits of food web members. Results of this work have important implications for understanding basic processes influencing fish in small, forested streams.

2. Materials and methods

2.1. Study area

This study is focused on four streams draining the headwaters of the Trask River, located in northwestern Oregon, USA (Fig. 1). The four streams were part of the Trask River Watershed Study: a manipulative field experiment conducted from 2006 through 2016. Headwater basins upstream of the four study reaches were logged and associated activities occurred (e.g., road building and maintenance) in 2011–2012. Harvest activity occurred 1 km or more upstream of three (Pothole Creek, Gus Creek, upper Trask River) of the four study reaches used in our model simulations. The area impacted by harvest upstream of the study reaches ranged from 24% to 44% of the contributing drainage area. The fourth study stream (Rock Creek) was maintained as an un-harvested reference; no logging, road construction or road maintenance occurred above this site during the study period (Reiter et al., 2020). Detailed datasets on the range of responses quantified as part of the Trask Watershed Study (Table 1) offered an ideal opportunity for evaluating spatial and temporal dynamics of food webs using the ATP model. The purpose of our study was not to model the impacts upstream harvest could have on fish and trophic pathways in downstream reaches. Field studies have suggested the effects of the upstream harvest were negligible to biota

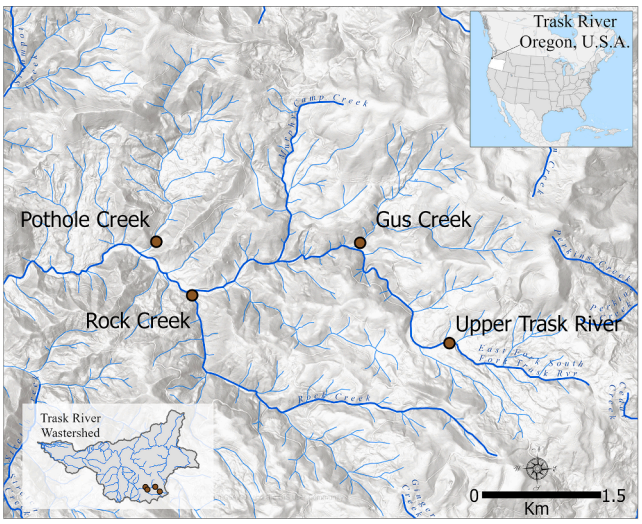

Fig. 1. Trask River watershed with study stream locations.

downstream over such distances (Jensen, 2017; Roon, 2021). Instead, we aimed to use the wealth of data and information collected in these downstream reaches to better understand how ecological interactions in forested streams influence fish communities (Table 1).

The study reaches were at or near the upstream extent of fish distribution within each stream. The fish assemblage consisted of reticulate sculpin (*C. perplexus*), riffle sculpin (*C. gulosus*), torrent sculpin (*C. rhotheus*), coastal cutthroat trout, juvenile coho salmon (*O. kisutch*) and steelhead (*O. mykiss*). Sculpins were considered as a functional guild, due to the difficulty of identifying species, and their similar benthic foraging behavior among conspecifics (Falke et al., 2020). Only sculpins and coastal cutthroat trout (hereafter referred to as trout) were present at all sites, and collectively out-numbered other fishes. Fish in the four streams were sampled in summer (mid-July to late September) by electrofishing in sites enclosed by weirs with one-way traps used to quantify immigration and emigration of all fishes (Jensen, 2017). Tagging of individuals using PIT tags and generic marking of fish with fin clips was used to estimate abundance and growth of individually tagged fish (Raggon, 2010, Jensen, 2017).

2.2. Model description

To explore the trophic dynamics influencing fish populations in our study streams, we used a modified version of the Aquatic Trophic Productivity (ATP) model (Bellmore et al., 2017; Whitney et al., 2019; see https://exchange.iseesystems.com/public/ryan-bellmore/atp/ to explore an online version). Different versions of this model have been used to explore the potential response of fish species to various restoration actions, including riparian management, nutrient supplementation, and stream channel modification (Bellmore et al., 2017; Benjamin et al., 2020; Whitney et al., 2020). Briefly, the ATP model simulates the capacity of stream ecosystems to sustain fishes via the transfer of organic matter among different components of a simplified food web. This model mechanistically links the dynamics of the food web, and the resultant performance of each web member, to the physical and hydraulic conditions of the stream and the structure and composition of the adjacent riparian area.

For each of the four study streams, we generalized the trophic structure of stream food webs using seven trophic biomass stocks: periphyton, terrestrial detritus, detritivorous and algivorous aquatic invertebrates, terrestrial invertebrates, coastal cutthroat trout, and sculpin (Fig. S1). For terrestrial detritus, we considered both deciduous and coniferous vegetation. In the model, periphyton and terrestrial detritus are preferentially selected by aquatic invertebrates that are algivores or detritivores, respectively; however, both basal resources can be consumed by either primary consumer (e.g., Mihuc and Minshall, 1995). In turn, the aquatic and terrestrial invertebrates are consumed by both fish taxa; however, trout are more likely to select terrestrial invertebrates relative to sculpin based on previous diet analysis (Raggon, 2010; Fig. S5). Within the ATP model, prey selection is a function of the quality (assimilation value; Table S2) and quantity (biomass) of a prey item (see Bellmore et al., 2017; Whitney et al., 2019 for details). Because fish were <1% of the diet biomass of trout or sculpin (Raggon, 2010), we did not consider piscivory in the model.

Biomass for each stock or food web member was calculated on a daily time step using mass balance equations (Table S1; see Bellmore et al., 2017; Whitney et al., 2019 for further details). The daily dynamics of each biomass stock are created from gains (e.g., consumption, upstream/lateral inputs, and production) and losses (e.g., respiration/decay, downstream export, predation, and background mortality). The structure and equations for periphyton, terrestrial detritus, terrestrial invertebrates, algivorous aquatic invertebrates, and trout stocks are similar to Whitney et al. (2019; see Table S3 for parameter values). For the Trask River watershed, we made two important structural changes to the ATP model: (1) we split the single aquatic invertebrate stock into a detritivore and algivore stock, although omnivory is possible and (2) we created an additional fish stock to model the dynamics of sculpin. Model structure and equations for these updated stocks are similar to those for aquatic invertebrates and fish in Whitney et al. (2019; see Table S3 for parameter values).

The dynamics of the food web members and their interactions are controlled by the environmental conditions of the stream, which were unique at each of our four streams (Table S4; Figs. S2, S3). These environmental conditions include discharge, channel morphology, water temperature, water clarity, dissolved nutrient concentrations, light availability, and riparian vegetation structure. Discharge and channel morphology (wetted width, depth, and gradient) affects channel hydraulics, such as water velocity and shear stress acting on the streambed, which, along with sediment size, influence the mobilization, transport, and retention of terrestrial and aquatic invertebrates and organic matter. The wetted area available influences the in-stream biological production. Water temperature influences the bioenergetics of fishes and aquatic invertebrates (consumption and respiration rates) as well as decay rates of periphyton and terrestrial detritus. Water clarity (e.g., turbidity and water depth) influences the amount of light, and along with dissolved nitrogen and phosphorus concentrations, may limit periphyton at the base of the food web.

In the model, we included additional effects of the physical environment on fish capacity (Fig. S3). The amount of habitat suitable for trout (Hickman and Raleigh, 1982) and sculpin (Mundahl et al., 2012) can be influenced by a suite of environmental attributes, including water velocity and depth. We chose velocity and depth to represent suitable habitat for fish because they were consistent parameters for both fish and because these two variables can be calculated using the daily discharge of the modeled stream. To estimate a daily proportion of suitable habitat available to trout and sculpin, we calculated the area with suitable velocity and depth separately based on daily discharge, and then averaged the proportions (Fig. S3).

The density and composition of riparian vegetation determined leaf litter and terrestrial invertebrate inputs to streams (Nakano and Murakami 2001; Kaylor and Warren, 2017). In the ATP model, riparian vegetation had two stocks: coniferous and deciduous. The two stocks allowed for differences in structure and composition among the streams in our study (Table S4), as well as differences in the flux of organic matter from the two vegetation types (Whitney et al., 2019; Fig. S4). The daily flux of terrestrial inputs was a product of the input (Fig. S4), proportion of vegetation covering the stream, and vegetation type (Table S4). For terrestrial invertebrates, we used measured input from a mixed vegetation cover (Romero et al., 2005).

The proportion of stream shading was measured separately (Table 1)

and used to adjust the amount of sunlight (i.e., PAR) reaching the stream bed for periphyton production. Shading has been shown to affect temperature and the stream heat budget (Johnson 2004; Arismendi et al. 2012). Within the ATP model, shading was not linked to potential effects on temperature (Reiter et al., 2020; Roon et al., 2021) because we were interested in exploring the influence of these environmental conditions separately.

2.3. Model simulations

For model simulations, we used available environmental data as parameter values for each stream in the ATP model (Table 1; Table S4; Figs. S2–S4). The environmental information was averaged across the 10 years (2007–2011, 2013–2016) of data collection or as the data were collected (Table S4; Figs. S2, S3). These years represent pre- and post-harvest time periods. Data were not collected in 2012 as logging activity occurring that year precluded access to the study sites. We justified averaging for these parameters across the pre- and post-harvest time frames because we were more interested in evaluating general system dynamics and not specific questions regarding the forest harvest treatments in the Trask Watershed Study. Moreover, consequences of harvest in upstream sections were not observed in the downstream sections used in this modeling exercise (Jensen, 2017). Environmental parameters were averaged on the finest time-scale possible (e.g., daily, monthly, seasonal) depending on data collection.

2.3.1. Corroboration.

For each of the four streams, we corroborated the ATP model output of the biomass of each stock (i.e., periphyton, aquatic invertebrates, trout and sculpin) to the biomass observed during field studies. Model runs for corroboration were based on average parameter values described above. Field collections for biomass estimates were typically conducted from the late spring (April or May) to early fall (September or October; Table 1). As such, our corroboration was restricted to these time periods.

2.3.2. Sensitivity analysis.

We identified commonly studied environmental variables to explore the direct and indirect effects on fish in forested streams. These included: temperature, discharge, dissolved nutrients, turbidity, stream shading, and riparian vegetation density. By considering these variables independently, we could better evaluate combinations of mechanisms driving fish response (biomass) that would be difficult or impossible to examine with field experiments. We evaluated response of fish biomass by highlighting different drivers of the model by means of a sensitivity analysis.

For sensitivity to environmental parameters, we used a uniform distribution adjusting each of the a priori identified environmental parameters by ±50% from the baseline value. For daily dynamic variables (temperature, discharge, nutrients, turbidity, and shading) we adjusted each day by the same percentage. The proportion of riparian vegetation cover was a state variable and did not require daily changes. To determine the relative importance of each variable, we used the Random Forest package in R (randomForest 4.6-13, The R Foundation, Vienna, Austria; Breiman and Cutler, 2011). The relative importance values represent the change in prediction error of a regression tree when the value of a given parameter is changed while values for all other parameters remain the same (see Harper et al., 2011 for details). For each stream, importance values for each parameter were normalized by the sum of the importance values across all parameters considered.

2.3.3. Scenarios.

In addition to the sensitivity analysis, we evaluated specific hypothetical scenarios that we viewed as most relevant both to natural processes and potential influences of human activities (i.e., contemporary forest management practices or climate change; Spies et al., 2019). We explored six scenarios in each of the four streams. (1) *Baseline scenario*, where no change occurred and environmental parameter inputs were as described above (see Table S4, Figs. S2–S4). (2) *Riparian disturbance scenario*, where canopy cover was reduced by 50%. This reduction in canopy cover resulted in a change in the flux of terrestrial invertebrates and detritus to the stream, and a reduction in stream shading. This scenario was not to emulate specific responses expected under likely management prescriptions, but rather to evaluate how larger changes in these parameters can influence system dynamics. (3) *Climate change scenario*, where we increased summer (July, August, September) daily temperature by 4 °C and decreased summer daily discharge by 50%; conditions that may be anticipated in response to longer-term (>30 yr) climate change (Mantua et al., 2010). (4) *Riparian disturbance and climate change scenario*, where we simultaneously made changes identified in the riparian disturbance and climate change scenarios of reduced canopy cover, increased temperature and decreased discharge. (5) *Sculpin removal scenario*, where we removed sculpin from the food web to explore the effect of inter-specific exploitative competition on trout biomass and the consequent changes in food web organization. (6) *Trout removal scenario*, where we removed trout to simulate responses of sculpin and other food web members. We assumed a change in biomass or food web pathways resulting from the removal of a fish stock would suggest the significance of exploitative competition.

For each scenario we conducted 1,000 model simulations to capture uncertainty in model outcomes. We adjusted 34 parameters to vary concurrently by ±25% of the mean value using a uniform distribution. These parameters were chosen because they have been previously shown to be influential in ATP model simulations (Bellmore et al., 2017). The 1,000 simulations were run using Latin hypercube sampling because it ensures adequate sampling across the entire range of each parameter while accounting for sufficient parameter combinations with limited simulations (Ford, 2010). These simulations allowed us to estimate the 10th and 90th percentiles of model outputs for each model scenario.

Model simulations ran on a daily time-step. Results of biomass and consumption by consumers (i.e., fish and aquatic invertebrates) were reported as either daily values or annual averages. These estimates were used to construct food web diagrams that show the biomass of each food web member and the flow of organic matter through the members. Means for calculating food web diagrams such as daily growth and biomass (e.g., bioenergetics) of a member, consumption rate, and assimilation efficiency were incorporated into the ATP model (Bellmore et al., 2017; Whitney et al., 2019). Results were presented in g-ash-free-dry-mass (AFDM) per m^2. We used a constant conversion factor of 0.2 g AFDM per 1.0 g wet weight (Whitney et al., 2019). All simulations were done in Stella Architect Version 2.0 (ISEE Systems, Lebanon, NH, USA).

3. Results

3.1. Model corroboration

The modeled biomass of periphyton, aquatic invertebrates, and fish in streams in the Trask River watershed were quantitatively similar to empirical observations (Fig. 2). Annual patterns of each food web member in the simulations were similar across the four streams considered. Subtle differences occurred because of stream specific environmental parameters. For example, Gus Creek. was higher gradient (10%) compared to the other streams (<4%). The higher gradient reduced habitat suitability via increases in velocity for sculpin (Fig. S3d), which decreased their biomass relative to the other streams.

Modeled proportions of terrestrial and aquatic invertebrates consumed by trout and sculpin were similar to summertime diets observed in 2008 (Raggon, 2010; Fig. S5). In general, the proportion of terrestrial invertebrates in the diet of trout increased throughout the summer up to approximately 0.7. In contrast, sculpin consumed predominantly aquatic invertebrates with terrestrial invertebrates

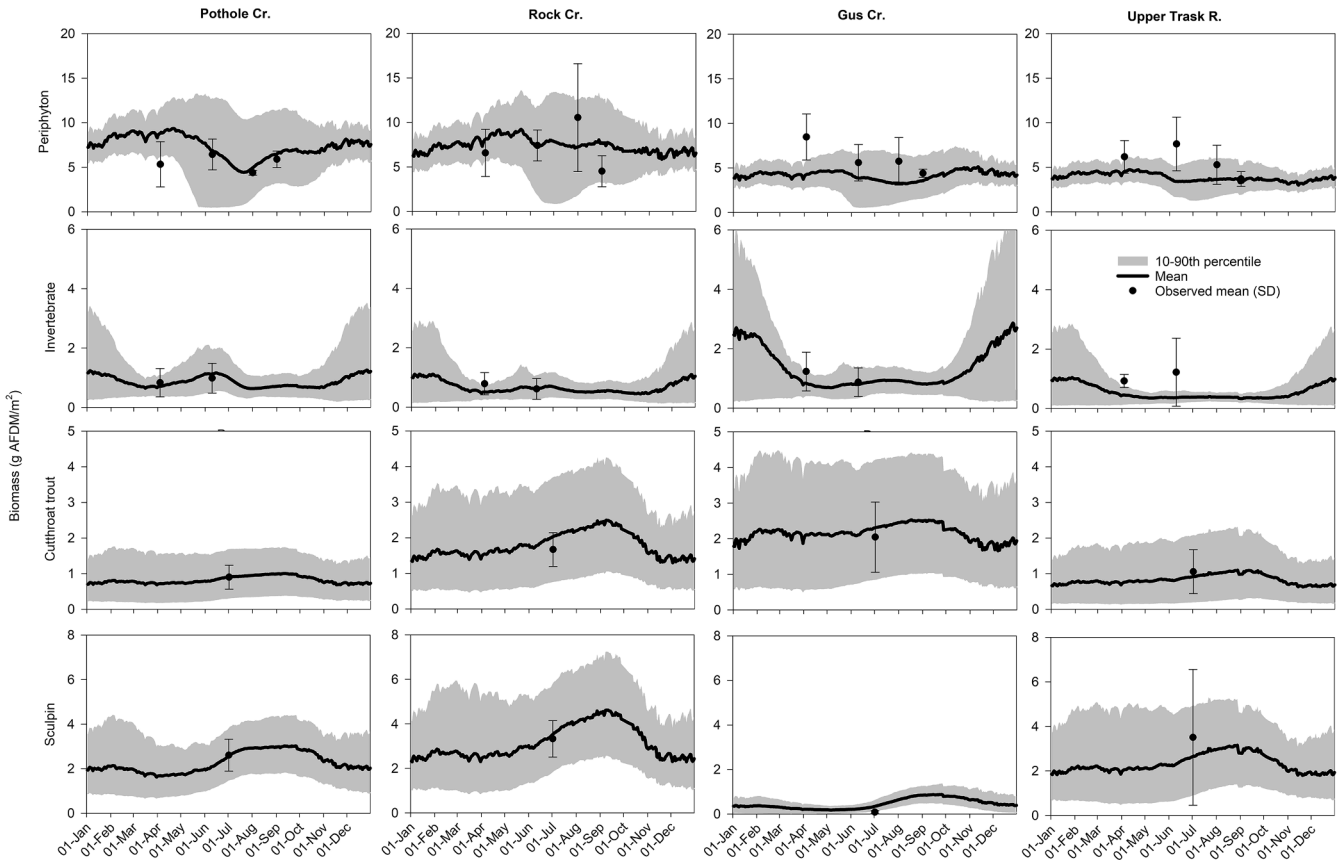

Fig. 2. Model parameter values (mean: black line and ±90th percentiles: shaded areas), and comparison to available empirical data for each stream averaged (±SD) from 2007 to 2016.

comprising only a small proportion of their diets (<0.25).

3.2. Sensitivity to environmental parameters

Sensitivity analysis showed a consistent set of model parameters were important, but the ranking of those parameters varied among streams and between species (Fig. 3). For trout, water temperature was the most influential followed by stream shading and terrestrial subsidies. However, with the exception of water temperature, the order of importance of these environmental variables was stream dependent. Terrestrial invertebrates, for example, were important to trout biomass in Rock Creek and upper Trask River but less so in Pothole and Gus Creeks. For sculpin, either stream shading or water temperature were most influential depending on the stream. Within the model simulations for the four streams, nutrients (DIN and SRP) and terrestrial subsidies were moderately important for the biomass of fish. Discharge, and turbidity had little importance for biomass of fish.

3.3. Scenarios

Simulated outcomes under baseline conditions indicated food webs differed slightly across the four streams (Fig. 4; Table S5). In Pothole Creek, the majority of organic matter that flowed to both trout and sculpin originated from periphyton, whereas most organic matter flow to fish the upper Trask River was from terrestrial detritus. In Rock and Gus Creeks, the dominant source of organic matter flowing to fish appeared to be more evenly distributed. However, some similarities occurred among the four streams. Sculpin consumed a larger overall biomass of both aquatic invertebrate groups while trout consumed larger biomass of terrestrial invertebrates (Fig. S5; Table S6).

Fishes exhibited variable responses to changes in canopy cover (i.e.,

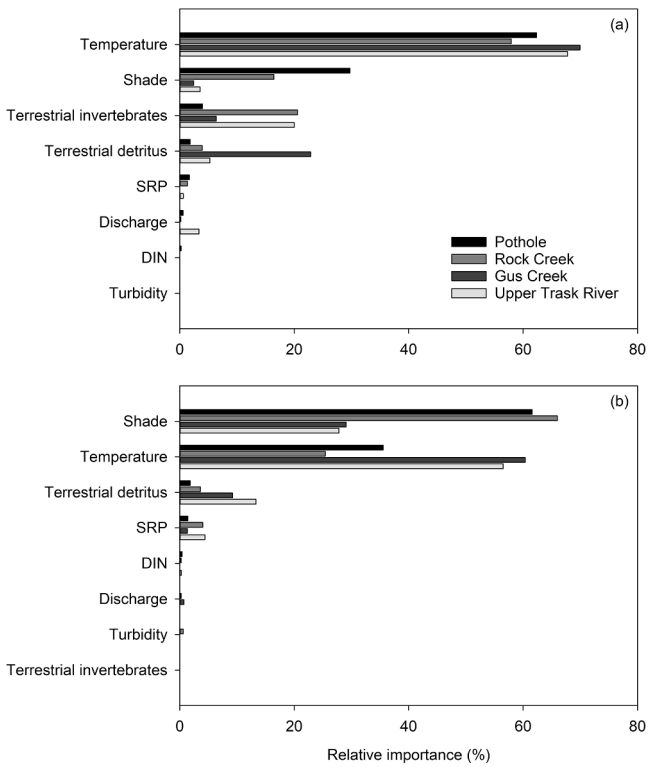

Fig. 3. Using sensitivity analysis, relative importance of environmental parameters in determining annual biomass of coastal cutthroat trout (a) and sculpin (b) for the four streams considered in the study.

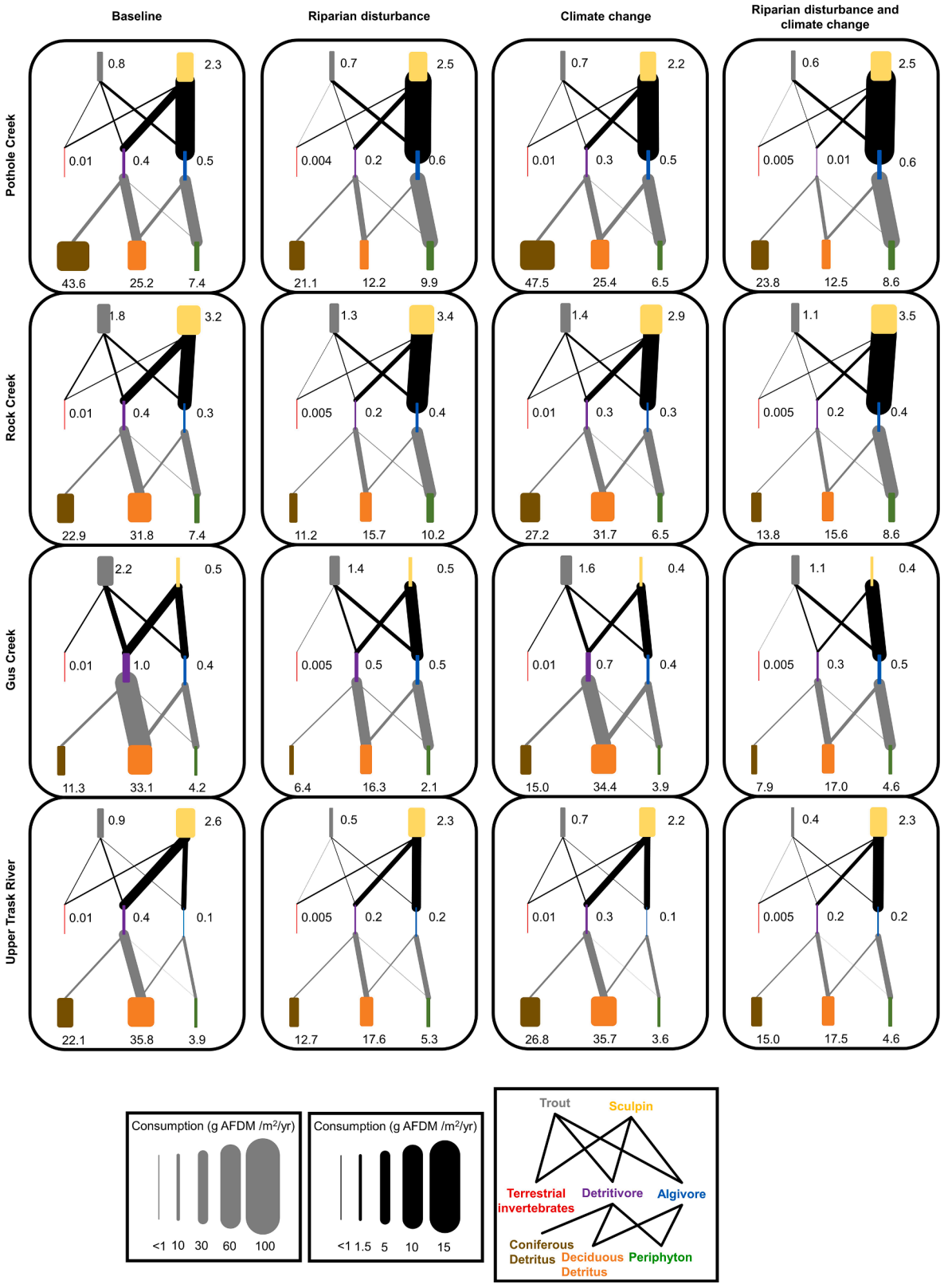

Fig. 4. Food web maps for each stream depicting the annual organic matter stocks (circles) and flows between consumers and resources (relative line width). Current conditions (baseline, left column) and three scenarios are shown: a reduction in canopy, climate change (increased temperatures and reduced discharge) and both (reduced canopy and climate change). Values on/next to circles are the annual average biomass (g AFDM/m2) for each food web member. See Tables S5 and S6 for mean (SD) of biomass and consumption rates, respectively.

terrestrial detritus and invertebrate subsidies; shade) or climate conditions (temperature and discharge) (Fig. 4; Table S5). Compared to baseline, trout biomass decreased by 10% to 48% when canopy cover was reduced. In contrast, reductions in canopy cover caused more variable responses in sculpin: some streams had small increases (7%; Pothole and Rock Creeks) in biomass et al., showed declines (12%; upper Trask River) or no change (Gus Creek). Under changes in temperature and discharge, simulations consistently produced decreases in the biomass of both trout (18–27%) and sculpin (6–21%). When canopy cover and climate conditions were changed simultaneously, simulations resulted in greater decreases in the biomass of trout (27–56%) in all four streams, but the biomass of sculpin decreased (5–14%) in two streams and increased (8–12%) in two.

Changes in the modelled average annual biomass of fishes were the result of the shifts in the pathways and magnitudes of organic matter flow through the food web (Fig. 4; Table S6) and the bioenergetic demands of food web members. The simulated reduction in canopy cover by 50% reduced the inputs of terrestrial invertebrates and detritus by a similar amount, which in turn reduced the flow of these subsidies to trout (51–81%) and to sculpin (2–50%; Table S6). In contrast, modelled increases in the average annual biomass of periphyton, owing to reduction in stream shade, was projected to increase the flow of autochthonous organic matter via algivorous invertebrates to sculpin (34–78%) and trout (27–55%). The modelled increases in summertime

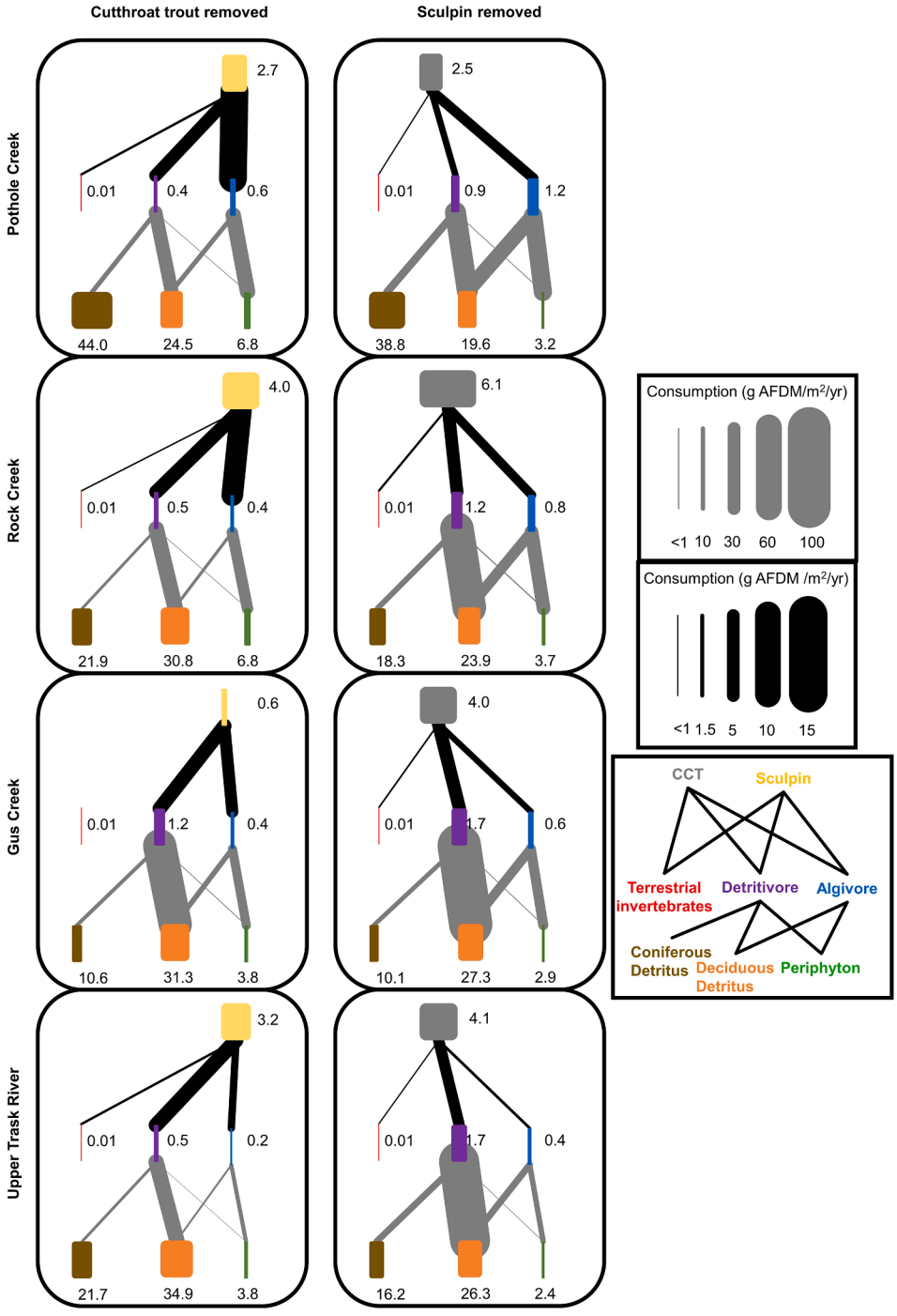

Fig. 5. Food web maps for each stream depicting the annual organic matter flow (relative line width) between consumers and resources (circles) when cutthroat trout or sculpin were removed. See Tables S5 and S6 for mean (SD) of biomass and consumption rates, respectively.

temperature increased rates of consumption more than respiration in both trout and sculpin. Aquatic invertebrate prey, however, had rates of respiration equal to or greater than consumption. Compared to baseline conditions, detritivores had a greater increase in respiration (approximately 57%) compared to consumption (up to 13% increase).

Removal of either trout or sculpin in the model resulted in an increase in the annual average biomass of the other (Fig. 5). For sculpin, the increase in annual biomass was minimal (17–28%) when trout were removed owing to an increase (12–34%) in the consumption of invertebrate prey resources (Tables S5, S6). When sculpin were removed from the food web, however, the average annual biomass of trout in most of the streams more than doubled (Tables S5, S6). Without sculpin, the proportion of aquatic invertebrates in the diet of trout increased by 92% or more. In addition, the removal of sculpin had cascading effects through the food web. Compared to baseline, without sculpin the biomass of aquatic invertebrates increased owing to less consumption by fish and basal resources (periphyton and detritus) decreased owing to increased consumption by invertebrates.

4. Discussion

The complexity of stream ecosystems is influenced by the number, strength, and nature of interactions within food webs and how they vary in space and time (Power and Dietrich, 2002). We addressed this complexity using the ATP model (Bellmore et al., 2017; Whitney et al., 2019) to better understand interactions among fish, their food resources, and riparian forests (Richardson and Danehy, 2007; Davis et al., 2013). Results of this work highlight four main findings. First, the magnitude of response of each top consumer differed with the simulated change, with trout more sensitive to changes in canopy cover and sculpin more sensitive to changes in climate parameters. Second, the pathways of energy transfer to fish could influence fish responses to changes in canopy cover, reaffirming that the forest is tightly linked to the stream. We found that trout were more responsive to changes in terrestrial subsidies from forest inputs whereas sculpin were more responsive to changes in light availability to the stream bottom. Third, the magnitude and direction of the response of fish to modeled changes can be mediated through fluxes of organic matter via autochthonous and allochthonous pathways suggesting some circumstances where riparian-aquatic conditions may buffer fish responses. Fourth, the impacts of climate change on food resources could have a greater influence on fish than the direct abiotic impacts that control physiology. In scenarios with increases in temperature, the consumption and respiration of detritivore aquatic invertebrates appeared to have more influence on fish biomass compared to the direct physiological responses of fish to increased temperature. Fifth, model simulations indicated strong interactions between the fish consumers, which manifested through consumption of shared resources and exploitative competition. Collectively, our results have implications for species conservation and forest management practices.

Most studies of fish responses to forest harvest in headwater streams in the Pacific Northwest have focused on trout (Martens and Dunham, 2021) because they are often the salmonid fish found furthest upstream in stream networks (Penaluna et al., 2021a). Sculpin, however, are often the most abundant fish in small to medium streams (Chelgren and Dunham, 2015). Sculpin also exhibit a more specialized pattern of foraging, based on comparisons of diets between sculpin and trout in this system (Raggon, 2010). Thus, changes that impact the benthic prey community may affect sculpin more than trout. In the four streams that we considered, model simulations indicated mixed results of the importance of sunlight (shade) and terrestrial subsidies for trout, whereas sculpin were consistently more sensitive to changes in shade-driven autotrophic production, as has been reported for trout (Murphy and Hall 1981, Kaylor and Warren, 2017, 2018). This result may be expected given the benthic foraging behavior of sculpin compared to the variable mix of terrestrial drift and benthic foraging exhibited by trout (Raggon, 2010, Li et al., 2016, Falke et al., 2020). Although early experimental work on streams in the Pacific Northwest highlighted the consumptive potential of sculpins (Davis and Warren, 1965, Warren and Davis, 1967, Brocksen et al., 1968), they have received little attention until recently (Raggon, 2010, Bellmore et al., 2013, Preston et al. 2018). Similar observations apply to other consumers in small streams, particularly for the coastal giant salamander (*Dicamptodon tenebrosus*) which are often very abundant across the Pacific Northwest (Hawkins et al., 1983), but were found in relatively low densities in our study streams.

The magnitude and direction of the response of fish to modeled changes in canopy cover was mediated through fluxes of organic matter via autochthonous and allochthonous pathways. In Gus Creek and upper Trask River, under baseline conditions a large proportion of energy consumed by fish originated from terrestrial subsidies, either directly from invertebrates or indirectly through detritivores feeding upon terrestrial detritus. When changes in canopy cover were modelled, increased energy contributed by autochthonous production to fish did not compensate for corresponding loss of allochthonous production and fish biomass declined. In contrast, in Pothole Creek, fish diets were more linked to insects associated with periphyton, which increased following reduction in canopy cover and resulted in a gain in sculpin and a loss in trout biomass. These results suggest the resilience of streams food webs to change may depend on multiple pathways to consumers that modulate responses to change.

Some empirical studies of trout in other Pacific Northwest streams have suggested higher productivity at sites with low canopy cover and low production associated with high canopy cover (Murphy and Hall, 1981, Kaylor and Warren, 2017, 2018), although others (e.g., De Groot et al., 2007; Roon, 2021) reported no associations. Much of this work has suggested increased sunlight and autotrophic production as a primary driver behind empirical associations, but a wide variety of process pathways can produce similar outcomes. For example, De Groot et al. (2007) noted that canopy removal in their study streams coincided with onset of cooler summer climates, which may have influenced ecosystem productivity, fish growth potential, or both. Increases in summer temperature are often observed in response to removal of riparian canopies (Reiter et al., 2020, Roon et al., 2021) and thus influences of temperature and light can be inherently confounded. More open canopy can also lead to reductions in terrestrial subsidies, including reductions in leaf litter (Wallace et al., 1997) or terrestrial invertebrates (Romero et al., 2005), which may be more important for trout than increasing sunlight (Erõs et al., 2012). Moreover, the composition of riparian vegetation may interact with the proportion of open canopy to influence the biomass of fish (Duncan et al., 1989). Although not manipulated with the model scenarios, nutrients, along with light, could limit periphyton growth that cascades to fish (Warren et al., 2017). It is clear that changes in riparian canopies lead to multiple, correlated responses in stream ecosystems, which are difficult to address via empirical statistical means. Accordingly, process-based models such as the ATP, which are not constrained by such limitations, can more completely account for these influences and offer complementary insights to empirical statistical studies.

The consistent decrease in fish biomass to the climate change scenario involving increased temperature and decreased flow was expected (Penaluna et al., 2015b). The model, however, enabled us to examine the alterations in ecosystem processes (Davis et al., 2013) and physiological characteristics of each food web member (Lefevre et al., 2021) likely responsible for decreased biomass. Increasing temperature had a strong negative effect on the bioenergetics of one stock of aquatic invertebrates, detritivores, considered in the model. This limited overall food resources available to fish, and, in turn, decreased their biomass. In Gus Creek and upper Trask River, where the allochthonous pathway was dominant, fish biomass exhibited a greater decline in the modelled scenarios compared to Pothole and Rock Creeks, where autochthonous pathways predominated. These results could be explained by the ATP

model's focus on trophic interactions, assumptions about algal responses, or the simplicity of the food web considered. The physiological equations we used for each food web member (Rutherford et al., 2000; Whitney et al., 2019) and parameter values (see supplementary material) were extrapolated from other studies, thus relative responses to climate change we simulated could be consistent with those observed in smaller forested streams (Woodward et al., 2010). However, additional research on how climate change may affect invertebrate prey, particularly physiological impacts, is needed.

Direct effects of simulated climate change on fish were minimal because the increased stream temperatures were closer to the optimal foraging temperature of both fish species (Jensen, 2017). In the modeling framework applied here, the effects of climate change on fish were focused on production of energetic resources (prey) and growth processes (i.e., bioenergetics). It is possible, however, that changes in demographic rates and phenology of the fish may be more important than bioenergetic consequences (Penaluna et al., 2015b, but see Campbell et al., 2020). Simulated influences of climate change and drought considered here also included reduced summer discharges, which only had minimal effects on fish biomass. This result may be owing to structure and parameterization of the model used, although reductions we considered were in percentages and produced only minimal changes in absolute discharge (Coble et al., 2020). The climate changes we simulated were based on mean values. It is possible that the inclusion of daily variability in temperature or discharge could have unforeseen effects on fish and is worth further investigation.

Although trout and sculpin in the streams we studied are influenced by different energetic pathways, their diets can overlap (Falke et al., 2020) with consequent potential for indirect or exploitative competition. In the streams we studied, Raggon (2010) reported significant seasonal overlap in diets of sculpin and trout with reduced overlap in summer as terrestrial invertebrates were more important in the diets of trout, whereas sculpins were more consistently linked to benthic prey. Simulated removals of sculpin or trout suggested exploitative competition is important as biomass of each species increased if the other was removed. This influence was asymmetrical, with trout exhibiting much greater increases in biomass as sculpins were removed. This finding is consistent with other studies indicating that sculpin can consume the majority of invertebrate prey resources in streams (Bellmore et al., 2013; but see Zimmerman and Vondracek, 2007; Naman et al., 2014). Variability in species responses to removals was apparent among simulations for the four study streams. In Rock Creek, for example, both species exhibited the strong responses to removal of the other. In this stream, availability of prey resources from allochthonous and autochthonous sources were relatively similar and thus either consumer (trout or sculpin) may be able to more readily adjust in the absence of the other. In Gus Creek, conditions were relatively unsuitable for sculpins (high gradient and low habitat suitability), and the increase in biomass of sculpins was correspondingly low when trout were removed in simulations. In this stream, trout were also relatively insensitive to removal of sculpins since the latter were not abundant. These findings indicate the likely presence of variable condition-specific factors influencing coexistence of these two consumers, including abiotic (Dunson and Travis, 1991) and biotic interaction modifiers (Silknetter et al., 2020). Accordingly, it may be difficult to draw conclusions regarding influences of natural or human-related changes on a focal fish species (e.g., trout; Martens and Dunham, 2021) if only one species is considered.

Our findings are consistent with variable outcomes where differential responses related to biotic and abiotic contexts can drive expected outcomes (Penaluna et al., 2015a, 2015b; Whitney et al., 2020). Among the four streams we considered, the relative importance of factors influencing fish biomass differed among streams. For example, results of simulations in Pothole and Rock Creeks suggested shade was most important influence on sculpin biomass, whereas temperature was more important for sculpin in Gus Creek and the upper mainstem Trask River. Responses of trout were influenced by a more complex portfolio of influences, but local variability in processes driving in-stream productivity, even among neighboring tributaries, was pronounced. Earlier application of an individual-based model focused on a different set of processes influencing trout also highlighted the idiosyncrasies of each of these study streams (Penaluna et al., 2015a, 2015b). Our study complements these findings by highlighting trophic dynamics among streams that can further influence the variability in fish responses. That said, our model analyses did not account for fish movement or predator avoidance behavior (e.g., cover use; Penaluna et al., 2021b), both of which may diminish or enhance stream specific responses of fish (Sheldon and Richardson, 2022).

The model we used should be thought of as a heuristic tool to explore dynamics of stream-riparian ecosystems. As such, caveats do exist. First, many abiotic and biotic parameters are needed to inform the model. In some cases, empirical data are available, such as the abiotic data (e.g., temperature, riparian composition) we used for the sites in the Trask River. However, data are not always available or limited such as the physiological parameters for aquatic invertebrates or habitat suitability curves for sculpin. In these cases, we used the best available information. Second, the model does not include all dynamics that could better represent local conditions such as fish movement or a more complex food web structure. The ATP model is flexible, however, and can be modified as we did in this study to represent the two dominant fishes (coastal cutthroat trout and sculpin). Additional complexity leads to more parameters and data needs, creating more challenging interpretations potentially decreasing the heuristic value of a modeling approach. Third, as with all models, our results may not be predictive, and in our view the results presented here should be thought of as hypotheses that could be tested with future empirical studies. Finally, it is worth reiterating that empirical studies alone cannot address the complexities in which mechanistic models are capable. Ultimately, both approaches are needed to gain a more robust understanding of ecosystem dynamics.

Insights from this study have many potential implications for management of the nexus of forests, streams, and fish. Much of the research involving this nexus involves study of abiotic factors (e.g., stream temperatures, discharges, geomorphic conditions), simple assessments of diets, or measures of fish responses involving only a single species (typically salmonids in the temperate forested regions). Accordingly, best management guidelines have been developed based on this information. This is a sensible approach, but as this study highlights, interactions among factors and influences are infrequently accounted for by research. For example, consumer interactions involving non-salmonid species contribute to an increasingly complex picture of forests, streams, and fish. Such complexity poses new challenges for adapting management practices to address them. It also highlights new opportunities for moving beyond past approaches that focus on a limited range of responses. Ultimately, riparian forest management or restoration that builds on a more complete understanding of how stream ecosystems function will have multiple benefits across landownerships. This is arguably true not only in the context of land uses such as forestry, but also in the face of increasing influences of climate change. We have highlighted the utility of ecosystem models, coupled with longer-term empirical data, to elucidate system dynamics in different places and under different environmental scenarios. Studies such as this provide key insights into variability of processes and food web linkages that could be important in terms of driving desired outcomes. As such, they can not only reveal the importance of system complexity, but also point to where uncertainty about key linkages occurs and could be addressed.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120046.

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