AN ABSTRACT OF THE DISSERTATION OF

Matthew Joseph Kaylor for the degree of Doctor of Philosophy in Fisheries Science presented on May 9, 2019.

Title: Bottom-up Drivers of Primary Producers and Predator Populations in Oregon Streams

Abstract approved: ____
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Humans have drastically altered the physical habitat and food web structure of stream ecosystems. Two major impacts humans have had on Pacific Northwest streams are modification of streamside forests (as a result of agriculture, land development, and timber harvest), and declines in the return of wild anadromous salmon to headwater ecosystems (due to a range of habitat degradation, dams, harvest, and hatcheries). Riparian forest impacts have altered stream light dynamics, while the loss of salmon has led to declines in the delivery of nutrients from the ocean to streams. While the initial impacts of the modifications took place decades or even centuries ago, they can have lasting effects on stream ecosystems and food webs. This dissertation evaluates 1) influences of long-term recovery from historic riparian harvesting on stream light, habitat, and food webs, and 2) how reduced salmon subsidies to streams may be impacting stream productivity and food webs.

Today most streams in the Pacific Northwest, and indeed across much of North America, have buffers of riparian forests that are regenerating from earlier land clearing. As stands recover, the trajectories of stand development will affect forest structure, which in turn affects stream light regimes. In the first half of my dissertation, I explore how stand age and structure

relates to stream light availability and then how spatial differences and temporal changes in stream light influence stream food webs and higher trophic level biomass in headwater streams. In Chapter 2, I explore how stream light availability differs with the age and stage of riparian forests. I found that stream light flux was lower and less variable when bordered by second-growth forests compared to old-growth forests within a stream network and more broadly across forests west of the Cascade Mountains. Numerous studies have evaluated how large differences in light availability (e.g. fully forested compared to complete removal of riparian forests) influence stream food webs, but smaller differences in light availability, such as those found in Chapter 2, have received less consideration. In Chapter 3, I conducted surveys across 18 stream reaches and evaluated how variables associated with stream habitat, light, primary production, and macroinvertebrate biomass account for variability in the biomass of cutthroat trout and total vertebrates (fish and salamanders). Habitat metrics were not well correlated with higher trophic level biomass. In contrast, factors associated with resource availability — as regulated through bottom-up, autotrophic pathways — were closely related to the biomass of fish and other consumers. In Chapter 4, I quantified long-term responses of stream biota to the regeneration of riparian forests following clear-cut harvest. I resampled five stream reach pairs that were originally sampled in 1976 shortly after canopy removal. This initial survey showed that periphyton chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout (*Oncorhynchus clarkii clarkii*) biomass were elevated in harvested reaches relative to reference reaches. After four decades of riparian regeneration, mean canopy openness, chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout biomass declined in harvested reaches relative to paired old-growth reference reaches. Changes in canopy cover were consistent with biotic responses and suggest that changes in light availability as stands regenerated exerted control on biota through bottom-up pathways in these streams.

While spatial and temporal light dynamics appear as important regulators of stream food webs in small forested streams of western Oregon, other factors may emerge as important constraints on food web productivity across stream networks in other regions. In the second half of my dissertation, I explore bottom-up drivers of fish production in a river network in eastern Oregon where canopies are more open than small western Oregon streams. I focus on nutrient and carbon subsides in this study as the loss of returning anadromous fish has been hypothesized as a key factor contributing to poor recovery of ESA-listed salmonids. In chapter 5, I evaluate network-scale spatial patterns of primary production, potential drivers of primary production, and juvenile salmonid abundance throughout two NE Oregon sub-basins. Primary production rates increased with watershed area and we were able to explain 72% of the variability in primary production across these basins using a combination of fixed-effects (e.g. light, nutrients, and temperature) and spatial autocorrelation. In contrast to other studies, juvenile salmonid abundance was greatest in cool headwaters where nutrient concentrations and rates of primary production were very low. To test the hypothesis that growth of juvenile salmonids and other biota in these low-productivity stream sections may be inhibited by the reduction of returning adult salmon and the associated loss of nutrient subsidies, I conducted a carcasses addition experiment in three locations of the Upper Grand Ronde River. In chapter 6, I focused on the responses of juvenile Chinook Salmon (*Oncorhynchus tshawytsca*) and steelhead (*O. mykiss*). Chinook and steelhead consumed an abundance of eggs and carcass tissue which resulted in greater growth rates and body condition of fish in treatment reaches relative to controls. To contextualize potential effects of increased growth on Chinook survival, I used an 18 year

tagging and detection dataset to evaluate Chinook length-survival relationships. The positive association between length and survival suggests that actions resulting in larger Chinook lead to increased survival rates. In chapter 7, I evaluate carcass addition effects on the broader food web. Periphyton, aquatic invertebrates, and non-salmonid fish assimilated carcass nitrogen, but enrichment was far less than observed in juvenile salmonids. In contrast to salmonids, diet analysis and stable isotope patterns indicated that non-salmonids were not consuming eggs and carcass material, suggesting carcass nitrogen assimilation occurred through bottom-up pathways. These results suggest that salmon subsidies have the potential to broadly impact stream food webs in this region, but that species able to directly consume eggs and carcass material (i.e. juvenile salmonids) clearly benefit more from these subsidies.

Bottom-up Drivers of Primary Producers and Predator Populations in Oregon Streams

by

Matthew Joseph Kaylor

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Doctor of Philosophy

Presented May 9, 2019

Commencement June 2019

Doctor of Philosophy dissertation of Matthew Joseph Kaylor presented on May 9, 2019.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Matthew Joseph Kaylor, Author

ACKNOWLEDGEMENTS

My time as a PhD student has truly been a gratifying experience that I have thoroughly enjoyed. For that, I first and foremost would like to sincerely thank my advisor, Dana Warren. I couldn’t have asked for a better advisor, mentor, and friend. He was passionate in his commitment to advancing my career and development as a scientist and went above and beyond to create opportunities for me to succeed. In addition, he truly cared about my personal well-being and happiness and recognized that good work-life balance was essential to being a productive graduate student. I look forward to our continued friendship and to continue working with Dana throughout my career.

I would like to sincerely thank my committee members; Ivan Arismendi, Sherri Johnson, Seth White, Johnny Armstrong, and Brian Haley. They were always there when I needed advice on project ideas, experimental design, and graduate school in general. They were a pleasure to work with and made it very clear that they cared about my advancement and success as a scientist. I would especially like to thank Seth White for his mentoring and commitment to advancing my research and skillset. He went above and beyond to set up collaborations, secure funding, and provide opportunities for me to advance as a scientist. In addition, I would like to thank collaborators who were crucial to the success of my research. Ted Sedell supported work in the Grande Ronde River and ensured I had all the resources necessary to conduct my research. Ryan Sponseller hosted me in Sweden and provided opportunities for me to gain research experience and exposure to new collaborators.

Prior to graduate school, I have been extremely fortunate to work with individuals who cared about my future and success, and they all played a role in shaping my career path. Jeremy “Grey Jay” Hubbard was a pleasure to work with while making arguably the best trout habitat in

northern Wisconsin. He introduced me to stream restoration and stream ecology and taught me many other non-fish related life lessons. Josh “Brad” VanDeMark was an excellent mentor that taught me about what graduate school was like and how to go about finding an advisor and mentor. Henry Carson advised my undergraduate research on beach microplastics and he introduced me to conducting research ranging from field work to scientific writing. The experience I gained from Hank, his advice about graduate school, and his mentoring played a crucial role in me getting into a graduate program and finding an advisor that was an excellent fit for me.

There are countless people I want to thank for their help with field work or for their friendship and general support throughout graduate school. I couldn’t have asked for a better group of people to work with throughout field sampling and lab processing. This list includes Brian VerWey, Ashley Sanders, Emily Heaston, Kate Pospisil, Chris Kopet, Emily Purvis, Jen King, Gavin Jones, Lauren Still, and Cassidy Hayes. Not only were they excellent workers, they were a pleasure to work with and made field sampling enjoyable. I also couldn’t have asked for a better group of other graduate students and friends to who supported me with their friendship and weekly, biweekly, and sometimes even triweekly trips to Squirrels Tavern and other Corvallis watering holes. These friendships were crucial to my overall wellbeing as a graduate student. My parents fostered my interest in natural resources and the outdoors at a young age. The trips my mom took me on to collect frogs, turtles, and fish from nearby ponds and streams for the numerous aquariums she helped me set up sparked my interest in aquatic ecosystems. My dad took me fishing and canoeing as a child and this furthered my interested in streams, lakes, and fish. My parents and sister were extremely supportive of me throughout graduate school and I can’t thank them enough.

Scholarships and funding throughout my education supported me financially and were incredibly important to my success. A National Science Foundation fellowship supported me for three years and allowed me to focus on my research. It also allowed me to travel to Sweden for five months to work with Dr. Ryan Sponseller through the Graduate Research Opportunities Worldwide (GROW) program. This was an amazing experience and I learned a tremendous amount from Ryan, his lab, and others at Umeå University. The Columbia River Inter-Tribal Fish Commission (CRITFC) supported me for multiple years and I thank Seth White for securing this funding. The Grande Ronde Model Watershed focused investment partnership provided funding that supported field work and lab preparation. I was additionally supported by the HJ Andrews Experimental Forest graduate research assistantship. Scholarships were provided by the James Sedell Graduate Scholarship, Flyfisher's Club of Oregon Graduate Scholarship, Charlie Taylor Memorial Fishin' Friends Graduate Scholarship, Carl Bond Memorial Scholarship, Neil Armantrout Graduate Scholarship, Washington County Fly Fisher's Scholarship, Oregon Council Fly Fisher's Scholarship, and Oregon Lottery Scholarship.

CONTRIBUTION OF AUTHORS

Dana R. Warren contributed to all aspects of this dissertation and associated manuscripts. Dana R. Warren and Peter M. Kiffney contributed to analysis, interpretation of results and writing of Chapter 2. Dana R. Warren contributed to all aspects of Chapters 3 and 4. Dana R. Warren, Seth M. White and W. Carl Saunders contributed to the study design, analysis, interpretation of results, and writing of Chapter 5. Dana R. Warren, Seth M. White, and Edwin R. Sedell contributed to the study design, field sampling, analysis, and writing of Chapter 6. Dana R. Warren, Seth M. White, Ashley M. Sanders, and Edwin R. Sedell contributed to the study design, field sampling, analysis, and writing of Chapter 7.

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CHAPTER 1: GENERAL INTRODUCTION

In stream ecosystems, food webs are supported by a variety of energy sources that may vary spatially and temporally (Wipfli and Baxter 2010), thereby influencing stream community composition and secondary production. Understanding drivers influencing the quantity and quality of these resources and associated impacts on stream food webs is therefore important to effective management of stream ecosystems and biota (Naiman et al. 2012). In the Pacific Northwest region, the focus of stream management is often the enhancement and recovery of salmonid populations. While studies have demonstrated how productivity at the base of the food web can regulate salmonid populations through controls on prey availability (Warren et al. 1964; Deegan and Peterson 1992), management efforts have overwhelmingly focused on improving physical habitat conditions (e.g. large wood and pools) with less of a focus on food resources and stream productivity (Wipfli and Baxter 2010; Naiman et al. 2012). These efforts are not always successful in achieving the goal of increasing fish carrying capacity or production (Roni et al. 2002; Roni 2019), potentially because consideration of the factors limiting populations was not holistic, encompassing both physical habitat constraints and food limitation (Naiman et al. 2012). Identifying abiotic and biotic factors that control stream productivity, and invertebrate, fish, and other consumer populations provides a more complete assessment of how management actions and spatial and temporal variability in associated drivers of productivity across stream networks may interact to shape consumer populations in streams.

Background on energy sources for stream food webs

In small forested headwater streams, a prevailing paradigm is that food webs are supported almost entirely by carbon delivered from adjacent riparian areas (allochthonous;

leaves, wood, and dissolved organic carbon). Indeed, one of the first studies to evaluate energy inputs to a forested stream found that over 99% of carbon inputs were of allochthonous origin (Fisher and Likens 1973). Later, the experimental exclusion of leaf litter from streams reduced secondary production of multiple trophic levels including predators (Wallace 1997; Wallace et al. 1999), further demonstrating the importance of terrestrial subsidies fueling food web productivity. Fish, particularly salmonids, may additionally benefit from terrestrial subsidies as they feed directly on terrestrial invertebrates that fall into streams, which can be a key prey resource (Nakano et al. 1999; Baxter et al. 2005; Saunders and Fausch 2007). It is clear that in heavily forested streams, energy budgets are dominated by allochthonous material and consumer communities can be reliant on detrital pathways (Rounick et al. 1982; Hicks 1997; Reid et al. 2008). However, the importance of these subsidies is relative to the quantity and quality of other carbon sources (Wipfli and Baxter 2010).

Primary producers within streams are a high quality food resource (low C:N; Cross et al. 2005), and rates of primary production can influence consumer community structure and secondary production. Forested low-order streams (1st to 3rd order) are typically light limited (Ambrose et al. 2004; Bernhardt and Likens 2004) where rates of autochthonous carbon production are low relative to inputs of allochthonous carbon. Light increases with distance downstream as streams widen and the River Continuum Concept (Vannote et al. 1980) postulates that changes in light from headwaters to mid-order streams shifts food web reliance from allochthonous carbon to autochthonous carbon. However, even in small forested headwaters, increases in light availability can alter community structure and increase the abundance or production of biota, even when allochthonous inputs are reduced. For example, Bilby and Bisson (1992) compared annual energy inputs to a stream section where the riparian forest was recently harvested compared to an upstream section bordered by old-growth forest. They found that the total allochthonous inputs were far lower in the clear-cut section (100 g m^{-2} y^{-1} compared to 300 g m^{-2} y^{-1}), but autochthonous carbon inputs were greater (175 g m^{-2} y^{-1} compared to 60 g m^{-2} y^{-1}). Despite lower total carbon flux to the harvested section, trout production was greater in the harvested reach. This demonstrates that energy budgets alone to not provide an estimate of energy transfer to consumers, and studies are increasingly finding that autochthonous carbon is disproportionately important relative to its availability. McCutchan and Lewis (2002) showed that autochthonous carbon contributions to the total carbon budgets ranged from 2-40% but consumer reliance on autochthonous carbon ranged from 40-80%. This study is consistent with a number of studies demonstrating that consumers are disproportionately reliant on autochthonous carbon relative to its availability (Hall et al. 2001; Brito et al. 2006; Lau et al. 2009). Spatial differences or temporal changes in light availability can have substantial influence on periphyton production (Hill and Knight 1988; Kiffney et al. 2003, 2004; Ambrose et al. 2004), autochthonous carbon contributions towards secondary production (Finlay 2001; McCutchan and Lewis 2002; Wootton 2012), and top predatory biomass (Murphy and Hall 1981).

Nutrients are also a fundamental constraint on productivity, and the availability of nutrients influences streams food webs through both autotrophic and heterotrophic pathways. In a small forested stream, the addition of nutrients increased the quality of detrital food resources and stimulated greater invertebrate secondary production through heterotrophic pathways (Cross et al. 2006). In larger streams, nutrients may influence consumers through autotrophic pathways or a combination of autotrophic and heterotrophic pathways. Numerous studies have demonstrated that the addition of nutrients to streams with little canopy cover stimulated greater primary production, invertebrate abundance, and the growth rates or abundance of fish, particularly juvenile salmonids (Johnston et al. 1990; Peterson et al. 1993; Pellett 2011; reviewed by Gerwing and Plate 2019). However, nutrient enrichment can also shift primary producer and invertebrate communities to species that are resistant to consumption by higher trophic levels (e.g. inedible primary producers or grazers), which may decouple the relationship between nutrient availability and consumer productivity (Slavik et al. 2004; Davis et al. 2010).

In oligotrophic streams accessible to anadromous fish, inputs of nutrient and carbon subsidies originating from marine environments can be major energy and nutrient resources fueling stream food webs (Schindler et al. 2003). Nutrients released from spawning salmon or carcasses can be assimilated by biofilms, stimulating primary production and thereby providing bottom-up increases in the productivity of invertebrates and fish (Kohler et al. 2008, 2012; Wipfli et al. 2010). Alternatively, biota can directly consume carcass eggs and flesh (Bilby et al. 1998; Armstrong and Bond 2013; Collins et al. 2016), or indirectly predate upon organisms that directly consumed eggs and carcass flesh (Collins et al. 2016). Drastic losses of anadromous fish have occurred globally which has reduced the delivery of marine-derived nutrient and carbon subsidies to these ecosystems. In contrast, anadromous species have been introduced to some regions where they were historically absent (e.g. Patagonia, New Zealand, and the Great Lakes region of North America) and the nutrient and carbon subsidies they now deliver to streams are incorporated by food webs (Collins et al. 2011; Arismendi and Soto 2012).

Dissertation goals

In the following chapters, I explore how external factors that affect basal resources in a stream ecosystem can impact food webs with a focus on fish and other apex predators in streams. In Chapters 2-4, I focus on how the age, stage, and structure of riparian forests in western Oregon can affect stream light availability, which, in turn, can influence rates of primary production and energy flow to higher trophic levels. I demonstrate the connections between riparian forest stand age, legacies of previous forest management, and light availability in Chapter 2 by sampling light availability through a basin with a mixed harvesting history and by conducting a meta-analysis of studies reporting stand age and canopy cover over streams. Riparian forests were extensively harvested across the Pacific Northwest, but regulations implemented to protect the function of riparian forests have resulted in riparian forest regeneration. In chapters 3 and 4, I demonstrate how spatial variability and temporal changes in light reaching forested streams can affect stream algal production and how relatively small increases this key basal resource can lead to local increases in the biomass and abundance of stream invertebrates, fish, and salamanders.

In the next three chapters I shift away from the light limited forest streams of western Oregon and focus on the Grande Ronde River in eastern Oregon. In this basin, light is rarely limiting owing to differences in vegetation, climate, and historic and ongoing land-use (White et al. 2017), potentially shifting limitation of productivity to nutrients. I first describe the spatial dynamics of nutrients, light, temperature, and stream primary production throughout the upper Grande Ronde River and the adjacent Catherine Creek watershed, and relate the spatial patterns of primary production to the spatial distribution of juvenile salmonids (Chapter 5). Keeping a focus on potential bottom-up drivers of fish production, we used the network study of stream production and nutrients to identify stream sections where low rates of productivity at the base of the food web may be limiting the production of consumers. One explanation for low nutrients and primary production in these sections may be the drastic reduction of returning adult salmon which transport large amounts of nutrients from the ocean to inland streams (Naiman et al. 2002; Schindler et al. 2003). To evaluate this hypothesis I added steelhead carcasses three stream sections and quantified juvenile salmonid growth, size, and diet responses (Chapter 6), as well as impacts to the broader food web including primary producers, invertebrates, and non-salmonid fish species (Chapter 7). Though carcass addition is a common management strategy to enhance juvenile salmonid production (Collins et al. 2015), this study provides an empirical evaluation of this management option in a region where evaluation has been limited and provides a more holistic evaluation of impacts to the food web in a region with diverse fish assemblages.

In these studies I sought to understand how underling drivers of stream food webs with a focus on bottom-up controls on consumer populations. I target two major changes that have impacted western stream ecosystems (1) changes in riparian forest structure and stand development processes owing to historic harvest and current regulations limiting harvest, and (2) the reduction of returning adult salmon and associated salmon-derived subsidies from many stream ecosystems. While these are seemingly disparate drivers of modifications to stream food webs, this work illustrates the link that these two factors have through their control on stream productivity and food availability, which in turn can influence salmonid and other consumer population densities and growth rates in streams. My specific objectives were to:

1) Understand how riparian stand development processes influence spatial and temporal light dynamics in western Pacific Northwest streams (Chapter 2)
2) Evaluate relationships between stream habitat, light availability, metrics of primary production, invertebrates, fish, and salamanders in forested streams of western Oregon (Chapter 3)
3) Quantify long-term impacts of riparian harvest and subsequent regeneration of riparian forests on stream habitat, light availability, primary producers, invertebrates, and ultimately cutthroat trout populations (Chapter 4)

4) Determine the spatial patterns and drivers of primary production in two NE Oregon sub-basins and relate spatial patterns of primary production to the spatial distribution of juvenile salmonids (Chapter 5)
5) Evaluate impacts of steelhead carcass additions to a NE Oregon stream on the growth rates, body condition, diet, and size of juvenile salmonids (Chapter 6)
6) Quantify carcass addition impacts to broader food webs including primary producers, invertebrates, salmonids, and non-salmonids and determine the pathways biota assimilate carcass-derived nutrients along three stream locations of a NE Oregon stream with varying fish assemblages (Chapter 7)

Literature cited

Ambrose, H. E., M. A. Wilzbach, and K. W. Cummins. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. The North American Benthological Society 23(4):701–712.

Arismendi, I., and D. Soto. 2012. Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from southern Chile. Knowledge and Management of Aquatic Ecosystems (405):01.

Armstrong, J. B., and M. H. Bond. 2013. Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. Journal of Animal Ecology 82(5):966–975.

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50(2):201–220.

Bernhardt, E. S., and G. E. Likens. 2004. Controls on periphyton biomass in heterotrophic streams. Freshwater Biology 49(1):14–27.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Brito, E. F., T. P. Moulton, M. L. De Souza, and S. E. Bunn. 2006. Stable isotope analysis indicates microalgae as the predominant food source of fauna in a coastal forest stream, south-east Brazil. Austral Ecology 31(5):623–633.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):1–18.

Collins, S. F., A. H. Moerke, D. T. Chaloner, D. J. Janetski, and G. A. Lamberti. 2011. Response of dissolved nutrients and periphyton to spawning Pacific salmon in three northern Michigan streams. Journal of the North American Benthological Society 30(3):831–839.

Cross, W. F., J. P. Benstead, P. C. Frost, and S. a. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshwater Biology 50(11):1895–1912.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detrital-based ecosystem. Ecology 87(6):1556–1565.

Davis, J. M., A. D. Rosemond, S. L. Eggert, W. F. Cross, and J. B. Wallace. 2010. Long-term nutrient enrichment decouples predator and prey production. PNAS 107(1):121–126.

Deegan, L. a, and B. J. Peterson. 1992. Whole-river fertilization stimulates fish production in an arctic tundra river. Canadian Journal of Fisheries and Aquatic Sciences 49:1890–1901.

Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82(4):1052–1064.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

Gerwing, T. G., and E. Plate. 2019. Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. Restoration Ecology 27(2):279–288.

Hall, R. O., G. E. Likens, and H. M. Malcom. 2001. Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. Journal of the North American Benthological Society 20(3):432–447.

Hicks, B. J. 1997. Food webs in forest and pasture streams in the Waikato region, New Zealand: A study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. New Zealand Journal of Marine and Freshwater Research 31(5):651–664.

Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125–132.

Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. Canadian Journal of Fisheries and Aquatic Sciences 47:862–872.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40(6):1060–1076.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23(3):542–555.

Kohler, A. E., T. N. Pearsons, J. S. Zendt, M. G. Mesa, C. L. Johnson, and P. J. Connolly. 2012. Nutrient Enrichment with Salmon Carcass Analogs in the Columbia River Basin, USA: A Stream Food Web Analysis. Transactions of the American Fisheries Society 141(September 2014):802–824.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53(3):446–460.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28(2):426–439.

McCutchan, J. H., and W. M. Lewis. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47(3):742–752.

Murphy, M. L., and J. D. Hall. 1981. Vaired effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109(52):21201–7.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nakano, S., H. Miyasaka, and K. Naotoshi. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80(7):2435–2441.

Pellett, K. 2011. A review of twenty years of nutrient enrichment in the salmon river watershed, Vancouver Island (1989-2010). Nanaimo, BC.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. Mckinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74(3):653–672.

Reid, D. J., G. P. Quinn, P. S. Lake, and P. Reich. 2008. Terrestrial detritus supports the food webs in lowland intermittent streams of south-eastern Australia: a stable isotope study. Freshwater Biology 53(10):2036–2050.

Roni, P. 2019. Does River Restoration Increase Fish Abundance and Survival or Concentrate Fish ? The Effects of Project Scale , Location , and Fish Life History. Fisheries 44(1):7–19.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. Michael, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22(1):1–20.

Rounick, J. S., M. J. Winterbourn, and G. L. Lyon. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. Oikos 39:191–198.

Saunders, W. C., and K. D. Fausch. 2007. Improved Grazing Management Increases Terrestrial Invertebrate Inputs that Feed Trout in Wyoming Rangeland Streams. Transactions of the American Fisheries Society 136(5):1216–1230.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Fronteirs in Ecology and the Environment 1(1):31–37.

Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of Kuparuk River ecosystem to phosphorus fertilization. Ecology 85(4):939–954.

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Wallace, J. B. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277(5322):102–104.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69(4):409–442.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. The Journal of Wildlife Management 28(4):617–660.

White, S. M., C. Justice, D. A. Kelsey, D. A. McCullough, and T. Smith. 2017. Legacies of stream channel modification revealed using General Land Office surveys, with implications for water temperature and aquatic life. Elem Sci Anth 5(0):3.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373–387.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, N. L. Mitchell, J. L. Lessard, R. A. Heintz, and D. T. Chaloner. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic levels in streamside experimental channels. Transactions of the American Fisheries Society 139:824–839.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7(12):1–9.

CHAPTER 2: CITATION INFORMATION

LONG-TERM EFFECTS OF RIPARIAN FOREST HARVEST ON LIGHT IN PACIFIC NORTHWEST (USA) STREAMS

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Freshwater Science, 2017

Issue 36(1), pp 1-13

CHAPTER 2: LONG-TERM EFFECTS OF RIPARIAN FOREST HARVEST ON LIGHT IN PACIFIC NORTHWEST STREAMS

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Abstract

Riparian forests exert strong influence on abiotic and biotic processes in adjacent streams by regulating light. Harvesting of riparian forests was once common practice, and consequently, many streamside forests across North America are in varying stages of development as they regenerate, thereby affecting stream light regimes. We used 2 approaches to evaluate the influence of riparian forest harvest and stand recovery on light availability in small mountain streams. We estimated light and canopy cover every 25 m along 11.5 km of a 4th-order stream network dominated by late-successional riparian forests that included 7 streamside harvest units 50 to 60 y old. Estimates of stream light fluxes were lower in harvest units than in upstream and downstream sections bordered by old-growth forests even though only 1 stream bank was harvested in 5 of 7 units. Differences in stream light between harvested reaches and adjacent old-growth sections were greater when both banks had been logged. We also conducted a space-for-time analysis based on a literature review of Douglas fir-dominated forests of the US Pacific Northwest. Canopy closure generally occurred within 30 y of harvest and was followed by a period of maximum canopy cover (minimum light) that lasted from 30 to 100 y. Data were limited for stands ranging from 100 to 300 y old, but mean canopy openness and variability in openness along the stream were greater in late-successional forests (dominant canopy trees >300 y old) than in stands that were 30 to 100 y old (18 vs 8.7%), a result consistent with the network analysis. Overall results from our study suggest that streams with mid-successional riparian forests probably are in a period of minimal summer light fluxes.

Introduction

Most North American forests have been cleared at least once within the last 2 centuries for timber harvesting, agriculture, or land development (Pan et al. 2011). Land clearing historically included streamside (riparian) forests with little consideration of potential negative effects on adjacent aquatic environments (Richardson et al. 2012). However, recognition of the ecological linkages between riparian forests and aquatic ecosystems led to increased regulatory protection to maintain key riparian functions, such as large wood recruitment to streams, nutrient and sediment retention, bank stability, and regulation of shade and stream temperature (FEMAT (Forest Ecosystem Management Assessment Team) 1993, Lee et al. 2004, Reeves et al. 2006, Richardson et al. 2012). In the Pacific Northwest region of North America, widespread implementation of riparian regulations did not occur until the late 20th century. By that time, most riparian forests had been harvested once (e.g. FEMAT 1993, British Columbia Ministry of Forests 1995). Therefore, most streamside forests today are still in the early stages of stand development. Forest development processes occur over long time scales, so the recovery of riparian forests will be an important consideration in stream ecosystems for decades and centuries to come. A number of investigators have explored how stand age/development affect key riparian functions including stream wood loading (Hedman et al. 1996, Benda et al. 2002, Warren et al. 2009), stream geomorphology (Fetherston et al. 1995), and stream nutrient processing (Valett et al. 2002, McClain et al. 2003, Cairns and Lajtha 2005). We focused on how stand development in the riparian forest affects stream light dynamics.

Light is an important driver of chemical, physical, and biological processes in streams. It is essential for stream primary production (Gregory 1980, Julian et al. 2011) and is a key component of stream thermal budgets (Caissie 2006, Moore et al. 2006). When light flux to streams is low, such as beneath closed riparian canopies, primary production is often low, and secondary production in the system depends largely on terrestrially-derived (allochthonous) C sources (leaves, needles, invertebrates) (Fisher and Likens 1973, Wallace et al. 1999). Therefore, reduced canopy cover and greater light fluxes can lead to elevated rates of in-stream primary production (Gregory 1980, Bilby and Bisson 1992, Hill et al. 1995, Clapcott and Barmuta 2010), nutrient demand (Sabater et al. 2000, Warren et al. 2016a), and autochthonous (produced in-stream) C contributions to stream food webs (McCutchan and Lewis 2002, Lau et al. 2009, Wootton 2012). Increased primary production commonly is accompanied by increased reach-scale invertebrate biomass (Stone and Wallace 1998) and enhanced invertebrate predator abundance (Aho 1976, Murphy and Hall 1981, Bilby and Bisson 1992, Wootton 2012). Drastic increases in light after canopy removal elevate stream temperatures (reviewed by Moore et al. 2006), but the magnitude and duration of temperature changes are influenced by local conditions and geomorphology (Johnson 2004, Pollock et al. 2009). Increased temperatures can negatively affect thermally sensitive species, and management of riparian shading has been a focus in assessments of stream warming (Groom et al. 2011). Considerable research has been done on the effects of canopy removal, but changes in light associated with recovery may have greater collective effects on streams than harvest given the long-term dynamics of stand regeneration.

Stand development and successional processes can influence riparian canopy structure and stream light availability (Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2016b). In riparian zones, fluvial disturbances and hydrologic conditions (e.g., soil moisture) often lead to forest communities and overall successional trajectories that differ from upland forests (Decamps et al. 1988, Cordes et al. 1997, Van Pelt et al. 2006). However, in small streams, differences in vegetation may be apparent only directly adjacent to streams (Villarin et al. 2009) where stand development processes in the upland and riparian zone interact to influence canopy structure and stream light over time. For example, in Douglas fir-dominated regions of the Pacific Northwest (PNW), deciduous alder (*Alnus* spp.) commonly becomes established directly adjacent to streams after riparian harvest and other disturbances. These alder stands can provide the majority of stream shade during summer (Summers 1982) until senescence shifts the canopy to upland coniferous species 40 to 60 y post-harvest (Van Pelt et al. 2006). Conceptual models of stream light following riparian harvest produced for the PNW region predict that light will decrease to preharvest levels within 25 y and then remain at minimal levels until late in stand development (>100 y) when canopy gaps increase insolation (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009).

This trajectory may be common in PNW forests, stands can develop along alternative trajectories and these alternative trajectories can alter the temporal dynamics of stream light (Warren et al. 2016b). For example, in the PNW, fluvial disturbances (Johnson and Jones 2000) and biological disturbance agents such as beavers (Naiman et al. 1988) can limit canopy closure and establish new cohorts of trees. Alternatively, lack of conifer recruitment or the establishment of shrub species may result in different successional trajectories (Henderson 1978, Minore and Weatherly 1994, Hibbs and Giordano 1996). Empirical data evaluating stream light as it relates to stand age and stage of development are critically needed to assess the long-term influences of riparian forest stand removal on associated biological and physical characteristics of the system.

We used 2 approaches to evaluate relationships between riparian forest stand age and stream light availability in Douglas fir-dominated forests of the PNW. First, we quantified light and canopy cover throughout a 4th-order stream network that encompasses reaches bordered by old-growth (>300 y old) and mid-successional (50–60 y old) riparian forests. The goals of this sampling effort were to evaluate: 1) characteristics of old-growth light regimes throughout the stream network, and 2) whether canopy openness and light (photosynthetically active radiation [PAR]) differed between stream sections flowing through harvested units and old-growth forest. We hypothesized that stream light and canopy openness would increase with stream size and that mean light and canopy openness would be lower in harvest units relative to upstream and downstream old-growth sections. Second, we evaluated canopy cover across a wider range of stand ages by conducting a space-for-time analysis based on a literature review of published studies in which both stand age and canopy cover over the stream were reported. We expected mean canopy openness to decline sharply within 20 y post-harvest, remain low in stands 30 to 100 y old, and then increase in later stages of stand development (>100 y), reflecting proposed conceptual models for this region (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009). We predicted that most data points would follow this trend, but we expected outliers that reflected alternative stand-development trajectories (Warren et al. 2016b). We predicted that both approaches would show variability in canopy openness (and light) that would be lower in streams in mid-successional than in old-growth forests.

Methods

Study system

We collected data for the longitudinal stream light assessment at the HJ Andrews Experimental Forest (HJA) in the Cascade Mountains, Oregon, USA. This region has a Mediterranean climate (wet, cool winters and warm, dry summers). We sampled ~11.5 km of stream length in the McRae Creek basin, a tributary to Lookout Creek, during summer low-flow conditions. This network included 8 km of the 4th-order (Strahler 1957) mainstem McRae Creek, ~3 km of a 3rd-order unnamed tributary on the west side of McRae Creek (MCTW), and 500 m of a 2nd-order unnamed tributary on the east side of McRae Creek (MCTE) (Figure 2.1). We sampled MCTE in 2014 and McRae Creek and MCTW in 2015.

The McRae basin is mostly old-growth forest mixed with small-patch clear-cuts (<30 ha), 7 of which were included in our sampling area. All 7 harvest units were cut within a relatively short time frame 50 to 60 y before our study (Table 2.1). Clearing on both stream banks occurred in units L503 and L504, whereas clearing on only 1 bank occurred in all other units (Figure 2.1). Trees were harvested to the stream bank with no riparian buffers, but in unit L505, a limited number of trees was left for bank stability because of steep slopes. Except unit L503, which was left to regenerate naturally, units were planted with Douglas fir (*Pseudotsuga menziesii*) within 3 y of harvest, a practice typical of managed forests across Oregon and Washington at the time.

We characterized broad patterns of PAR and canopy openness with regard to landscape position by dividing McRae Creek and MCTW into 2 reaches based on distinctive geomorphic and network features that coincided with differences in gradient and bankfull width. The lower reach of McRae Creek (4100 m long) began on the downstream end at the confluence with Lookout Creek and extended upstream to a series of steep waterfalls just downstream of harvest unit L504. The waterfalls prevented assessment of a 200-m reach directly downstream of unit L504. The upper reach of McRae Creek (2900 m long) began just upstream of the waterfall section and extended to a distance of 7200 m. The waterfall section marked a change in gradient, and the upstream section was steeper and more confined than the downstream reach. At MCTW, the lower reach (950 m long) began at the confluence of MCTW and McRae Creek and continued upstream to unit L503, which was the only harvest unit in MCTW and a logical place to split the stream. The upper reach of MCTW (1250 m long) began at the upstream edge of unit L503 and ended at the crossing with road 320. We surveyed only one 500-m reach in MCTE.

Stream-network light dynamics

To evaluate relationships between channel and riparian characteristics and stream light, we quantified stream bankfull width, wetted width, canopy openness, % red alder (*Alnus rubra*) and estimated PAR. At McRae Creek and MCTW, we collected these data at 25-m intervals. At MCTE, we estimated PAR at 5-m intervals (in concurrence with a study by DRW, unpublished data) and canopy openness at 10-m intervals in the 120-m old-growth section and 120 m of the 380-m second-growth section. We measured all other variables at the standard 25-m intervals.

Canopy openness was quantified by 2 individuals with a convex spherical densiometer (Model A; Forestry Suppliers, Jackson, Mississippi) and reported values are the means of 4 measurements, one in each cardinal direction. We evaluated user bias before the network surveys to ensure that estimates by the 2 individuals were comparable (<5%) at each point. Small light gaps, such as those between branches and leaves, may not be detected as well with a spherical densiometer as with other methods (e.g., hemispherical photos) (Julian et al. 2008a). Therefore, our sampling was focused on detecting relatively large canopy gaps (>1 m).

We assessed light flux to the stream bottom every 25 m throughout the sampling network with the aid of photo-degrading fluorescein dye (Bechtold et al. 2012). Fluorescein degrades at a predictable rate when exposed to light and can be used to quantify relative light availability in streams (Bechtold et al. 2012, Warren et al. 2013). We mixed concentrated fluorescein with deionized water to a concentration of 400 μg/L and added 36 g/L of commercial aquarium salt (Instant Ocean) to buffer the solution. We filled 3.7-mL clear glass vials with the premixed solution and used zip ties to attach 3 vials to a single wire flag at each sampling location. Every 4th flag had a vial wrapped in aluminum foil to serve as a ‘field-dark’ control to correct for drift in concentration. In McRae Creek and MCTW, we placed fluorescein flags (n = 360) over two 2-

d periods in early summer 2015 (6–7 July and 8–9 July). In MCTE, we placed fluorescein flags (n = 101) in early summer 2014 (30 June–1 July). All sampling days were sunny and cloudless. We placed the vials in the stream between 0500 and 0800 h, when light levels reaching the stream were still very low, and retrieved them at approximately the same time after 24 h. We placed flags with fluorescein vials attached in the thalweg and secured them by placing a small rock on top of the flag.

Upon retrieval, we returned the flags to the laboratory and allowed them to warm to room temperature because fluorescence readings are affected by solution temperature (Bechtold et al. 2012). We measured fluorescence with an AquaFluor handheld fluorometer (Turner Designs, San Jose, California). Fluorescence readings for each flag/location were averaged across the 3 replicates and subtracted from the mean fluorescence value of the field-dark controls to produce a single, corrected photodegradation value for each location. We noted in the field those vials covered by leaves or rocks and removed them from analysis.

We used Odyssey PAR sensors (Dataflow Systems, Christchurch, New Zealand) to collect PAR data needed build a relationship between fluorescein-dye photodegradation and measured PAR for the 2 field seasons (2014–2015). We attached PAR sensors to rebar pounded into the stream substrate within 0.25 m of a set of flags containing fluorescein vials and left them in place for 24 h to measure total daily accumulated PAR. Total daily accumulated PAR (mol $m^{-2} d^{-1}$) was compared to mean fluorescein decay for each location at 56 locations and a curve was fitted using a 3-factor polynomial function (Figure A2.1). Measured PAR and fluorescein-converted PAR estimates were calculated as % full sun based on accumulated PAR measured at the HJ Andrews CENMET metrological station. Flags with attached fluorescein-filled vials were situated directly on the stream bottom, whereas PAR sensors were situated directly above the water surface. Water depth, water clarity, and reflection from the water surface can affect light penetration in the water column (Julian et al. 2008b). However, during mid-summer, water in the study streams was clear with little turbidity and all fluorescein vials were in shallow water (0.1–0.25 m) where turbulence was minimal. Julian et al. (2008a) found that ~10% of PAR was reflected by water in a stream. Thus, PAR reaching the stream bottom (and fluorescein vials) probably was reduced even in clear, shallow water. Nevertheless, we found a strong relationship between PAR and fluorescein decay (Figure A2.1).

We visually estimated and scored the abundance of alder as % riparian trees within 10 m upstream and downstream of the sampling location and 5 m into the riparian zone on each bank based on the following categories: 0 = not present, 1 = 1–20, 2 = 20–40, 3 = 40–60, 4 = 60–80, and 5 = >80% (Figure A2.2).

We used 2 approaches to analyze PAR and canopy openness data. First, we characterized PAR and canopy openness in each of the 5 stream sections (Lower McRae, Upper McRae, Lower MCTW, Upper MCTW, and MCTE) and evaluated trends based on channel characteristics. Second, we compared PAR and canopy openness values in each harvest unit to values in old-growth reaches directly upstream and downstream of each unit. We used the same linear distance in upstream and downstream old-growth reaches as the linear distance in the harvest unit (e.g., if the harvest unit bordered 300 m of stream, we used the 300 m downstream and 300 m upstream of the unit) unless the distance overlapped with another harvest unit, in which case we used the maximum length of the old-growth reach. We examined data in each reach for normality and ln(*x*)-transformed data if needed. We used a *t*-test in R (version 3.1.3; R Project for Statistical Computing, Vienna, Austria) for each comparison. We evaluated variance by examining the standard deviations (SDs) in PAR and canopy cover in each harvest unit and associated upstream and downstream sections and used *F*-tests of homogeneity of variance to compare SDs between reaches. We used linear regression to evaluate the relationships between PAR and canopy openness and PAR/canopy openness and bankfull width.

Literature review of canopy cover-to-riparian forest stand age relationships

We used the Web of Science® (Thomson Reutter, Philadelphia, Pennsylvania) to initiate our literature review with the goal of identifying studies that contained estimates of riparian forest stand age (or mean age of dominant canopy trees) and canopy cover over the stream in the Pacific Northwest of North America. Forest development and recovery from harvest is a process occurring across much of North America, but the PNW is the best place to conduct this analysis because of the large number of studies in which influences of forest practices on stream ecosystems were evaluated.

To account for potential stream size and forest community effects, we restricted our search to studies pertaining to small mountain streams (<10 m bankfull) of the Coast and Cascade mountain ranges of Oregon, Washington, and British Columbia where the dominant tree species is Douglas fir. We conducted 3 primary searches based on the following criteria: 1) stream, canopy, Oregon; 2) stream, canopy, Washington; and 3) stream, canopy, British Columbia. We searched the methods, results, and appendices of the resultant 201 papers to find studies in which stand age and an estimate of canopy cover were both reported. We excluded sites where buffer strips were present because buffer strips can affect stream light (Kiffney et al. 2003). When means were reported, we searched citations in those papers and other established references (including appendices and theses) to see whether data were available on individual streams rather than in aggregate. If no data on the individual streams could be found, we used the reported mean values (Table A2.1). If a relatively narrow range of stand ages were provided for the mean estimate of cover, we used the average of the range of ages reported.

We focused on canopy openness as a proxy for stream light (per Lamberti and Steinman 1997) because direct quantification of stream light flux (e.g., use of PAR sensors) is relatively uncommon, and we could not find enough studies with light and stand age to build a comprehensive synthesis. Canopy cover is quantified much more regularly in stream studies, and canopy architecture strongly influences stream shading and, by proxy, PAR exposure (McTammany et al. 2007). The most common method used to characterize canopy cover in streams is a spherical densiometer. Other methods to estimate cover include hemispherical photography, the line-intercept method, and the use of a moosehorn (a gridded mirror aimed upwards but with a narrower view than a densiometer). In a comparison of these methods, hemispherical photography and densiometer estimates were similar but moosehorn and line-intercept methods were substantially different from densiometer and hemispherical photography estimates, especially when cover was limited (Fiala et al. 2006). Therefore, we included only studies in which spherical densiometer estimates or hemispherical photography was used and excluded studies in which the moosehorn (e.g., Romero et al. 2005) or line-intercept method was used (e.g., De Groot et al. 2007).

We plotted canopy openness vs stand age of the riparian forest as reported in each study. We placed all studies characterized as old-growth or late-successional into a single group (old-growth; >300 y) because the time since a stand-replacing event or the average age of dominant trees is difficult to measure and usually is not reported for forests >200 y old. Canopy closure rates and stand development processes may differ among Douglas fir-dominated regions of the Coast Range and Cascade Range (Summers 1982), so we classified each point as either Coast or Cascade Range. We grouped studies from the Coast Mountains, British Columbia, with those from the Coast Range. We fit a negative exponential decay curve to data from 0 to 100 y to examine rates of canopy closure and to estimate when canopy openness values returned to preharvest conditions (Sigmaplot, version 13.0.0; SYSTAT Software, San Jose, California).

Results

Stream network light dynamics

Within the McRae network, streams bordered by old-growth riparian forests exhibited a wide range of PAR and canopy openness values (Figs 2A, B, 3A–D). Individual measurements of PAR ranged from 0.6 to 26.3 mol m^{-2} d^{-1} (1–58% of full sun values) and canopy openness values ranged from 0 to 69%. Across all sites, canopy openness explained 36% of the variation in PAR estimates ($n = 377$). When streams were evaluated separately, canopy openness explained more variation of PAR estimates in McRae ($R^2 = 0.44$, $n = 266$) than in MCTW ($R^2 = 0.23$, $n = 90$) and MCTE ($R^2 = 0.02$, $n = 21$).

When the stream network was broken up into 5 larger sections, mean PAR in streams bordered by old-growth forest was greatest in the lower section of McRae (9.9 mol m^{-2} d^{-1}), followed by the upper section of McRae (6.4 mol m^{-2} d^{-1}), the lower section of MCTW (4.7 mol m^{-2} d^{-1}), MCTE (3.3 mol m^{-2} d^{-1}), and the upper section of MCTW (2.0 mol m^{-2} d^{-1}) (Table 2.2). Mean canopy openness was greatest in lower McRae (22.4%), followed by upper McRae (18.4%), lower MCTW (10.2%), MCTE (10.1%), and upper MCTW (6.5%) (Table 2.2). The larger mainstem McRae had greater mean PAR and canopy openness than the smaller tributaries, but bankfull width explained <5% of the variation in PAR and canopy openness values across all data points within the stream network.

Mean estimated PAR was lower in the harvest unit than in adjacent upstream and downstream reaches bordered by old-growth forests for all comparisons ($n = 14$), but only 6 comparisons were significant at $p < 0.05$ (Figure 2.4A). Estimated PAR was, on average, 2.78 mol m^{-2} d^{-1} lower in harvest units than in upstream and downstream old-growth sections (range: 0.55–6.16 mol m^{-2} d^{-1}). Thus, PAR values in old-growth reaches averaged 1.70× greater than PAR values in adjacent harvest units (range: 1.14–2.54× greater). The contrast between harvest units and adjacent old-growth sections was most pronounced when harvesting occurred on both banks (e.g., L503, L504) or when a dense and uniform alder canopy was established (e.g., L602). The SD of PAR estimates was lower in the harvest unit in 13 of 14 comparisons (Figure 2.4A), but only 5 of these comparisons had $p < 0.05$ (comparison of variances F-test).

Mean differences in canopy openness were largely comparable to the PAR results. Openness was lower in the harvest unit in 12 of 14 comparisons and 6 comparisons were significantly different ($p < 0.05$; Figure 2.4B). Percent canopy openness was 6.1% greater on average (range: –2.2–14.5%) in old-growth sections than in adjacent harvest units. The SD of canopy openness estimates was lower in harvest units in 8 of 14 comparisons and 5 of these had $p < 0.05$ (comparisons of variances F-test).

The relationship between canopy openness and PAR was much stronger at the reach-scale than at individual locations. Mean canopy openness explained 78% of the variation in mean PAR estimates for the 22 reaches used to evaluate differences in canopy openness and PAR between harvest units and old-growth forests.

Literature review of canopy cover-to-riparian forest stand age relationships

Despite an extensive literature search, we found relatively few studies in which authors reported both stand age and canopy openness and that met our other criteria (e.g., Douglas fir dominated, no riparian buffers, densiometer or hemispherical photography). We identified 10 studies encompassing a total of 92 individual points: 54 from the Coast Range or Coast

Mountains and 37 from the Cascade Range. Of these, 72 sites had been previously harvested and ranged in age from 0 to 100 y, 2 sites were 100 to 300 y old, and 17 sites were old-growth where a stand-replacing disturbance had not occurred within 300 y.

Across the full data set, maximum canopy openness occurred shortly after a stand-replacing event but rapidly declined over a 40-y period, eventually reaching minimum levels between 30 and 100 y (Figure 2.5A). Based on a fitted negative exponential decay curve, canopy openness reached preharvest, old-growth levels (see below) ~28 y after harvest (Figure 2.5B). Canopy openness over streams in old-growth forests averaged 18.0% but was highly variable and ranged from 3.4 to 34.0% (SD = 7.9). Mean canopy openness in stands between 30 and 100 y old was 8.7% and ranged from 1.2 to 32.0% (SD = 5.7), but canopy openness was >15% at 1 site (SD = 3.7 with outlier removed). Variance between old-growth and stands 30 to 100 y old were significantly different when this outlier was removed (*F*-test; *p* = 0.001) but not when the outlier was included (F-test, *p* = 0.14). Data on stream size, aspect, elevation and gradient, were not available for all studies, so we could not examine relationships between these covariates and changes in canopy cover over time Figure A2.2).

Discussion

Stand recovery from timber harvest is widespread in stream riparian zones across North America. Our results indicate that stream light regimes are affected by both initial canopy removal and recovery. Light regimes continue to shift as conditions change through stand development and forest successional processes. Network sampling indicated that stream light availability and canopy openness were lower in harvest units where the forest ages ranged from 50 to 60 y than in old-growth forests (>300 y). These results are consistent with those of other studies in which investigators found greater mean canopy openness in streams of late-successional forests than in second-growth forests (Murphy and Hall 1981, Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2013). We observed this difference in light regimes even in the 5 harvest units where the clearing had been done on only 1 stream bank, but the contrast in light between harvest units and adjacent stream reaches with old-growth riparian forests was generally greater in units where harvesting occurred on both stream banks. Data from the literature review were relatively consistent with conceptual models of summer light availability over time for Douglas fir-dominated forests of the PNW region (Sedell and Swanson 1984, Gregory et al. 1987). Canopy openness values decreased rapidly after harvest, reflecting a negative exponential decay curve, and returned to preharvest (old-growth) levels after ~30 y. Between 30 and100 y later, mean canopy openness was less than the mean values for streams bordered by forests where stand-replacing disturbances had been absent for ≥300 y. Consistent with other studies evaluating light in streams bordered by second-growth vs old-growth riparian forests (Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2013), canopy openness values were far less variable along the stream when stands were between 30 and 100 y old compared to streams with old-growth riparian forests. Data were limited for stands between 100 and 300 y old, and we were not able to assess canopy patterns for this time frame.

The type of plant community that regenerates after a stand-replacing event can affect how forests influence stream light (Warren et al. 2016b). In the western PNW, red alder commonly occupies riparian zones after harvest and can form a closed canopy relatively quickly—within 12 y for the Coast Range and 25 y for the Cascade Range (Summers 1982). However, alder is a short-lived species, and initial cohorts can senesce after 40 to 60 y, giving way to a coniferous overstory (Van Pelt et al. 2006). Gregory et al. (1987) suggested that light may briefly increase during this transition before canopy closure by coniferous species. Harvested units in the McRae basin were between 50 and 60 y old and, consistent with the prediction of a short period of increased light following alder senescence, we observed signs of alder mortality and associated canopy gaps in some units. However, results from our literature review, in which alder was a dominant canopy species in most early stands, did not indicate any period of elevated canopy openness between 30 and 100 y. Even within the small geographic extent of the McRae Creek basin, alder was not evenly distributed. In the lower sections of the McRae network, alder was typically more abundant in harvest units but still common in old-growth sections. On the other hand, alder was nearly absent from the 3-km upstream section of mainstem McRae Creek above 850 m in elevation. Here, deciduous vine maple (*Acer circinatum*) provided substantial shade in some sections, but overstory canopies were dominated by conifers. The lower reach of McRae Creek is alluvial and less steep than the more confined upper McRae, which may provide more favorable hydrologic and disturbance conditions for alder establishment and maintenance (Villarin et al. 2009). Alternatively, the loss of red alder may be a consequence of elevation change because red alder is typically more common at elevations <750 m (Harrington 2006). These differences in vegetative communities may, in part, explain why bankfull width explained little of the variation in light or canopy cover across the McRae Creek network.

Canopy openness explained far less of the variation in PAR at a given single location than when mean values were compared at the reach scale. This result is consistent with findings by Warren et al. (2013) and suggests that stream light availability is not well correlated with direct overhead canopy cover at a single point. The angle of the sun may cause an offset in light penetration to the understory such that the gap responsible for an local increase in light may not be within the field of view for a spherical densiometer. However, gaps and associated areas of elevated light are more likely to be surveyed during multiple measurements along the length of a reach. Therefore, mean PAR and mean canopy openness are likely to be more strongly correlated at the reach scale than at individual locations. Other factors, such as stream orientation and topographic shading, also may affect relationships between canopy cover and PAR. East–west-oriented streams receive more shading from trees on the south than on the north stream bank because of the sun angle (Julian et al. 2008a). In McRae Creek and MCTW (more north–west oriented streams), canopy openness explained much more of the variation in PAR than in MCTE (east–west oriented), indicating that canopy openness in east–west streams may not be a good metric of light availability. Topographic shading can influence stream light availability substantially in areas with steep valley walls or in areas with minimal shading from the riparian forest (Yard et al. 2005), but we do not think it was a dominant control on light in streams in our study. Hillslopes were generally not steep enough to provide topographical shade except for very early and late in the day when the sun is at a lower angle. Moreover, streams were densely forested and, at these time periods, vegetation typically already shaded streams.

The River Continuum Concept hypothesizes that stream light availability follows an orderly pattern of increasing light with distance downstream as widening channels create larger canopy gaps (Vannote et al. 1980). In our network study, results were consistent with this hypothesis when we evaluated the smallest headwaters down to the largest section of the mainstem. Across this range in stream size, mean PAR and canopy openness in old-growth forests were greater in the larger mainstem than in the narrower tributaries, and in the mainstem, canopy openness and PAR were greater in the larger downstream section than in the narrower upstream section. However, at individual locations across the stream network, bankfull width explained very little (<5%) of the variation in PAR and canopy openness. This finding may be attributable to the high variability in PAR and canopy openness values in all old-growth sections of the stream network. Even the widest stream sections (lower McRae = 9.6 m on average) were narrow enough to allow canopies to close entirely over the stream. At larger spatial scales, increasing channel width will inevitably be a dominant factor influencing light flux to the stream surface, but water depth and water clarity may reduce light reaching the stream bottom (Vannote et al. 1980, Julian et al. 2008a, b).

Our data show that changes in canopy openness associated with canopy closure are large but differences in stream canopy openness and light between previously harvested riparian forests and old-growth forests are relatively small. Most investigators who studied the influence of light on stream biotic processes have evaluated large increases in light associated with clear-cut harvesting. Comparatively few investigators have evaluated small changes in light, but their results suggest these changes can be biologically significant. For example, in a field manipulation (Kiffney et al. 2003) and an experimental study in streamside channels (Kiffney et al. 2004), small increases in light (<25% full sun) resulted in greater periphyton accrual and biomass of some invertebrates. Quinn et al. (1997) observed increasing algal standing stocks and invertebrate biomass when light increased from 2 to 10% ambient sun and again when light increased from 10 to 40%. These studies suggest that small changes in mean canopy cover can alter biological processes, but they are few in number and geographic extent and more research is needed in this area.

Stream light is typically more heterogeneous in old-growth forests than in younger stands because of spatially variable canopy gaps (Stovall et al. 2009, Warren et al. 2013). In our network sampling, the SD of PAR estimates was greater in most old-growth sections than in harvest units, and this difference was most pronounced where harvesting occurred on both banks or where alder formed a closed canopy (e.g., L602). Both Stovall et al. (2009) and Warren et al.

(2016a) found significant relationships between local light availability and local periphyton chlorophyll *a* accrual in streams in late-successional forests. Warren et al. (2016a) found that the relationship between light and chlorophyll *a* accrual was much steeper when substrates were augmented with nutrients than where they were not augmented and that spatial variability in light created spatial variability in nutrient limitation and ultimately reach-scale colimitation. However, the influences of spatially variable light on local (patch-scale) and reach-scale primary production, invertebrate communities, temperature, and other ecosystem processes remains largely unexplored (but see Julian et al. 2008b, 2011).

The overall trend in canopy cover from our literature review is consistent with conceptual models for this region that predict temporal changes in stream light (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009), but our results should be interpreted with some caution. First, most studies were from 4 research forests; the HJ Andrews Experimental Forest, the Hinkle Creek watershed study, the Alsea watershed study, and the Malcolm Knapp Forest. Trajectories of canopy cover over time did not appear to differ among these forests or between Coastal and Cascade Ranges, but we acknowledge that a more spatially balanced distribution of sites would provide a more comprehensive evaluation of stream light dynamics. Second, we were not able to quantify how abiotic and biotic disturbances influence stand trajectories. Fluvial disturbances can alter riparian vegetation, limit riparian canopy closure, and establish new cohorts of alder (Johnson and Jones 2000), which would alter timing of alder senescence. In addition, organisms such as beaver (Naiman et al. 1988, Pollock et al. 1995) and insect defoliators (Obedzinski and Shaw 2001) can substantially alter riparian vegetation and, thus, stream light dynamics over time. Last, our literature review showed that canopy openness was greater in old-growth reaches than in reaches bordered by 30- to 100-y-old forests that were clear-cut harvested. However, we had very limited data from streams bordered by stands 100 to 300 y old, which reduced our ability to assess if, and when, a transition to late-successional gap-dynamic structure may occur. A lack of studies from this age range is not surprising given widespread 20th century harvesting (Pan et al. 2011), but given reduced harvest and the establishment of riparian reserves, progression to these ages probably will become more prevalent, warranting further evaluation of light dynamics.

Future conditions may differ substantially from those observed in the last century, and therefore, future developmental trajectories and ultimately stream light also may differ (Warren et al. 2016b). Climate change, in particular, is anticipated to shift tree species distributions (Iverson and Prasad 1998, Hamann and Wang 2006), increase stress related mortality (Allen et al. 2010), alter growth rates and productivity (Pastor and Post 1988), and affect disturbance processes (Overpeck et al. 1990, Dale et al. 2001). For example, climate change is expected to expand the geographic extent of insect pest species that can cause selective morality (Carroll et al. 2004, Paradis et al. 2008, Cudmore et al. 2010, Liang and Fei 2013). As noted by Reilly and Spies (2015), disturbance that removes only a portion of dominant trees can substantially alter developmental trajectories, forest structure, and canopy coverage. Moreover, climate change effects on the frequency, magnitude, and extent of forest disturbance are anticipated to alter forest structure and successional patterns (Dale et al. 2001). The influence of these changes on forest development trajectories, stream light, and light-associated stream processes will be an important area of research as we evaluate stream responses to climate change.

Conclusions

Many riparian areas that historically were old-growth forests are currently dominated by younger stands because of landuse legacies (Pan et al. 2011), and we suggest that as a result, the distribution of stream light availability has shifted. Most PNW second-growth forests are <100 y old (Pan et al. 2011), and our results indicate that streams adjacent to these forests probably are exhibiting either: 1) decreasing light availability as canopies close, or 2) minimum light levels associated with closed canopies and stands in the stem-exclusion phase of development. Stand development is an ongoing process and successional processes may be reset by natural or anthropogenic stand replacement events. In the absence of new stand-replacing disturbances, these forests probably will develop greater complexity and increased stream light as dynamic canopy gaps form. Overall, understanding the interactions among riparian forest stand development, canopy cover, and stream light will enhance our understanding of stream ecosystems and how they may change in the future.

Acknowledgements

Author contributions: MJK contributed to the initial study design and field work, and wrote most of the manuscript. DRW contributed to the initial study design, helped frame ideas, produced some of the figures, and wrote some of the manuscript. PMK helped frame and edit the manuscript.

We thank Brian VerWey, Emily Heaston, Graham Takacs, Gavin Jones, and Lauren Still for their field sampling efforts. Comments from Michael Pollock, Ivan Arismendi, Jonathan Armstrong, and 2 anonymous reviewers substantially improved this manuscript. Results from this study were presented at the 2015 Society for Freshwater Science meeting by MJK and an award for this presentation has covered publishing costs in *FWS,* which we greatly appreciate. Summer 2015 fieldwork was supported by NSF DEB 1547628 awarded to DRW. Facilities and logistical support at the HJ Andrews Experimental Forest were provided through funding from the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), from the US Forest Service Pacific Northwest Research Station, and from Oregon State University.

Literature cited

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. MS thesis. Oregon State University, Corvallis, Oregon.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Bechtold, H. A., E. J. Rosi-Marshall, D. R. Warren, and J. J. Cole. 2012. A practical method for measuring integrated solar radiation reaching streambeds using photodegrading dyes. Freshwater Science 31:1070–1077.

Benda, L. E., P. Bigelow, and T. M. Worsley. 2002. Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A. Canadian Journal of Forest Research 32:1460–1477.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

British Columbia Ministry of Forests. 1995. Riparian management area guidebook. British Columbia, Ministry of Forests, Victoria, British Columbia. (Available from: https://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/riparian/rip-toc.htm)

Cairns, M. A., and K. Lajtha. 2005. Effects of succession on nitrogen export in the west-central Cascades, Oregon. Ecosystems 8:583–601.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Carroll, A. L., S. W. Taylor, J. Regniere, and L. Safranyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223–232 *in* T.L. Shore, J.E Brooks and J.E. Stone (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. Natural Resources Canada, Canadian Forest Service, and Pacific Forestry Centre. Victoria, BC.

Clapcott, J. E., and L. A. Barmuta. 2010. Forest clearance increases metabolism and organic matter processes in small headwater streams. Journal of the North American Benthological Society 29:546–561.

Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography 24:675–695.

Cudmore, T. J., N. Björklund, A. L. Carroll, and B. Staffan Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. Journal of Applied Ecology 47:1036–1043.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. H.

Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and M. B. Wotton. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Decamps, H., M. Fortune, F. Gazelle, and G. Pautou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology 1:163–173.

De Groot, J. D., S. G. Hinch, and J. S. Richardson. 2007. Effects of logging second-growth forests on headwater populations of coastal cutthroat trout: a 6-year, multistream, before-and-after field experiment. Transactions of the American Fisheries Society 136:211–226.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Forest Ecosystem Management Assessment Team, Portland, Oregon. (Available from: http://www.blm.gov/or/plans/nwfpnepa/FEMAT-1993/1993_%20FEMAT_Report.pdf)

Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology 13:133–144.

Fiala, A. C. S., S. L. Garman, and A. N. Gray. 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232:188–197.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. PhD Dissertation, Oregon State University, Corvallis, Oregon.

Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influences of forest practices on aquatic production. Pages 233–255 *in* E. O. Salo and T. W. Cundy (editors). Streamside Management: Forestry and Fishery Interactions. University of Washington, Institute of Forest Resources, Seattle, Washington.

Groom, J. D., L. Dent, L. J. Madsen, and J. Fleuret. 2011. Response of western Oregon (USA) stream temperatures to contemporary forest management. Forest Ecology and Management 262:1618–1629.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

Harrington, C. 2006. Biology and ecology of red alder. Red alder—a state of knowledge. General Technical Report PNW-GTR-669. US Department of Agriculture, Forest Service, Portland, Oregon.

Hedman, C. W., D. H. Van Lear, and W. T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26:1218–1227.

Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. Northwest Science 70:213–222.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465–485.

Johnson, S. L. 2004. Factors influencing stream temperatures in small streams : substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61:913–923.

Johnson, S. L., and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57:30–39.

Julian, J. P., M. W. Doyle, and E. H. Stanley. 2008a. Empirical modeling of light availability in rivers. Journal of Geophysical Research 113.

Julian, J. P., S. Z. Seegert, S. M. Powers, E. H. Stanley, and M. W. Doyle. 2011. Light as a first-order control on ecosystem structure in a temperate stream. Ecohydrology 4:422–432.

Julian, J. P., E. H. Stanley, and M. W. Doyle. 2008b. basin-scale consequences of agricultural land use on benthic light availability and primary production along a sixth-order temperate river. Ecosystems 11:1091–1105.

Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecological Applications 17:852–868.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40:1060–1076.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23:542–555.

Lamberti, G.A., and A.D. Steinman. 1997. Primary production in stream ecosystems. Journal of the North American Benthological Society. 16:95-104.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28:426–439.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165–180.

Liang, L., and S. Fei. 2013. Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change. Climatic Change:1–12.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. a. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

McCutchan, J. H., and W. M. Lewis, Jr. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742–752.

McTammany, M.E., E.F. Benfield, and J.R. Webster. 2007. Recovery of stream ecosystem metabolism from historical agriculture. Journal of the North American Benthological Society. 26:532-545.

Mellina, E., and S. G. Hinch. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Canadian Journal of Forest Research 39:1280–1301.

Minore, D., and H. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. New Forests 8:249–263.

Moore, R. D., D. L. Spittlehouse, and A. Story. 2006. Riparian microclimate and stream temperature response to forest harvesting : a review. Journal of the American Water Resources Association 41:813–834.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.

Obedzinski, R. A., and C. G. Shaw. 2001. Declining woody vegetation in riparian ecosystems of the western United States. Western Journal of Applied Forestry 16:169–181.

Overpeck, J., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbances and vegetation. Nature 343:51–53.

Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–732.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Pastor, J., and W. Post. 1988. Response of northern forests to CO_2-induced climate change. Nature 334:55–58.

Pollock, M. M., T. J. Beechie, M. Liermann, and R. E. Bigley. 2009. Stream temperature relationships to forest harvest in Western Washington. Journal of the American Water Resources Association 45:141–156.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Jones and J. H. Lawton (editors). Linking species and ecosystems, Springer Science and Business Media, Dordrecht, The Netherlands.

Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. New Zealand Journal of Marine and Freshwater Research 31:665–683.

Reeves, G. H., J. E. Williams, K. M. Burnett, and K. Gallo. 2006. The aquatic conservation strategy of the Northwest Forest Plan. Conservation Biology 20:319–329.

Reilly, M. J., and T. A. Spies. 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland northern California. Ecosphere 6:1-27.

Richardson, J. S., R. J. Naiman, and P. A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshwater Science 31:232–238.

Romero, N., R. E. Gresswell, and J. L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797–1807.

Sabater, F., A. Butturini, E. Martí, and I. Muñoz. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. Journal of the North American Benthological Society 19:609–620.

Sedell, J. R., and F. J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. Pages 9–16 *in* W. R. Meehan, T. R. Merrell, and T. A. Hanley (editors). Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska. American Institute of Fisheries Research Biologists, Morehead City, North Carolina.

Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39:151–169.

Stovall, J. P., W. S. Keeton, and C. E. Kraft. 2009. Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams. Canadian Journal of Forest Research 39:2343–2354.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions American Geophysical Union 38:913–920.

Summers, R. P. 1982. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. MS Thesis, Oregon State University, Corvallis, Oregon.

Valett, H. M., C. L. Crenshaw, and P. F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. Ecology 83:2888–2901.

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Van Pelt, R., T. C. O'Keefe, J. J. Latterell, and R. J. Naiman. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecological Monographs 76:277–298.

Villarin, L. A., D. M. Chapin, and J. E. Jones. 2009. Riparian forest structure and succession in second-growth stands of the central Cascade Mountains, Washington, USA. Forest Ecology and Management 257:1375–1385.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of Resource Limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Warren, D. R., S. M. Collins, E. M. Purvis, M. J. Kaylor, and H. A. Bechtold. 2016a. Spatial variability in light yields co-limitation of primary production by both light and nutrients in a forested stream ecosystem. Ecosystems. doi: 10.1007/s10021-016-0024-9

Warren, D. R., W. S. Keeton, H. A. Bechtold, and E. J. Rosi-Marshall. 2013. Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. Aquatic Sciences 75:547–558.

Warren, D. R., W. S. Keeton, P. M. Kiffney, M. J. Kaylor, H. A. Bechtold, and J. Magee. 2016b. changing forests – changing streams: riparian forest stand development and ecosystem function in temperate headwaters. Ecosphere 7:1–19.

Warren, D. R., C. E. Kraft, W. S. Keeton, J. S. Nunery, and G. E. Likens. 2009. Dynamics of wood recruitment in streams of the northeastern US. Forest Ecology and Management 258:804–813.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7:e51839.

Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins, L. E. Stevens, S. Hueftle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. Ecological Modelling 183:157–172.

Table 2.1: Characteristics of harvest units and the stream surveyed in harvest units along McRae Creek, McRae Creek Tributary West (MCTW), and McRae Creek Tributary East (MCTE).

Stream	Harvest unit	Stand age (y)	Banks harvested	Stand area (ha)	Stream bankfull width (m)	Reach distance (m)
McRae	L501	59	1	7.4	10.12	425
	L502	52	1	11.5	8.47	375
	L404	58	1	22.8	8.84	325
	L602	52	1	15.9	7.81	375
	L504	55	2	8.7	8.02	300
	L505	56	1	20.2	6.95	550
MCTW	L503	60	2	18.4	3.6	225
MCTE	L504	55	2	8.7	2.80	375

Table 2.2: Mean (± SD) canopy openness (%) and photosynthetically active radiation (PAR) for streams in old-growth riparian forests of the McRae Creek network (upper and lower reaches of McRae Creek and McRae Creek Tributary West [MCTW], and McRae Creek Tributary East [MCTE]).

Stream	Bankfull width (m)	Gradient (%)	Canopy openness (%)	PAR (mol m^{-2} d^{-1})	*n*
McRae (Lower)	10.0 (3.4)	5.4	22.4 (12.6)	9.9 (6.8)	100
McRae (Upper)	6.6 (2.3)	10.6	18.4 (10.8)	6.4 (5.0)	86
MCTW (Lower)	5.7 (2.7)	9.8	10.2 (7.4)	4.7 (3.3)	38
MCTW (Upper)	3.1 (0.9)	8	6.5 (5.1)	2.0 (1.4)	51
MCTE [a]	3.5 (0.7)	6.8	10.1 (5.9)	3.3 (2.6)	27 (12)

[a] PAR was estimated at 5-m intervals (*n* = 26) whereas canopy openness was measured at 10-m intervals (*n* = 12).

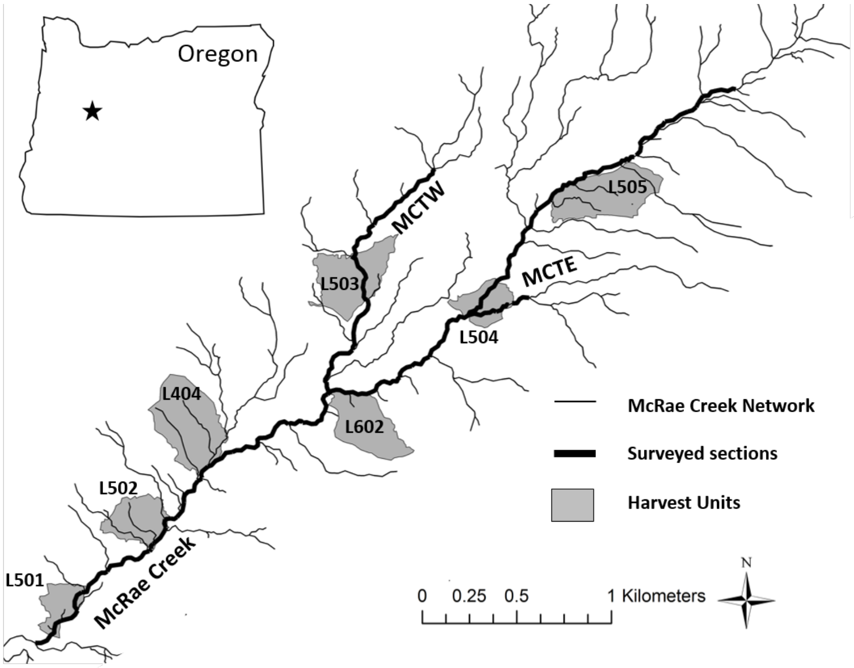

Figure 2.1: Map of the McRae Creek basin and surveyed sections of the stream network (bold) within the HJ Andrews Forest, Oregon, USA. Grey polygons represent previously harvested, now secondary growth forests (Table 2.1). The remainder of the stream network was bordered by unharvested forest.

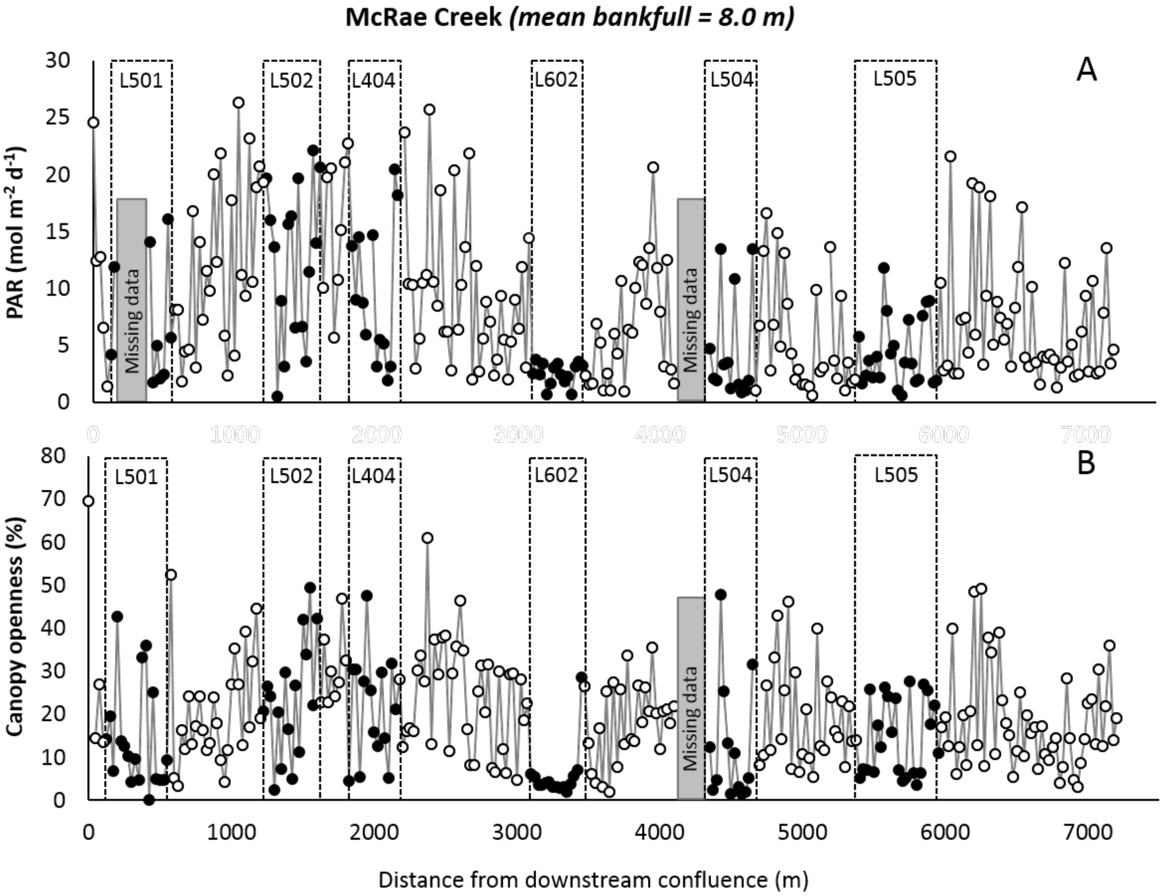

Figure 2.2: Estimated photosynthetically active radiation (PAR) (A) and canopy openness (B) measured every 25 m for 7400 m on McRae Creek. PAR was estimated using photodegrading fluorescein dye. Filled dots represent areas bordered by previously harvested riparian forest on ≥1 stream bank, whereas open dots represent areas bordered by old-growth riparian forest on both banks. Dashed lines indicate harvest units.

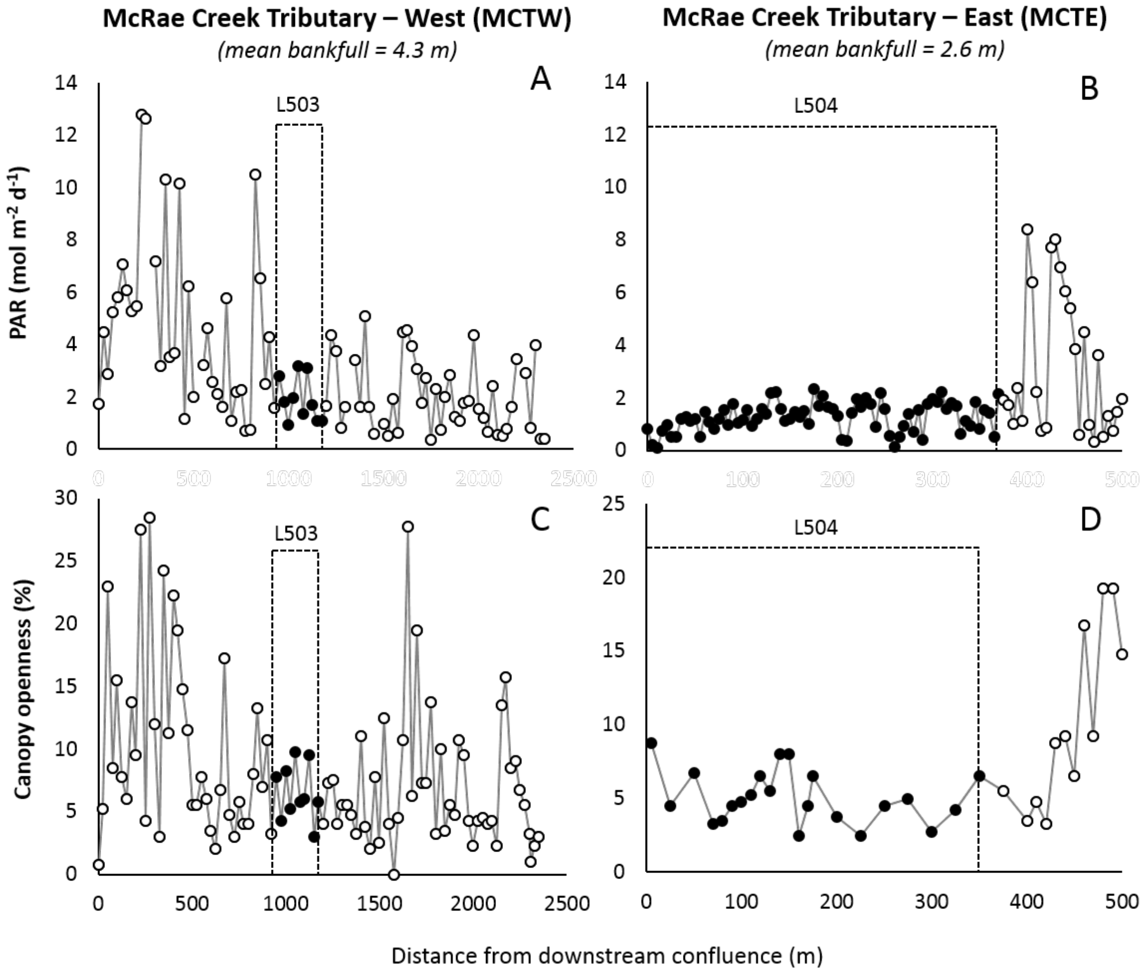

Figure 2.3: Estimated photosynthetically active radiation (PAR) (A, B) and canopy openness (C, D) on McRae Creek Tributary West (MCTW) (A, C) and McRae Creek Tributary East (MCTE) (B, D). PAR was measured every 5 m for MCTE. See Figure 2.2 for explanation of details.

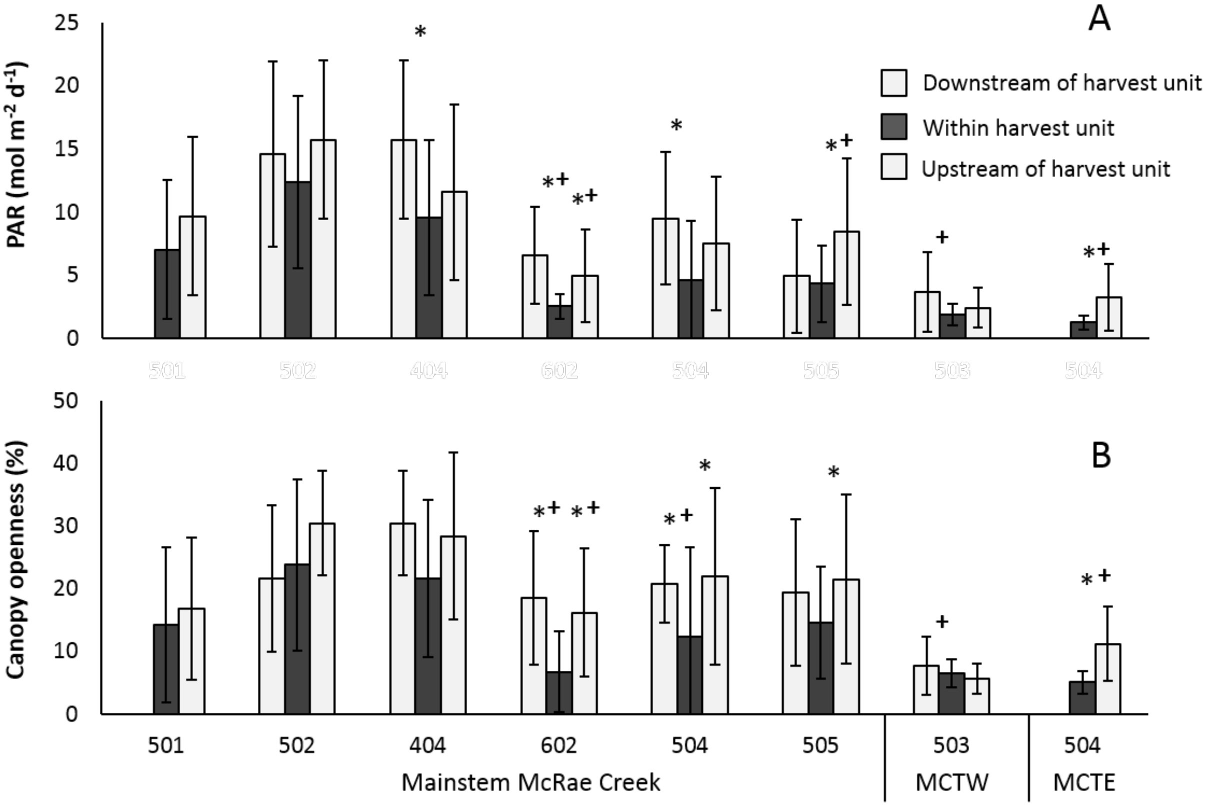

Figure 2.4: Estimated mean (± SD) photosynthetically active radiation (PAR) (A) and canopy openness (B) in harvest units and unharvested upstream and downstream sections of equal linear stream distance along McRae Creek, McRae Creek Tributary West (MCTW), and McRae Creek Tributary East (MCTE). Asterisks indicate significant difference ($p < 0.05$) between harvest unit and unharvested section and plus signs indicate significantly different standard deviations.

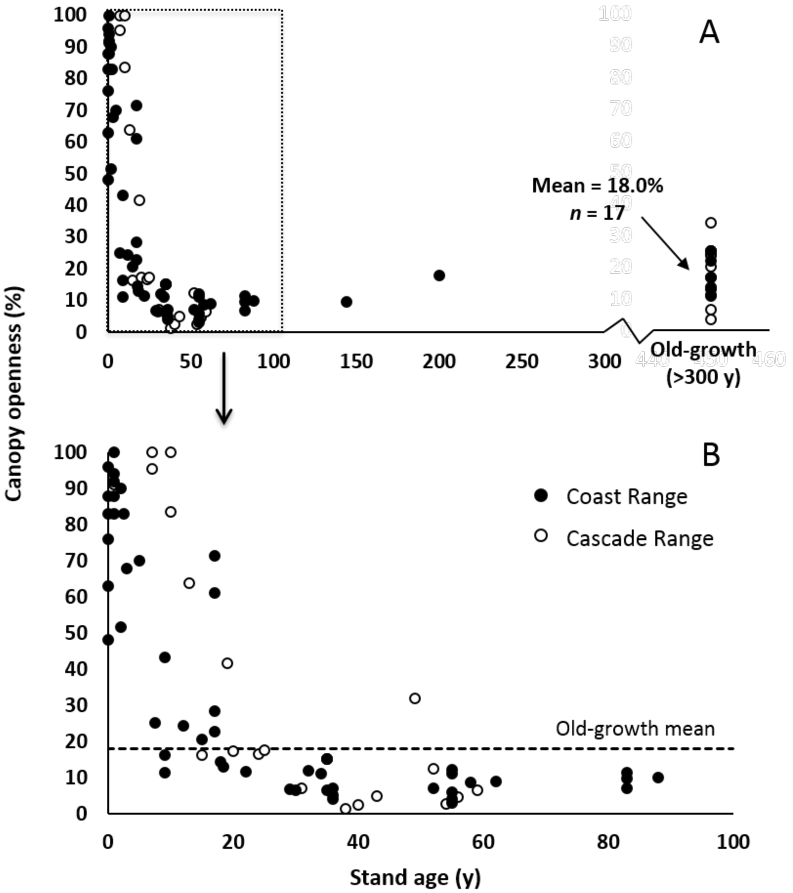

Figure 2.5: Stand age (years since a stand-replacing event) vs canopy openness for 92 sites in Coastal and Cascade Mountains (A) and expanded view of the first 100 y (B). Stands >300 y old were grouped. Coast = sites in the Coast Range, Oregon, and the Coast Mountains, British Columbia.

CHAPTER 3: CITATION INFORMATION

LINKING RIPARIAN SHADE AND THE LEGACIES OF FOREST MANAGEMENT TO FISH AND VERTEBRATE BIOMASS IN FORESTED STREAMS

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Ecosphere, 2017

Volume 8 (6), e01845

CHAPTER 3: LINKING RIPARIAN SHADE AND THE LEGACIES OF FOREST MANAGEMENT TO FISH AND VERTEBRATE BIOMASS IN FORESTED STREAMS

Matthew J. Kaylor and Dana R. Warren

Abstract

Determining the factors that limit abundance and biomass of fish is fundamental to effective fisheries management. In streams, pool availability, cover, and habitat complexity often limit fish—particularly salmonids—and many restoration efforts are directed toward addressing physical habitat factors. However, the availability of prey, and the factors that influence prey abundance, can also influence the abundance, biomass, and growth of fish and other consumers. Both habitat and prey availability can be influenced by characteristics of the riparian forest in headwaters. In this study, we evaluate how variables associated with stream habitat, primary production, and macroinvertebrate biomass account for variability in the biomass of cutthroat trout and total vertebrates (fish and salamanders) across a series of paired stream reaches with contrasting forest structure. Each of nine stream pairs consisted of an old-growth reach and a reach bordered by 40- to 60-yr-old second-growth riparian forest. We evaluated relationships between response and explanatory variables for each forest structure type using correlation analysis, regression analysis, and AICc model comparison analyses. We also conducted correlation and regression analyses on within-stream reach pair differences across the nine study streams. Canopy openness, nitrate concentration, periphyton chlorophyll *a* accrual, total invertebrate biomass, predatory invertebrate biomass, cutthroat trout biomass, and total vertebrate biomass were all positively correlated with each other, while temperature was negatively correlated with biotic variables. Within reach pairs, canopy openness emerged as the strongest correlate with top predators, with differences in canopy openness explaining 84% of

the variation in vertebrate biomass differences in the paired analysis. Other habitat metrics were poorly correlated with invertebrate, fish, and salamander biomass for all analyses. Overall, these results suggest that for the stream reaches surveyed here, resource availability—as regulated through bottom-up, autotrophic pathways—is a dominant control on fish and other consumers. This highlights the importance of food resource limitation for fish and top predators in headwater streams, and illustrates how differences in canopy structure can affect bottom-up drivers of stream food webs.

Introduction

Riparian zones are key areas of exchange between aquatic and terrestrial ecosystems. In many regions, riparian zones are dominated by forests, which exert strong controls on stream habitat and the quantity and quality of food resources at the base of food webs. Riparian vegetation influences stream primary production via controls on stream light (Gregory 1980, Bilby and Bisson 1992, Hill et al. 1995), and terrestrial vegetation in the riparian zone subsidizes stream food webs by contributing nutrients, leaves, needles, and terrestrial invertebrates (Gregory et al. 1991). Riparian vegetation also stabilizes banks, reduces erosion, and provides streams with wood that can create pools and promote habitat heterogeneity (Montgomery et al. 1995). Given their strong influence on streams, differences in the community composition, age distribution, and structural characteristics of riparian forests have the potential to exert control on stream biota.

The availability and quality of stream habitat is commonly identified as a factor limiting abundance of stream fishes (Poff and Huryn 1998, Rosenfeld 2003). For salmonids, pools are key habitat elements that provide deep water cover (Berg et al. 1998) and thermal refuge

(Matthews et al. 1994), and can minimize energetic costs of feeding (Fausch 1984, Rosenfeld and Boss 2001). In forested streams, pool creation, overhead cover, and habitat complexity are often associated with large wood (Beechie and Sibley 1997, Montgomery et al. 1995). The removal of large wood from streams, which was once a common practice associated with timber harvesting (Richardson et al. 2012), has been linked to reductions in pool area and fish abundance (Fausch and Northcote 1992, Mellina and Hinch 2009). In streams lacking large wood and structural complexity, the artificial addition of wood or other structures intended to promote pool formation and habitat complexity often increases salmonid abundance (Roni and Quinn 2001, Roni et al. 2002). Consequently, stream restoration efforts over the past 30 yr often involve large wood additions and physical manipulations to promote pool formation, structural heterogeneity, and habitat complexity, particularly in the Pacific Northwest ecoregion (Naiman et al. 2012). In addition, riparian zones are commonly managed to promote future large wood inputs to streams (Richardson et al. 2012). However, some studies have found little to no response in salmonid abundance following habitat restoration (Roni et al. 2002, 2008), suggesting that factors beyond habitat and wood may be limiting fish populations in some streams.

When evaluating factors limiting target populations, it is important to consider other species that may interact with that target species. In many streams, especially in the Pacific Northwest, salmonid fish are a key species around which management decisions are structured. However, stream salamanders are also important vertebrate predators in headwater ecosystems with diets that may overlap with salmonids and that may prey upon juvenile salmonids (Parker 1994). Pools appear to be the preferred habitat of large Pacific giant salamanders (*Dicamptodon* spp.) as well as salmonids (Roni 2002), but it is less clear how pool area influences reach-scale abundance or biomass. For example, Roni (2002) did not observe significant differences in salamander density between pool and riffle habitats, and Roni (2003) did not find differences in salamander abundance in reaches where large wood was artificially added.

The availability of prey has also been linked to fish and salamander biomass in streams (Hawkins et al. 1983, Kiffney and Roni 2007). In forested streams, light availability influences fish feeding efficiency (Wilzbach and Hall 1985) and is critically important for benthic primary production (Hill et al. 1995), which, combined with terrestrial subsides (allochthonous), provides the energy for invertebrate communities (Cummins and Klug 1979). Primary producers in forested low-order streams (first to third order) are often light limited (Ambrose et al. 2004, Bernhardt and Likens 2004) or partially light limited (Warren et al. 2017). Differences in canopy coverage—as a result of natural or anthropogenic processes—can have substantial influence on periphyton production (Hill and Knight 1988, Bilby and Bisson 1992), autochthonous carbon contributions to consumers (Finlay 2001, McCutchan and Lewis 2002), and the reach-scale biomass of invertebrates (Noel et al. 1986, Danehy et al. 2007) and fish (Murphy and Hall 1981, Bilby and Bisson 1992, Mellina and Hinch 2009, Wootton 2012).

Riparian stand development processes and the legacies of forest management can affect stream habitat and productivity. Streams bordered by old-growth riparian forests typically exhibit greater large wood loading, large wood volume, and total pool area than streams where riparian harvesting occurred (Bilby and Ward 1991, Keeton et al. 2007, Warren et al. 2007). Light availability is highest following riparian clear-cutting or a stand-replacing event but as the riparian forest regenerates, canopies close, typically reaching maximum cover when stands are 30–100 yr of age (Kaylor et al. 2017). In late stages of stand development (e.g., old growth), the formation of canopy gaps results in greater and more spatially variable light (Keeton et al. 2007, Kaylor et al. 2017). To evaluate the relative strength of habitat and productivity metrics in explaining fish and salamander biomass, we created a study design in which we selected adjacent stream sections with these contrasting riparian forest conditions.

In this study, we evaluated relationships between metrics of habitat and productivity relative to fish and salamander biomass in nine stream reach pairs. Each pair had one stream reach bordered by old-growth riparian forest and one reach bordered by previously harvested, second-growth riparian forest. Considering differences among streams and between reaches within each stream, we evaluated relationships between both biotic and abiotic covariates and the biomass of coastal cutthroat trout (*Onchorhynchus clarkii clarkii*), coastal giant salamanders (*Dicamptodon tenebrosus*), and total vertebrates (fish and salamanders). Among streams and within reach pairs, we expected fish and vertebrate biomass to be correlated with both habitat metrics (percentage of pool area, large wood volume) and productivity metrics (canopy openness, nutrients, periphyton chlorophyll a [hereafter chl *a*], and invertebrate biomass). Although pool area and large wood are important factors for fish in many Pacific Northwest systems, given results from earlier work on headwaters on the west slope of the cascades (Aho 1976, Murphy and Hall 1981, Hawkins et al. 1983), we expected productivity metrics to be stronger predictors of trout and total vertebrate biomass.

Materials and methods

Study site

The nine reach pair sites evaluated in this study were located within the McKenzie River Basin in the western Cascade Mountains of Oregon (Figure 3.1). Seven of the sites were located within the HJ Andrews Experimental Forest (HJA), a 6400-ha research forest encompassing the entire Lookout Creek drainage basin. Cook Creek and Fritz Creek were located outside of the HJA. Cook Creek is a tributary of Blue River upstream of Blue River reservoir and Fritz Creek is a tributary of Deer Creek, which flows directly into the McKenzie River. The Mediterranean climate of this region is characterized by wet winters with high stream discharge and dry summers with annual minimal flows occurring between late August and early September.

Each site consisted of two reaches: one within a section of stream with old-growth riparian forest and another in a nearby section of stream bordered by second-growth riparian forest on at least one stream bank. Harvesting in the previously managed reaches occurred on just one stream bank in three reach pairs (MR404, LO701, and LO703) and on both banks for all other pairs. Sites were selected based on the presence of old-growth and second-growth riparian forests close in proximity on the same stream (within 500 m). Having distinctly different forest types along two nearby sections of the same stream reduces inherent stream-to-stream environmental variability (e.g., temperature, gradient, geology, substrate) that often arises in comparisons between whole-stream systems in basins with managed vs. unmanaged, late-successional forests. Reaches ranged from 90 to 200 m, and reaches within a reach pair were separated by a 90- to 325-m buffer section.

The previously harvested cutblocks were cleared 40–60 yr prior to this study (Table 3.1). In all cases, timber was removed down to the stream bank with no riparian buffer. Trees were replanted within 5 yr post-harvest in seven of the nine cuts in accordance with forest management practices at the time. Stands in McRae Creek Tributary-West (MCTW) and Mack Creek were regenerated without any post-harvest planting. In 2014, the second-growth riparian forests were predominantly Douglas fir (*Pseudotsuga menziesii*) but red alder (*Alnus rubra*) was also a common canopy species in areas directly adjacent to streams and provided substantial stream shading. Old-growth forests were comprised of Douglas fir, western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Red alder was present adjacent to streams within old-growth forests as well, but it was not as common as in second-growth sections.

Coastal cutthroat trout and coastal giant salamanders (*D. tenebrosus*) were present in all 18 stream reaches and were the dominant vertebrates. Sculpin (*Cottus* spp.) were present in both reaches of MR404, but were not found in any other reaches. Tailed frogs (*Ascaphis truei*) were found in low abundance in some of the streams, but were not evaluated in this study.

Field sampling – abiotic variables

All data were collected in the summer of 2014 during low-flow conditions. Across all nine pairs, we collected a suite of physical habitat variables in each reach including canopy cover, bankfull width, wetted width, pool area, large wood abundance and volume, temperature, nutrient concentration, and stream gradient. Canopy cover was quantified using a convex spherical densiometer (Forestry Suppliers Model A). Measurements were taken in each cardinal direction at 11 regularly spaced locations in each reach. All densiometer measurements were taken by the same individual to avoid user bias. Bankfull width and wetted width were measured at transects across the same 11 reach locations. The mean wetted width for each reach was multiplied by reach length to obtain total reach wetted area, which was used to standardize fish, salamander, and invertebrate abundance and biomass estimates per square meter of stream. Pools were identified during summer low-flow conditions as slow velocity habitats connected to the main channel. Pool area was calculated using the length and width of each pool, and percent pool area was calculated as the total pool area divided by total wetted reach area. We quantified all large wood pieces greater than 1 m in length and 10 cm in diameter (Richmond and Fausch 1995, Young et al. 2006, Warren et al. 2009). We only measured the portion of wood pieces located within the bankfull channel for wood volume estimates. Total channel area (mean bankfull width multiplied by reach length) was used to standardize large wood volume among reaches. Temperature loggers (HOBO Pro v2, Onset Computer Corporation, Bourne, Massachusetts, USA) were deployed for 2 weeks during mid-summer to evaluate relative temperature among streams and differences between paired reaches. Due to a limited number of sensors, not all sensors were deployed for the same time interval. Sensors were deployed from 20 July 2014 to 3 August 2014 in Cook Creek and Fritz Creek and from 4 August 2014 to 24 August 2014 in all other streams. Water samples were collected in September 2014 at all reaches during a two-day period prior to the onset of autumn rain events in this region. Water samples were filtered (25-mm Whatman GF/F filters), frozen, and analyzed for nitrate-N (NO_3-N) and phosphate-P (PO_4-P) using a Dionex 1500 Ion Chromatograph (Sunnyvale, California, USA). Nitrogen is the limiting nutrient for stream autotrophy in the streams evaluated in this study (Gregory 1980, Warren et al. 2017). Phosphate-P was poorly correlated with all biotic response variables, and we therefore present only nitrate-N results.

Field sampling – biotic variables

Periphyton chl *a* accrual was quantified on 10 ceramic tiles (15 × 15 cm) per reach. Tiles were placed in the stream in mid-July and were retrieved after six weeks. Tiles were spaced at regular intervals and positioned within riffle sections of the stream at a depth of 10–25 cm. After six weeks, tiles were scraped using a wire brush and the slurry was filtered through 47-mm glass fiber filters (Whatman GF/F). Filters were placed in 20-mL glass vials and frozen for 24–48 h. 15 mL of 90% acetone was then added to vials to extract chl *a*. After 2–4 h of dark storage at room temperature, chl *a* was quantified using fluorometric methods (Arar and Collins 1997).

Fluorescence of a subsample of the extraction solution was measured before and after the addition of 0.1 N HCl (0.15 mL/5 mL solution).

Benthic invertebrates were sampled in late July (15 July 2014 to 29 July 2014). Both reaches within a reach pair were always sampled on the same day. In each reach, six Surber samples (363 μm, 0.0625 m^2) were collected from riffle habitats at regular intervals. Substrate within the Surber sample quadrate was disturbed to a depth of 10 cm for approximately 30 s. Samples were stored in 90% alcohol until laboratory processing. In the laboratory, the contents of each of the six Surber samples from each reach were combined into a single pooled sample. This pooled sample was then subsampled using a plankton splitter until a minimum of 500 individuals were picked from the subsample. We conducted a 60-s visual search of the remaining sample (less the subsample) to collect large-bodied predators to more effectively quantify invertebrate predator biomass. Invertebrates were identified to Family or Genus (Merritt et al. 2008) and individually measured using an ocular micrometer mounted on the dissecting microscope. Invertebrate lengths were converted to biomass using established length–weight relationships (Sample et al. 1993, Sabo et al. 2002, M. Wipfli, *unpublished data*). We summed the biomass of individuals within a subsample and divided this summed value by the proportion of the total sample that was subsampled. The addition of this value and the biomass of the 60-s sample to identify large-bodied individuals (which was not subsampled) was then divided by the total area sampled (0.375 m^2) to obtain biomass estimates per square meter (g/m^2).

Fish and salamanders were collected using a backpack electroshocker (Smith-Root model LR-20B). Block nets were set at the upper and lower ends of each reach to prevent movement and close the system for the duration of the surveys. Population estimates were conducted using single-pass mark–recapture methods for all reach pairs except Mack Creek. For mark–recapture surveys, fish and salamanders were anesthetized using AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand), weighed (nearest 0.01 g), measured (total length for fish and snout-vent length for salamanders), and marked. Fish were marked with a small caudal clip and salamanders were marked with a visual elastomer tag (Northwest Marine Technology, Shaw Island, Washington, USA). Fish and salamanders were released and the reach was resurveyed after approximately 24 h. The number of marked and unmarked individuals was recorded for each species. Abundance was estimated using the Lincoln-Peterson mark–recapture model, modified by Chapman (1951), and biomass was estimated by multiplying abundance estimates by mean weight. Juvenile (0+) and adult (1+) trout were analyzed separately. Trout were distinguished as juvenile or adult based on length frequency histograms and, in general, trout <65 mm were classified as juveniles.

Multiple-pass depletion methods were used to survey fish and salamanders at Mack Creek. Mack Creek is a long-term ecological research (LTER) site where fish and salamanders are sampled annually using depletion estimates. The long-term research project provided the 2014 fish and salamander data used in this study (S. V. Gregory, *unpublished data*). Multiple-pass depletion and mark–recapture methods can produce significantly different population estimates (Rosenberger and Dunham 2005). To standardize population estimates across all reaches, we applied a correction factor that was obtained from simultaneous mark–recapture and depletion estimates conducted in Mack Creek in 2015 (S.V. Gregory) per Thompson and Seber (1994).

In addition to the primary fish and salamander surveys conducted in mid-summer, a second single-pass survey was conducted in late September 2014 to capture juvenile (age 0+) cutthroat trout and assess summertime relative growth rates for this age class. We did not sample

Mack Creek in the second juvenile assessment as we did not want to interfere with long-term research efforts occurring annually at this site. In LO701, McRae Creek Tributary-East (MCTE), and Fritz Creek, juvenile trout were surveyed on two sampling dates but there were few surveyed fish in at least one of these surveys ($n < 5$). Therefore, we were only able to evaluate juvenile relative growth rates in five of the nine sites. Relative growth rates were determined by subtracting the mean weight at survey date 2 from the mean weight of survey date 1 and then dividing this number by the number of days between sampling events.

Statistical analysis

Data from the 18 stream reaches were used to explore relationships between habitat and biotic variables and the biomass of cutthroat trout, salamanders, and total vertebrates. We used three approaches: (1) We examined correlations (Pearson's correlation coefficient (r) and r-squared) between all explanatory and response variables among sites, blocked by riparian forest age class, (2) we examined correlations of all explanatory and response variables using reach pair differences, and (3) we evaluated the relative support of sets of a priori models for cutthroat trout biomass, salamander biomass, and total vertebrate biomass across old-growth and previously harvested reaches using Akaike Information Criteria adjusted for small sample sizes (AICc, Hurvich and Tsai 1989).

Total reach biomass for trout, salamanders, and total vertebrates were converted to biomass per unit area (g/m^2) to standardize this response across sites and to account for differences in reach area across study reaches. Biomass was used rather than abundance, as biomass can be a better approximation of a stream's productive capacity (Stoneman and Jones 2000). Similarly, covariates were also converted to unit-area metrics or a percentage (e.g., percentage of pool area). Vertebrate biomass included the summed biomass of trout, salamanders, and sculpin, although sculpin were only present at a single site (MR404).

We first evaluated correlation (Pearson's *r* and *r*-squared) between all explanatory and response variables. Related studies have evaluated relationships between abiotic and biotic explanatory variables and similar response variables using linear regression (Murphy and Hall 1981, Hawkins et al. 1983, Kiffney and Roni 2007), and thus, results from this analysis can be evaluated in the context of these other studies. Correlation values were examined separately for each riparian forest type (old growth and previously harvested) allowing for evaluation of the degree to which relationships are dependent on covariates vs. factors associated with riparian forest age class and associated structural differences. To evaluate the hypothesis that bottom-up drivers exert strong influence on multiple aspects of the food web in these oligotrophic headwater ecosystems, we examined correlations among chl *a,* total invertebrate biomass, predatory invertebrate biomass, cutthroat trout biomass, salamander biomass, and total vertebrate biomass.

We also evaluated relationships between reach pair differences for biotic and abiotic factors. Using reach pair differences reduces stream-to-stream variability of certain variables (e.g., temperature, nitrate concentration, gradient, bankfull width) which allows for more explicit evaluation of how local habitat and metrics of productivity, which often differ on small spatial scales (e.g., large wood, pool area, canopy openness), relate to differences in stream biota. We examined correlations between all biotic and abiotic covariate differences (old growth minus previously harvested) and the differences in response variables: chl *a*, invertebrate biomass, predatory invertebrate biomass, trout biomass, salamander biomass, and total vertebrate biomass ($n = 9$).

Lastly, we formulated a set of a priori models for abiotic and biotic covariates that could be related to trout, salamander, and total vertebrate biomass. We used AICc to evaluate the relative support for the candidate models. Each candidate model consisted of a single covariate and an interaction with reach type (old growth, previously harvested) as a binary (0, 1) indicator variable. Reach type was included as an interaction with each model variable to allow the slope and intercept to vary by reach type and because reach type may be representative of other unmeasured variables that are not included in the model (e.g., potential effects of harvesting beyond the measured explanatory variables used in this study). Interactions among multiple covariates are possible, but the inference of these interactions was limited by our sample size. With only nine pairs and 18 total reaches, we were constrained to a comparison of single-factor regression relationships with the reach-type covariate. We produced a total of eight models, one for each of the following variables: canopy openness (%), invertebrate biomass (g/m^2), pool area (%), large wood volume ($m^3/100\ m^2$), gradient (%), bankfull width (m), nitrate-N concentration (µg/L), and mean August temperature (°C). To account for non-independent error in the models, we used linear mixed-effects models and included a random effect that corresponded to stream pair. Candidate models were fit using the lme4 package (Bates et al. 2015) in the program R (R Development Core Team 2012). We examined model-fitted residuals to assess model assumptions of normality and constant variance.

With only five reach pairs in which we were able to quantify juvenile cutthroat trout relative growth rates, we focused on differences in relative growth between reaches within reach pairs. We hypothesized that differences in canopy cover and invertebrate biomass would reflect differences in juvenile trout relative growth rates, but habitat variables would not. We used linear regression (n = 5) to evaluate correlations between differences in explanatory variables and differences in juvenile trout relative growth rates between reaches within reach pairs.

Results

Cutthroat trout biomass (g/m^2) varied by nearly an order of magnitude among streams (from an estimated 0.9 to 8.0), and coastal giant salamander biomass ranged from an estimated 4.4 to 14.9 g/m^2 among all reaches (Table 3.2). The biomass of sculpin, present at just the two MR404 reaches, ranged from 1.5 to 3.1 g/m^2. Estimated capture probabilities ranged from 0.54 to 0.94 for adult cutthroat trout, from 0.28 to 1 for age-0 cutthroat trout, and from 0.08 to 0.22 for coastal giant salamanders.

Across old-growth and previously harvested reaches, correlations were generally consistent with a bottom-up-driven food web. There were strong positive correlations between chlorophyll a, invertebrate biomass, predatory invertebrate biomass, cutthroat trout biomass, and salamander biomass (Figure 3.2). Chlorophyll *a* was positively correlated with both canopy openness (r^2 old growth [OG] = 0.49; r^2 previously harvested [PH] = 0.81) and nitrate-N concentration (r^2 OG = 0.66; r^2 PH = 0.60). Invertebrate biomass (r^2 OG = 0.58; r^2 PH = 0.55) and predatory invertebrate biomass (r^2 OG = 0.67; r^2 PH = 0.62) were positively correlated with chl *a*. Both cutthroat trout biomass (r^2 OG = 0.67; r^2 PH = 0.82) and total vertebrate biomass (r^2 OG = 0.64; r^2 PH = 0.73) were, in turn, positively correlated with total invertebrate biomass. Salamander biomass was positively correlated with invertebrate biomass, but less so than for cutthroat trout or total vertebrate biomass (r^2 OG = 0.30; r^2PH = 0.47).

Among all potential explanatory variables, cutthroat trout biomass was positively correlated with nitrate-N concentration (r OG = 0.71, r PH = 0.69), canopy openness (*r* OG = 0.68; *r* PH = 0.85), chl *a* (*r* OG = 0.88; *r* PH = 0.76), and invertebrate biomass (*r* OG = 0.82; *r* PH = 0.90) across both old-growth and previously harvested reaches (Figure 3.3A, B). Cutthroat trout biomass was negatively correlated with temperature (*r* OG = −0.68; *r* PH = −0.77); however, this relationship was largely driven by the two coldest sites, LO701 and LO703, that were just downstream of a ground water-fed tributary, which also exhibited high nitrate-N concentrations, canopy openness, chl *a*, and invertebrate biomass relative to other sites. All Pearson's correlation coefficients for large wood volume, percent pool area, gradient, and bankfull width were less than 0.5 across both reach types (Figure 3.3A, B; Figures A3.1 and A3.2). When reach pair differences (old growth less previously harvested) were evaluated, differences in temperature, large wood volume, percent pool area, gradient, bankfull width, and nitrate-N concentration were all poorly correlated (all *r* values <0.40) with differences in cutthroat trout biomass (Figure 3.3C). However, differences in canopy openness (*r* = 0.53; Figure 3.4A), chl *a* (*r* = 0.64), and invertebrate biomass (*r* = 0.62) were all positively correlated with differences in cutthroat trout biomass (Figure 3.3C).

Coastal giant salamander biomass was not as well correlated as cutthroat trout biomass was with nitrate-N concentration (*r* OG = 0.32; *r* PH = 0.41), canopy openness (*r* OG = 0.30; *r* PH = 0.59), chl *a* (*r* OG = 0.30; *r* PH = 0.59), or invertebrate biomass (*r* OG = 0.55; *r* PH = 0.68) across old-growth and previously harvested reaches (Figure 3.3A, B). Temperature (*r* OG = −0.74; *r* PH = −0.93) and large wood volume (*r* OG = −0.87; *r* PH = −0.36) were strongly negatively correlated with salamander biomass (Figure 3.3A, B). Pearson's correlation coefficients for percent pool area, gradient, and bankfull width were all less than 0.3 across both reach types (Figure 3.3A, B; Figures A3.1 and A3.2). When reach pair differences were evaluated, differences in bankfull width (*r* = 0.66) and canopy openness

($r = 0.79$; Figure 3.4B) were positively correlated with differences in salamander biomass. Differences in all other variables, including temperature, chl *a*, and invertebrate biomass, were poorly correlated ($r < 0.40$) with differences in salamander biomass (Figure 3.3C).

Total vertebrate biomass was positively correlated nitrate-N concentration (r OG = 0.60; r PH = 0.53), canopy openness (r OG = 0.67; r PH = 0.80), chl *a* (r OG = 0.76; r PH = 0.79), and invertebrate biomass (r OG = 0.80; r PH = 0.80), but negatively correlated with temperature (r OG = −0.78; r PH = −0.87) and large wood volume (r OG = −0.71; r PH = −0.47) across old-growth and previously harvested reaches (Figure 3.3A, B). Pearson's correlation coefficients for percent pool area, gradient, and bankfull width were all less than 0.5 across both reach types (Figure 3.3A, B; Figure A3.3). Differences in bankfull width ($r = 0.57$), canopy openness ($r = 0.92$; Figure 3.4C), and total invertebrate biomass ($r = 0.64$) were positively correlated with differences in total vertebrate biomass, while differences in all other variables were weakly correlated ($r < 0.30$) with differences in total vertebrate biomass (Figure 3.3C).

Canopy openness was lower in the previously harvested reach of six of the nine reach pairs, but greater in three of the nine pairs. The differences in canopy cover between reaches explained over 80% of the variability in the difference in vertebrate biomass between reaches. This correlation was stronger for total vertebrate biomass ($r^2 = 0.84$) than for salamanders ($r^2 = 0.62$) and cutthroat trout biomass ($r^2 = 0.28$; Figure 3.4). Surprisingly, differences in canopy openness were only weakly correlated with differences in chl *a*($r^2 = 0.12$). However, the difference in chl *a* was strongly positively correlated with the difference in invertebrate biomass ($r^2 = 0.73$). The difference in invertebrate biomass was, in turn, positively correlated with the difference in cutthroat trout biomass ($r^2 = 0.38$) and total vertebrate biomass ($r^2 = 0.41$), but less so for salamanders biomass ($r^2 = 0.15$). Despite substantial differences in large wood volume (range 0.5–9.7 m^3/m^2) and percent pool area (range −3.6% to 21.8%) between reaches within reach pairs, these metrics were not well correlated with differences in cutthroat trout biomass, accounting for less than 10% of the variation in differences in trout biomass, salamander biomass, and total vertebrate biomass (Figure A3.3). Differences in gradient, temperature, and nitrate-N were relatively small between reach pairs and were not well correlated with cutthroat trout biomass, salamander biomass, or total vertebrate biomass (all r^2 values <0.10).

Model selection (AICc) of candidate models generally found further support for the importance of variables associated with bottom-up processes in accounting for cutthroat trout and vertebrate biomass in these headwater streams, but not for salamander biomass (Appendix S1: Table A3.1). Among old-growth and previously harvested reaches, the model containing invertebrate biomass was the highest ranked model accounting for cutthroat trout biomass and was 27 times more likely to be the best-approximating model than the second-ranked model, which contained canopy openness. The models for nitrate concentration, temperature, and physical habitat in the stream were highly unlikely to be the best model (AICc weights < 0.005). For salamanders, the model containing temperature was the best-approximating model (AICc weight = 0.99) and was far more likely than the second-ranked model (invertebrate biomass). For total vertebrates, the model containing canopy openness was the highest ranked model (AICc weight = 0.66) followed by the model containing invertebrate biomass (AICc weight = 0.30). The model containing temperature was ranked third (AICc weight = 0.036). All other models were highly unlikely to be the best model (AICc weights < 0.001).

Relative growth rates of juvenile cutthroat trout (age–0+) were higher in the old-growth reach compared to the previously harvested reach in four of the five streams for which we had access and adequate samples sizes for an assessment of juvenile summer growth (Figure 3.5). Juvenile relative growth rates were greater in the previously harvested reach of LO703 compared to the old-growth reach; however, this is a site where canopy openness remained greater in the previously harvested reach. In the paired analysis, the reach in each reach pair with more open canopy (and therefore more light) generally exhibited greater juvenile relative growth rates (Figure 3.5). MR404 is the exception, but canopy openness and relative growth rates were largely comparable between reaches at this site and differences were small. Differences in canopy openness explained 77% of the variation in the difference in relative juvenile growth rates (n = 5) and differences in total invertebrate biomass explained 76% of the variation in the differences in juvenile relative growth rates (n = 5). Differences in bankfull width, large wood volume, percent pool area, gradient, nitrate concentration, and temperature all explained less than 30% of the variation in the differences in juvenile relative growth rates. Differences in relative growth rates were not related to differences in the biomass or abundance of juvenile trout, adult trout, or total vertebrates. The 95% confidence intervals of estimated juvenile abundance and biomass (during sampling event 1) were overlapping for four of the five reach pairs. In addition, relative growth rates were greater in the reach that had greater adult trout biomass and abundance in Cook Creek, MR404, and LO703 (Table 3.2). These trends are generally consistent when comparing vertebrate biomass and abundance between reaches within reach pairs (Table 3.2).

Discussion

We found strong positive correlations between (1) chl *a* and total invertebrate biomass, (2) total invertebrate biomass and trout biomass, and (3) total invertebrate biomass and total vertebrate biomass among both old-growth and previously harvested stream sections, which is consistent with the hypothesis that bottom-up processes are dominant drivers of fish and total vertebrate biomass in these forested headwater streams. Canopy openness and nitrate concentration, the primary limiting factors for benthic autotrophy in streams surveyed in this study (Gregory 1980, Warren et al. 2017), were both positively correlated with periphyton chl *a*, invertebrate biomass, trout biomass, salamander biomass, and total vertebrate biomass. In contrast, most habitat variables (large wood volume, percent pool area, gradient, and bankfull width) were poorly correlated with all biotic variables among old-growth and previously harvested reaches. The exception is temperature, which was negatively correlated with all biotic variables across old-growth and previously harvested reaches. However, in the analysis using reach pair differences, differences in temperature were poorly correlated with differences in all biotic metrics. In contrast, in the reach pair difference analysis, canopy cover remained a strong correlate with biotic metrics and explained 28%, 62%, and 84% of the variation in differences in cutthroat trout, salamander, and total vertebrate biomass, respectively. Collectively, these relationships suggest that within the stream reaches evaluated in this study, variability in metrics associated with bottom-up controls exert stronger influence on consumer population biomass than physical habitat variables during summer.

These results are consistent with observational studies that have found that light (or proxies for light) and prey availability can correlate strongly with predator populations in streams. For example, in the Coast Range of Oregon and northern California, the density of invertebrates in the collector–gatherer functional feeding group explained a substantial proportion of the variance in cutthroat trout and total vertebrate biomass (fish and salamanders) across shaded and unshaded sites (Hawkins et al. 1983). Similarly, Murphy (1979) found a positive correlation between canopy openness and total vertebrate biomass across 31 stream reaches in the Cascade Mountains. These studies sampled sites ranging from fully closed canopies to recently harvested sites with open canopies (e.g., 0–100% open). Kiffney and Roni (2007) observed a positive relationship between light input and total vertebrate (fish and salamanders) biomass in streams ranging in canopy openness from 0% to 50%, comparable values to those observed in this study. While increases in primary production and consumer population biomass following removal of all or most riparian shading have been well documented (Bilby and Bisson 1992, Wilzbach et al. 2005, Wootton 2012), harvesting has been greatly reduced in riparian zones (Richardson et al. 2012), and the distribution of current canopy coverage has shifted toward more closed canopies (Kaylor et al. 2017). Results from Kiffney and Roni (2007) along with results from the work presented here highlight the potential for smaller differences in canopy openness (and light) to influence aquatic biota via increased stream primary production in light-limited headwater streams.

Although forested headwater streams are often predominantly heterotrophic with food webs deriving the majority of basal carbon from allochthonous resources (Fisher and Likens 1973, Vannote et al. 1980, Wallace 1997, Tank et al. 2010), autochthonous carbon can be a disproportionately important food resource for stream consumers in these systems (Bilby and Bisson 1992, McCutchan and Lewis 2002, Lau et al. 2009). The potentially disproportionate influence of autochthonous carbon production on stream secondary consumers is illustrated well by Bilby and Bisson (1992) in which carbon budgets were compared between a stream section bordered by old-growth riparian forest and a stream section where the riparian forest was recently harvested. The old-growth section received 300 $g \cdot m^{-2} \cdot yr^{-1}$ of allochthonous carbon and 100 $g \cdot m^{-2} \cdot yr^{-1}$ of autochthonous carbon (total carbon inputs = 400 $g \cdot m^{-2} \cdot yr^{-1}$), while the harvested reach received 60 $g \cdot m^{-2} \cdot yr^{-1}$ of allochthonous carbon and 175 $g \cdot m^{-2} \cdot yr^{-1}$ of autochthonous carbon (total carbon inputs = 235 $g \cdot m^{-2} \cdot yr^{-1}$). Despite lower total carbon flux to the harvested section compared to the old-growth section, fish production was greater in the harvested reach, which they suggest is a result of higher biomass of high-quality autochthonous carbon at the base of the food web. In an assessment of carbon isotopes, McCutchan and Lewis (2002) found that 40–80% of secondary consumer production was supported by autochthonous production, whereas availability of this carbon source was disproportionally low (<2–40% of total available organic carbon). The disproportionate influence of autochthonous carbon on secondary production relative to its availability is likely due to the lower C:N ratio in periphyton compared to allochthonous litter (Cross et al. 2005). With more N per unit biomass, the energetic benefits of assimilation increase for the same amount of material consumed, making periphyton a higher-quality food source for consumers. Consequently, relatively small changes in light availability and primary production may have disproportionate influences on consumer communities.

Temperature was negatively correlated with chl *a,* invertebrate biomass, cutthroat trout biomass, salamander biomass, and total vertebrate biomass for both old-growth and previously harvested reaches in this study. All streams were relatively cool, even in mid-summer, and therefore, the relationship with cutthroat trout is unlikely attributed to thermal stress. The negative relationships with temperature observed in this study were largely driven by the two coldest pairs (LO701 and LO703), which also exhibited among the highest nitrate concentrations, canopy openness, periphyton chl *a*, invertebrate biomass, trout biomass, salamander biomass, and total vertebrate biomass compared to other surveyed reach pairs. At these two reach pairs, as well as other reach pairs, differences in canopy openness were accompanied by similar differences in the biomass of invertebrates, cutthroat trout, salamanders, and total vertebrates. Further, across all nine pairs, differences in temperature explained very little variation in the differences in biotic metrics. We therefore suggest that productivity at these sites drove the negative relationship with temperature. Alternatively, the cold temperatures of these streams may be indicative of other key habitat factors that we did not account for directly in our surveys, such as cooler and more stable ground water inputs that could influence thermal refuge and flow stability. During the summer low-flow period, in which temperatures are high, habitat availability is at an annual minimum, and competition is elevated (Power et al. 2013), stable flows may provide increased pool habitat relative to similarly sized streams with less ground water input.

Habitat covariates beyond canopy cover and temperature explained little variation in cutthroat trout and total vertebrate biomass in correlations across streams or in the reach pair difference analysis. Indeed, numerous studies have found positive relationships between large wood or pool area and salmonid metrics (Fausch and Northcote 1992, Connolly and Hall 1999, Roni and Quinn 2001), and there are a few potential reasons why we did not find similar responses. First, our nine study streams are high-gradient with large substrates (cobble-boulder) and step-pool or cascade geomorphology (Montgomery and Buffington 1997). In these systems, boulders are a dominant agent of pool formation (Frissell et al. 1986), and in boulder-dominated systems, wood may be less important as a habitat feature for fish (Burgess 2001, Warren and Kraft 2003). Another potential explanation for the apparent lack of a large wood relationship is that the size of the harvested stands in this study were small (4–20 ha) and consisted of patches within a largely unharvested (old-growth) watershed. Larger cuts, or entire basin harvesting and removal of large wood, may yield different relationships, spatially and temporally, between large wood, pool habitat, and trout biomass (see Mellina and Hinch 2009). Despite substantial differences in large wood volume among and within reach pairs, the range of percent pool area was much smaller and may have influenced our ability to determine an effect of this variable in a regression analysis. In contrast, canopy openness, nitrate, chl *a*, and invertebrate biomass ranged considerably among streams. In streams with larger contrasts between reaches, pool area may be a stronger determinant of trout biomass. Lastly, previous research in this region, the western Cascade Mountains of Oregon, provides support that bottom-up processes exert controls on cutthroat trout and total vertebrate biomass. For example, in a study in the HJA, Murphy and Hall (1981) evaluated cutthroat trout biomass in stream sections where the riparian forest had been recently harvested and stream wood had been removed relative to upstream sections bordered by old-growth forest. They found that cutthroat trout biomass was greater in the recently harvested sections even though pool area and wood volume were both lower in harvested reaches.

Within reach pairs, juvenile cutthroat trout relative growth rates were greater in the reach with more canopy openness in four of the five pairs, regardless of the riparian forest stage/age. This is consistent with other studies in which differences in resident salmonid growth rates, including adults, were linked to differences in light availability (Johnson et al. 1986, Murphy et al. 1986, Bilby and Bisson 1992, Wilzbach et al. 2005, Kiffney et al. 2014). However, the greater size of juvenile salmonids in harvested reaches has at times been attributed to stream warming associated with canopy removal resulting in earlier emergence timing (Thedinga et al. 1989). The biomass of trout can also influence growth rates through density-dependent processes (Ramirez 2011), but in the study reaches in which juvenile trout growth was evaluated, the biomass of juvenile trout, adult trout, and total vertebrates did not explain observed differences in growth. Juveniles were similar in size during the first capture event for each reach pair, and thus, greater growth rates in the more open site are not attributable to larger initial sizes. However, it is unclear whether greater growth rates translate to increased survival and reproductive success. For example, in clear-cut streams in Alaska, juvenile coho salmon (*Oncorhynchus kisutch*) abundance (Murphy et al. 1986) and growth rates (Thedinga et al. 1989) were greater in clear-cut reaches relative to unharvested reaches in summer, but in winter, few juveniles remained in clear-cut reaches due to loss of large wood, pool habitat, and cover (Heifetz et al. 1986, Murphy et al. 1986). Additionally, while juvenile (age 0+) coho were larger in clear-cut reaches, there were no observable differences in size in age 1+ fish (Thedinga et al. 1989), suggesting that greater growth rates in juveniles may not always translate to older age classes.

Conclusions

Results from our study do not invalidate previous work highlighting the importance of stream wood and pool habitat for fish in western U.S. headwater streams. Rather, they demonstrate the relative importance of considering bottom-up forces (e.g., light and nutrients) in addition to habitat as factors that can limit invertebrate, fish, and vertebrates in a stream ecosystem. Results from this study, combined with previous studies (Murphy and Hall 1981, Hawkins et al. 1983, Bilby and Bisson 1992, Kiffney and Roni 2007, Wootton 2012), provide evidence that in light-limited streams, changes (temporally) or spatial variability in canopy coverage and light during summer has the potential to influence consumer biomass via controls on bottom-up processes. More broadly, studies have documented that changes in labile carbon (Warren et al. 1964), inorganic nutrients (Peterson et al. 1993, Cross et al. 2006), allochthonous litter inputs (Wallace 1997, Wallace et al. 1999), salmon subsidies (Bilby et al. 1998, Collins et al. 2016), and terrestrial invertebrate subsidies (Kawaguchi and Nakano 2001, Saunders and Fausch 2012) can alter carbon quantity and quality at the base of the food web, which can resonate through higher trophic levels, ultimately influencing fish abundance, biomass, and growth. This concept—that consumers can be limited by food availability—is a fundamental concept in ecology, but as Naiman et al. (2012) discussed, the dominant focus of stream and river restoration efforts to improve suppressed salmonid stocks in the Columbia Basin has been improving in-stream habitat. Consideration of both habitat quality and food web structure and productivity will provide a more holistic understanding of the factors limiting target populations (Roni et al. 2002).

Acknowledgments

We thank B. VerWey, K. Pospisil, E. Heaston, C. Kopet, and E. Purvis for their work in the field. We thank E. Heaston, W. Cross and two anonymous referees for manuscript reviews that substantially improved this work. S. Gregory and R. Wildman provided 2014 fish and salamander data from the HJ Andrews LTER long-term fish sites at Mack Creek. J. Li, W. Gerth, D. Lytle, and R. Van Dreische provided logistical support and critical expertise for invertebrate identification and analysis. Stream water analyses were conducted at the Oregon State University Institute for Water and Watershed's Collaboratory. This research was supported by a National Science Foundation Graduate Research Fellowship (Grant No. 1314109-DGE), the Oregon State University Fish and Wildlife Habitat in Managed Forests Research Program, the US Department of Agriculture National Institute of Food and Agriculture McIntire Stennis program (award 1009738), the HJ Andrews Experimental Forest research program (which is funded by the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), the US Forest Service Pacific Northwest Research Station, and Oregon State University. All animal

collections were conducted in compliance with Oregon State University's Animal Care and Use Committee (Permit no. 4439).

Literature cited

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. Oregon State University.

Ambrose, H. E., M. A. Wilzbach, and K. W. Cummins. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. The North American Benthological Society 23:701–712.

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. Page US Environmental Protection Agency Method 445.0 Revision 1.2. Cincinnati, Ohio.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126:217–229.

Berg, N., A. Carlson, and D. Azuma. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Canadian Journal of Fisheries and Aquatic Sciences 55:1807–1820.

Bernhardt, E. S., and G. E. Likens. 2004. Controls on periphyton biomass in heterotrophic streams. Freshwater Biology 49:14–27.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48:2499–2508.

Burgess, J. A. 2001. Response of trout, sculpins, and salamanders to experimental manipulation of large wood in Cascade Mountain streams. Oregon State University.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution, with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7:1–

18.

Connolly, P. J., and J. D. Hall. 1999. Biomass of Coastal Cutthroat Trout in unlogged and previously clear-cut basins in the central Coast Range of Oregon. Transactions of the American Fisheries Society 128:890–899.

Cross, W. F., J. P. Benstead, P. C. Frost, and S. a. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshwater Biology 50:1895–1912.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detrital-based ecosystem. Ecology 87:1556–1565.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

Danehy, R. J., S. S. Chan, G. T. Lester, R. B. Langshaw, and T. R. Turner. 2007. Periphyton and macroinvertebrate assemblage structure in headwaters bordered by mature, thinned, and clearcut Douglas-fir stands. Forest Science 53:294–307.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–551.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82:1052–1064.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

Frissell, C. a., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. Oregon State University.

Gregory, S. V, J. Swanson, W. A. Mckee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Hawkins, C. P., M. L. Murphy, N. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173–1185.

Heifetz, J., M. L. Murphy, and K. V Koski. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaskan streams. North American Journal of Fisheries Management 6:52–58.

Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125–132.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Hurvich, C., and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Johnson, S. W., J. Heifetz, and K. V Koski. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. North American Journal of Fisheries Management 6:532–537.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46:303–316.

Kaylor, M. J., D. R. Warren, and P. M. Kiffney. 2017. Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams. Freshwater Science 36.

Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecological Applications 17:852–68.

Kiffney, P. M., E. R. Buhle, S. M. Naman, G. R. Pess, and R. S. Klett. 2014. Linking resource availability and habitat structure to stream organisms: an experimental and observational assessment. Ecosphere 5:1–27.

Kiffney, P. M., and P. Roni. 2007. Relationships between productivity, physical habitat, and aquatic invertebrate and vertebrate populations of forest streams: an information-theoretic approach. Transactions of the American Fisheries Society 136:1088–1103.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28:426–439.

Matthews, K. R., N. H. Berg, D. L. Azuma, and T. R. Lambert. 1994. Cool water formation and trout habitat use in a deep pool in the Sierra Nevada, California. Transactions of the American Fisheries Society 123:549–564.

McCutchan, J. H., and W. M. Lewis. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742–752.

Mellina, E., and S. G. Hinch. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Canadian Journal of Forest Research 39:1280–1301.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An introduction to the aquatic insects of North America. Kendell Hunt Publishing Company.

Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. GSA Bulletin 109:596–611.

Murphy, M. L. 1979. Predator assemblages in old-growth and logged sections of small cascade streams. Oregon State University.

Murphy, M. L., and J. D. Hall. 1981. Vaired effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Murphy, M. L., J. Heifetz, S. W. Johnson, K. V Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43:1521–1533.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109:21201–7.

Noel, Di. S., C. W. Martin, and C. A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. Environmental Management 10:661–670.

Parker, M. S. 1994. Feeding ecology of stream-dwelling Pacific Giant Salamander larvae (Dicamptodon tenebrosus). American Society of Ichthyologists and Herpetologists 1994:705–718.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. Mckinley, M. C. Miller, J. R. Vestal, R. Ventullo, S. Ecology, and N. Apr. 1993. Biological responses of a tundra river to fertilization. Ecology 74:653–672.

Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (Salmo salar) streams. Canadian Journal of Fisheries and Aquatic Sciences 55:201–217.

Power, M. E., J. R. Holomuzki, and R. L. Lowe. 2013. Food webs in Mediterranean rivers. Hydrobiologia 719:119–136.

Ramirez, B. S. 2011. Experimental analysis of intra- and interspecific competitive interactions between cutthroat trout and sculpins in small streams. Oregon State University.

Richardson, J. S., R. J. Naiman, and P. A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshwater Science 31:232–238.

Richmond, A. D., and K. D. Fausch. 1995. Characteristics and function of large woody debris in suba pine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and

Aquatic Sciences 52:1789–1802.

Roni, P. 2002. Habitat use by fishes and Pacific Giant Salamanders in small western Oregon and Washington streams. Transactions of the American Fisheries Society 131:743–761.

Roni, P. 2003. Responses of benthic fishes and giant salamanders to placement of large woody debris in small Pacific Northwest streams. North American Journal of Fisheries Management 23:1087–1097.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. Michael, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1–20.

Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management 28:856–890.

Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:282–292.

Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for Rainbow Trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395–1410.

Rosenfeld, J. S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953–968.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585–593.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. North American Bentholocial Society 21:336–343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Saunders, W. C., and K. D. Fausch. 2012. Grazing management influences the subsidy of terrestrial prey to trout in central Rocky Mountain streams (USA). Freshwater Biology 57:1512–1529.

Stoneman, C. L., and M. L. Jones. 2000. The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. Transactions of the American Fisheries Society 129:639–657.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118–146.

Thedinga, F., M. L. Murphy, J. Heifetz, K. V Koski, and S. W. Johnson. 1989. Effects of logging on size and composition of juvenile Coho Salmon (Oncorhynchus kisutsch) and density of presmolts in southeast Alaska streams. Canadian Journal of Fisheries and Aquatic Sciences 46.

Thompson, S. K., and G. A. F. Seber. 1994. Detectability in conventional and adaptive sampling. Biometrics 50:712–724.

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Wallace, J. B. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. The Journal of Wildlife Management 28:617–660.

Warren, D. R., E. S. Bernhardt, R. O. Hall, Jr., and G. E. Likens. 2007. Forest age, wood and nutrient dynamics in headwater streams of the Hubbard Brook Experimental Forest, NH. Earth Surface Processes and Landforms 32:1154–1163.

Warren, D. R., S. M. Collins, E. M. Purvis, M. J. Kaylor, and H. A. Bechtold. 2016. Spatial variability in light yields co-limitation of primary production by both light and nutrients in a forested stream ecosystem. Ecosystems.

Warren, D. R., C. E. Kraft, W. S. Keeton, J. S. Nunery, and G. E. Likens. 2009. Dynamics of wood recruitment in streams of the northeastern US. Forest Ecology and Management 258:804–813.

Wilzbach, M. A., and J. D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. Verhandlungen International Verein Limnologie 22:2516–2522.

Wilzbach, M. A., B. C. Harvey, J. L. White, and R. J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:58–67.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7:1–9.

Young, M. K., E. A. Mace, E. T. Ziegler, and E. K. Sutherland. 2006. Characterizing and contrasting instream and riparian coarse wood in western Montana basins. Forest Ecology and Management 226:26–40.

Table 3.1: Physical attributes of stream reach pairs. OG = old-growth riparian forest and PH = previously harvested riparian forest on at least one stream bank.

Site	Riparian type	Harvest Year	Stand Area (ha)	Bankfull Width (m)	Canopy Openness (%)	Gradient (%)	Wood Volume ($m^3/100m^2$)	Pool Area (%)	NO_3-N (µg/L)	Temp (ºC)
MCTE	OG	-	-	3.46	11.2	6.8	6.0	29.3	1.3	12.3
	PH	1958	9	3.06	5.1	7	1.4	10.3	5.8	12.6
MCTW	OG	-	-	4.1	8.6	6.7	10.8	24.4	4.0	13.1
	PH	1953	17	3.4	6.1	4.3	1.2	13.1	3.3	13.3
MR504	OG	-	-	6.9	22.4	6.8	2.6	37.9	3.0	11.2
	PH	1958	9	6.3	8.4	6.8	3.1	30.8	4.0	11.4
LO703	OG	-	-	7.8	34.0	6.4	2.0	16.8	48.9	9.1
	PH	1960	7	7.4	53.8	6.4	0.7	15.4	44.2	9.3
Fritz	OG	-	-	9.7	11.1	16	2.6	27.3	9.6	13.9
	PH	1960	7	7.8	2.6	13.8	2.8	29.9	11.3	14.2
Mack	OG	-	-	9.8	23.9	9.5	6.0	27.0	63.7	12.4
	PH	1965	4	9.3	32.2	9.9	1.5	21.4	58.0	12.7
LO701	OG	-	-	9.9	20.2	7.1	2.7	40.2	42.0	9.9
	PH	1959	12	9.0	10.5	6.0	0.9	42.4	38.5	10.3
Cook	OG	-	-	10.55	23.8	4.6	6.6	17.5	37.5	13.8
	PH	1971	7	8.6	4.8	4	0.6	21.2	31.9	13.9
MR404	OG	-	-	10.4	29.0	7.6	6.8	41.0	20.4	13.7
	PH	1953	20	8.6	32.7	4.0	0.3	19.2	20.6	13.6

Table 3.2: Biotic variables estimated in each reach.

Site	Riparian type	Chl a ($\mu g/cm^2$)	Total invertebrate biomass (g/m^2)	Predatory invertebrate biomass (g/m^2)	Cutthroat trout biomass (g/m^2)	Salamander biomass (g/m^2)	Total vertebrate biomass (g/m^2)
MCTE	OG	0.04 (0.02)	1.16	0.22	2.66 (2.66-2.74)	6.91 (5.75-8.07)	9.58 (8.42-10.81)
	PH	0.12 (0.06)	1.67	0.82	3.44 (3.44-3.44)	7.56 (6.33-8.79)	11.10 (9.87-12.34)
MCTW	OG	0.46 (0.15)	0.75	0.36	1.88 (1.88-2.36)	6.00 (3.34-8.65)	7.92 (5.26-11.05)
	PH	0.27 (0.11)	0.89	0.26	1.87 (1.87-1.93)	8.36 (4.84-11.88)	10.31 (6.76-13.98)
MR504	OG	0.16 (0.04)	1.70	0.91	2.68 (2.47-2.89)	8.94 (2.78-15.09)	11.76 (5.34-18.17)
	PH	0.15 (0.06)	0.84	0.50	2.87 (2.36-3.38)	7.67 (3.10-12.24)	10.64 (5.52-15.77)
LO703	OG	1.28 (0.25)	2.56	0.96	5.13 (4.68-5.59)	9.82 (5.79-13.96)	15.22 (10.66-19.77)
	PH	1.28 (0.54)	3.55	1.01	8.01 (7.53-8.48)	14.95 (7.41-22.48)	23.14 (15.09-31.20)
Fritz	OG	0.18 (0.07)	1.05	0.37	0.87 (0.72-1.04)	8.36 (4.41-12.32)	9.25 (5.14-13.36)
	PH	0.09 (0.05)	0.68	0.43	2.46 (2.46-2.23)	5.75 (1.78-9.72)	8.28 (4.06-12.49)
Mack	OG	1.08 (0.33)	2.61	1.48	4.15 (4.11-4.21)	6.91 (6.22-7.59)	11.18 (10.47-11.93)
	PH	0.97 (0.21)	1.72	1.01	4.70 (4.55-4.87)	7.95 (7.06-8.84)	12.79 (11.74-13.83)
LO701	OG	1.36 (0.10)	2.53	1.62	6.29 (5.72-6.86)	10.58 (1.46-19.70)	16.99 (7.27-26.71)
	PH	0.82 (0.14)	1.07	0.73	4.20 (3.96-4.44)	12.86 (3.95-21.78)	17.08 7.93-26.24)
Cook	OG	0.62 (0.19)	1.09	0.71	3.29 (2.97-3.61)	8.09 (5.14-11.05)	11.46 (8.14-14.77)
	PH	0.39 (0.15)	0.64	0.39	2.93 (2.67-3.20)	4.41 (2.81-6.02)	7.45 5.55-9.35)
MR404	OG	1.09 (0.24)	1.50	1.08	4.17 (3.70-4.64)	5.87 (2.04-9.71)	11.87† (6.82-16.93)
	PH	1.09 (0.17)	1.83	1.18	3.26 (2.93-3.59)	6.69 (3.55-9.83)	13.35† (8.68-18.02)

†Total vertebrate biomass for MR404 includes sculpin (*Cottus spp.*).

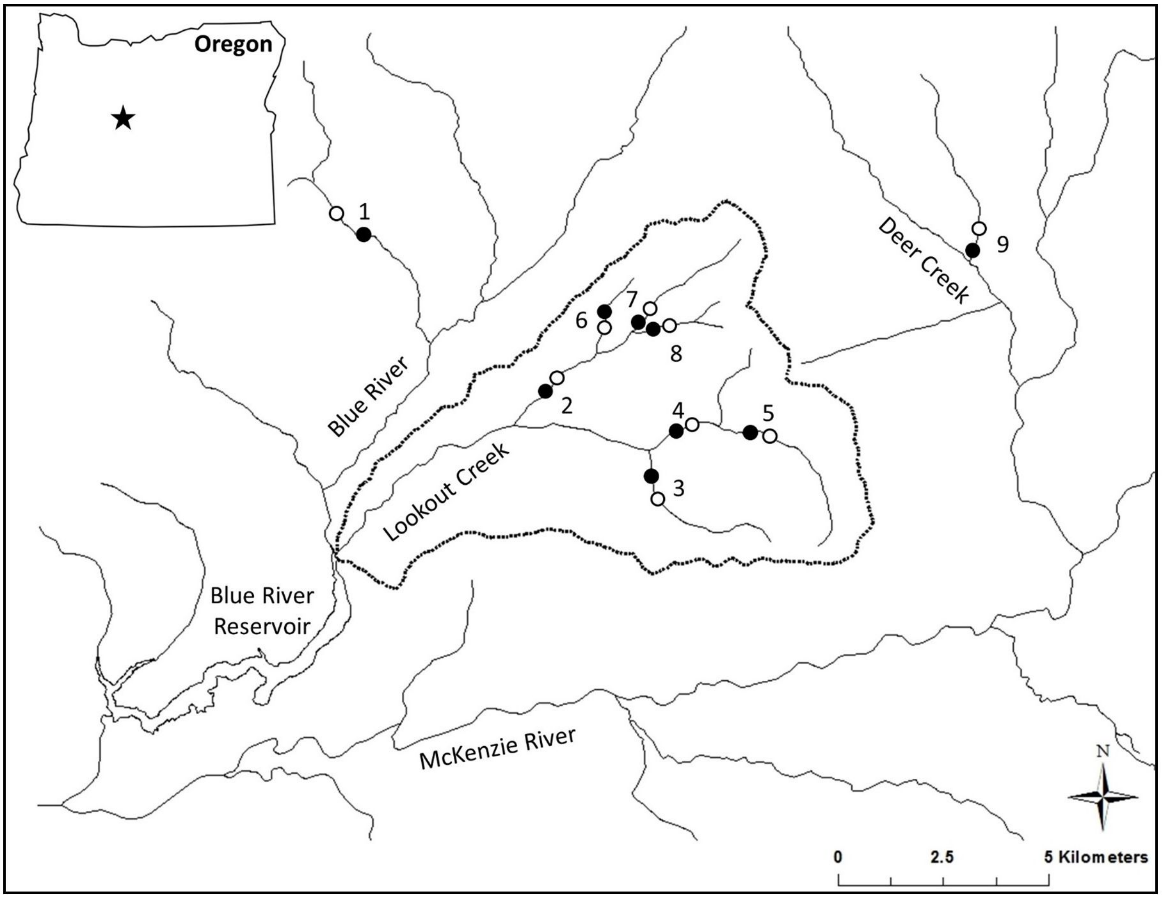


Figure 3.1: Map of the nine reach pair locations in the McKenzie River Basin, Oregon. Each reach pair consists of a reach within old-growth forest (open circles) and a reach bordered by previously harvested riparian forest (closed circles). Pair 1 = Cook; 2 = MR404; 3 = Mack; 4 = LO701; 5 = LO703; 6 = MCTW; 7 = MR504; 8 = MCTE; 9 = Fritz.

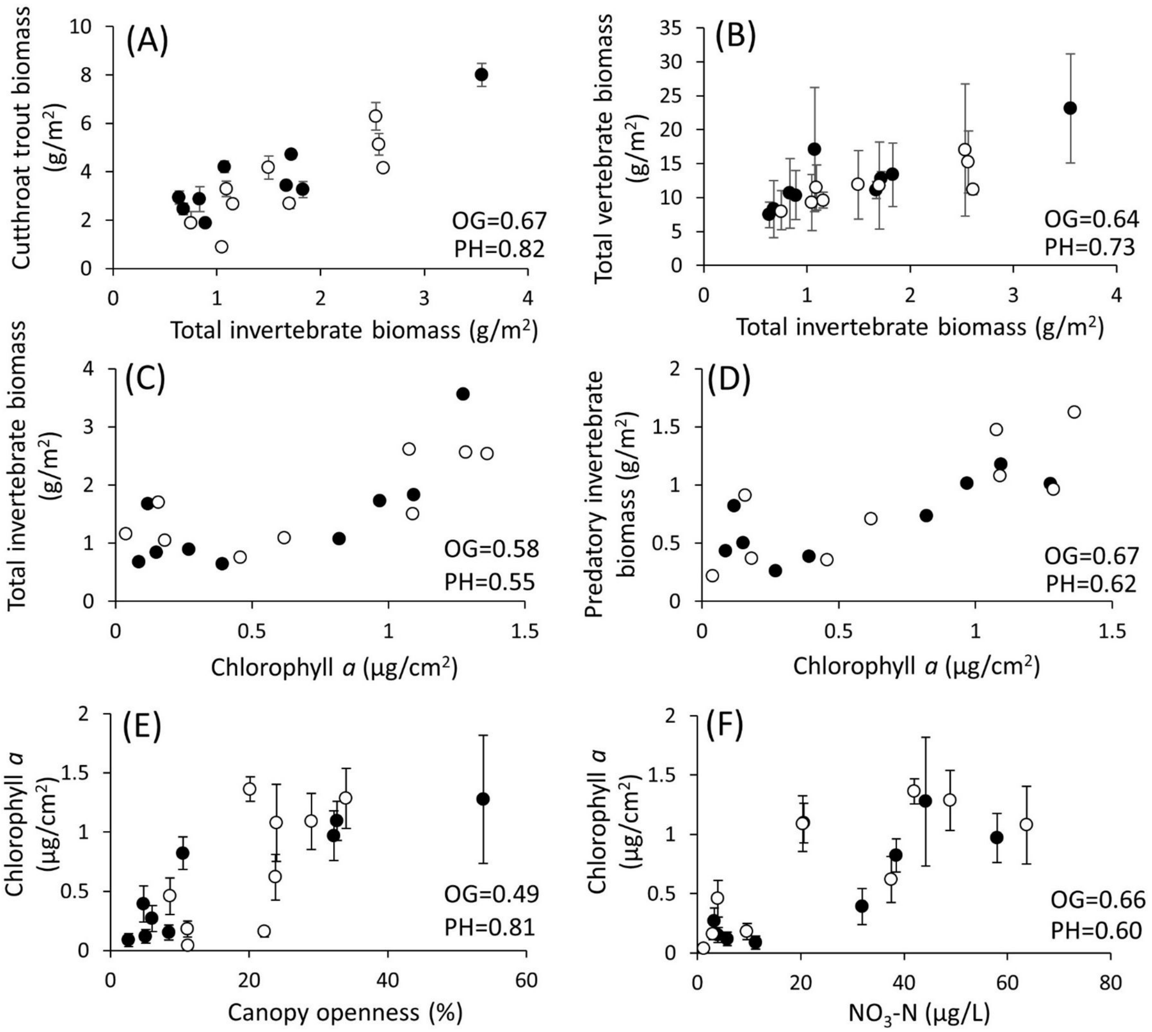
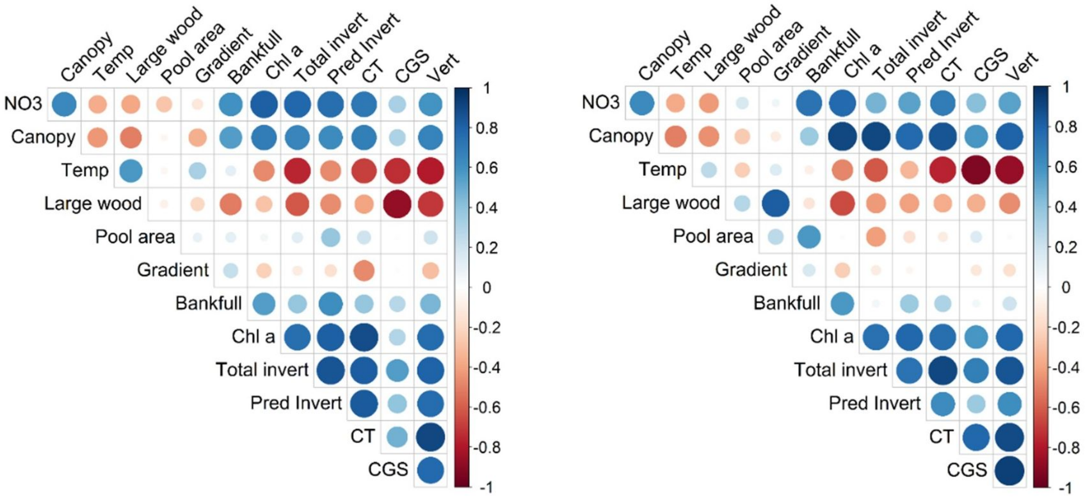


Figure 3.2: Relationships between total invertebrate biomass and cutthroat trout biomass (A), total invertebrate biomass and total vertebrate biomass (B), chl *a* and total invertebrate biomass (C), chl *a* and predatory invertebrate biomass (D), canopy openness and chl *a* (E), and nitrate-N and chl *a* (F). Open circles indicate old-growth reaches, while closed circles indicate previously harvested site reaches. Values in lower right corner of each panel indicate *r*-squared values, which were evaluated separately across old-growth (OG) and previously harvested (PH) reaches.


(A) Old-growth

(B) Previously harvested

(C) Reach pair differences (OG-PH)

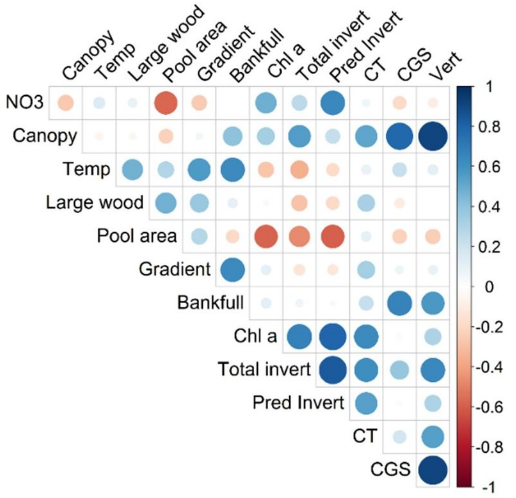


Figure 3.3: Correlation matrix for reaches bordered by old-growth forests (A), reaches bordered by previously harvested forests (B), and reach pair differences (C). CT = cutthroat trout biomass (g/m^2); CGS = coastal giant salamander biomass (g/m^2); Vert = total vertebrate biomass (g/m^2); Chl = chlorophyll *a* content (µg/cm^2); Invert = total invertebrate biomass (g/m^2); PredInvert = predatory invertebrate biomass (g/m^2); Canopy = canopy openness (%); BF = bankfull width (m); LW = large wood volume (m^3/100 m^2); Grad = gradient (%); NO₃ = nitrate-N concentration (µg/L); Temp = mean daily mean temperature (°C). See Appendix S1: Figs. S1–S3 for correlation coefficients and *P*-values.

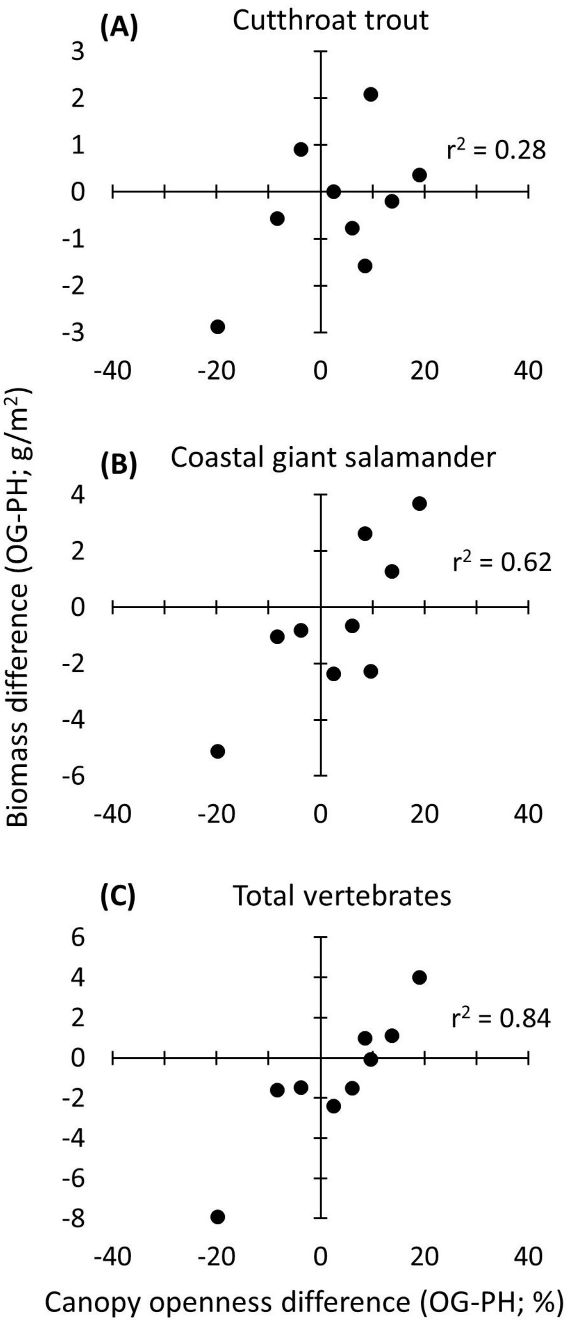


Figure 3.4: Relationships between reach pair differences (old growth minus previously harvested) in canopy openness vs. trout biomass (upper), salamander biomass (middle), and total vertebrate biomass (lower).

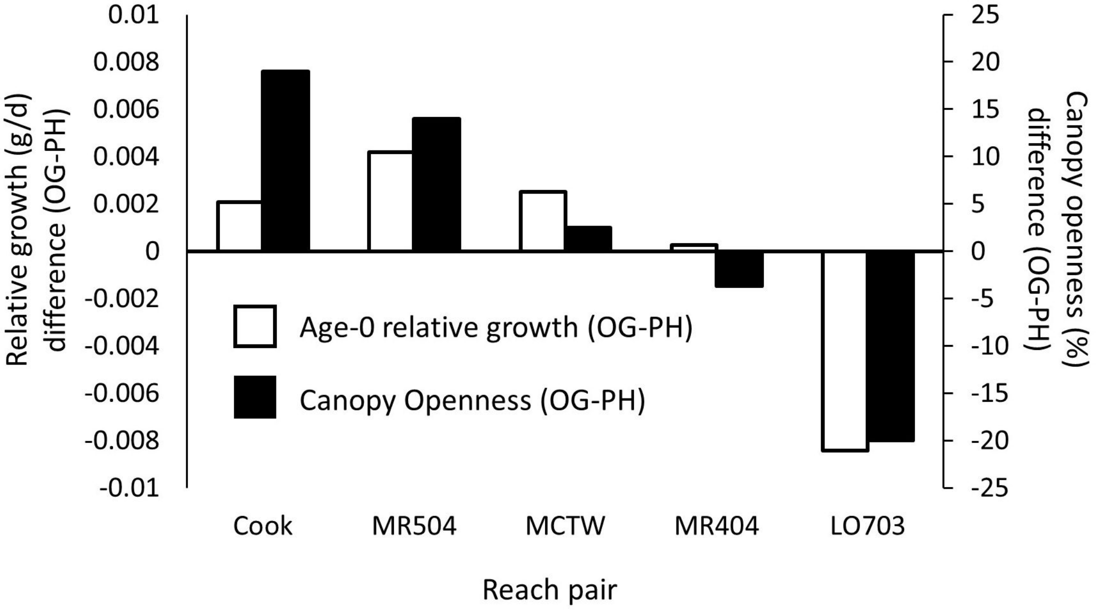


Figure 3.5: Reach pair differences (old growth [OG] minus previously harvested [PH]) for juvenile (age-0+) relative growth rates (open bars; left *y*-axis) and canopy openness (filled bars; right *y*-axis).

CHAPTER 4: CITATION INFORMATION

CANOPY CLOSURE AFTER FOUR DECADES OF POSTLOGGING RIPARIAN FOREST REGENERATION REDUCES CUTTHROAT TROUT BIOMASS IN HEADWATER STREAMS THROUGH BOTTOM-UP PATHWAYS

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Canadian Journal of Fisheries and Aquatic Sciences, 2018

Issue 75, pp 513-524

CHAPTER 4: CANOPY CLOSURE AFTER FOUR DECADES OF POSTLOGGING RIPARIAN FOREST REGENERATION REDUCES CUTTHROAT TROUT BIOMASS IN HEADWATER STREAMS THROUGH BOTTOM-UP PATHWAYS

Matthew J. Kaylor and Dana R. Warren

Abstract

Recovery from timber harvest is widespread across North America, but few studies have evaluated long-term stream responses to riparian harvest. We revisited five stream reach pairs where in 1976, periphyton chlorophyll a, predatory invertebrate biomass, and cutthroat trout (Oncorhynchus clarkii clarkii) biomass were elevated in reaches where canopies were more open following timber harvest. After four decades of riparian regeneration, mean canopy openness, chlorophyll a, predatory invertebrate biomass, and cutthroat trout biomass declined in harvested reaches relative to paired old-growth reference reaches. In one reach pair, the harvested reach remained more open than the control reach. In accordance with the hypothesis that light exerts strong controls on predator biomass via bottom-up processes in these forested headwaters, trout biomass was also greater in the harvested reach in this pair in 2014. Changes in large wood and pool area over this time interval do not account for chlorophyll a, predatory invertebrate biomass, or cutthroat trout biomass responses. These results provide empirical support for conceptual models relating changes in riparian canopy cover to primary production and bottom-up controls on consumer populations.

Introduction

The removal or loss of streamside (riparian) forests have clear acute impacts on associated aquatic environments, particularly headwater streams where interaction between aquatic and terrestrial environments are maximized. Stream responses to riparian harvest have been relatively well studied for the initial years following canopy removal (<10 years), but few studies have evaluated long-term recovery from this disturbance or its effects on stream biota. Conceptual models based on results from comparative studies evaluating stream abiotic and biotic differences between stream reaches of contrasting forest type (e.g., clear-cut, second-growth, old-growth) have been developed to suggest likely trajectories of change in stream biota and stream ecosystem processes over the decadal time scales associated with riparian forest stand development (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009; Warren et al. 2016). These conceptual trajectories portray increases in primary production, with subsequent bottom-up driven increases in invertebrate production and top consumer (usually salmonids) biomass shortly after riparian canopy removal. Then, following canopy closure that reduces light availability, these conceptual models suggest decreasing primary production with associated declines in consumer biomass. Throughout North America, recovery from 20th century timber harvest is a widespread process that affects riparian zones as well as the upland forest (Pan et al. 2011; Kaylor et al. 2017). Evaluating both short-term and long-term impacts of riparian forest removal and recovery provides a more complete understanding of the impacts of riparian forest harvest on adjacent stream ecosystems.

Removing riparian forests can impact stream habitat, physiochemical conditions of a stream, and the productivity and food web structure of streams (Bilby and Ward 1991; Bilby and Bisson 1992; Wootton 2012). The removal of streamside vegetation reduces allochthonous carbon subsidies (e.g., litter and terrestrial invertebrate inputs), and without any compensatory increases in autochthonous carbon, a reduction in detrital and terrestrial invertebrate inputs can lead to decreased abundances and growth of secondary consumers and predators (Wallace 1997;

Nakano et al. 1999; Wallace et al. 1999). But riparian timber harvest also reduces stream shading, which may lead to increases in primary production and autochthonous carbon availability (e.g., stream benthic algal communities) by alleviating light limitation (Bilby and Bisson 1992; Ambrose et al. 2004; Wilzbach et al. 2005). When an increase in autotrophy compensates for loss of litter inputs following riparian canopy loss, the abundances and biomass of food-limited invertebrates and fish can increase (Noel et al. 1986; Bilby and Bisson 1992; Wootton 2012). Decreased shading can also lead to increases in stream temperature (Beschta et al. 1987; Moore et al. 2006; Groom et al. 2011), and this can be a concern in systems dominated by cold-water salmonid fishes. Historical timber harvest operations in the riparian zone and upland forest can also negatively impact the stream shortly after logging by increasing sediment inputs (Kreutzweiser and Capell 2001; Croke and Hairsine 2006), decreasing stream habitat complexity (Murphy et al. 1986; Ralph et al. 1994; Sweeney et al. 2004), and creating chemically stressful stream conditions (e.g., pH; Baldigo et al. 2005).

Short-term stream responses to timber harvest have been well studied, particularly the response of salmonid species in the Pacific Northwest region of North America (Hall and Lantz 1969; Murphy and Hall 1981; Bilby and Bisson 1992). However, results from this work have been equivocal, with substantial variation in the magnitude and directionality of fish population responses (reviewed in Mellina and Hinch 2009). The extent of habitat modification (loss) associated with riparian forest management, particularly the removal of large wood from streams and loss of pool habitat, appears to be a key determinant of whether salmonid populations respond positively or negatively on short time scales (Mellina and Hinch 2009). When habitat is not severely degraded, alleviation of light limitation can lead to gains in primary production, thereby enhancing invertebrate production and ultimately top consumer (fish) biomass and growth due to greater prey availability (Murphy and Hall 1981; Bilby and Bisson 1992). Whether initial population responses to harvest are positive (increased biomass) or negative (decreased biomass), few studies have empirically evaluated long-term responses on the decadal time scales riparian forests take to regenerate (Bisson et al. 2008).

One of the earliest and most widely cited studies evaluating the influences of riparian harvest on fish populations is Murphy and Hall (1981), which documented greater summertime periphyton stocks, predatory invertebrate biomass, and coastal cutthroat trout (*Oncorhynchus clarkii clarkii)* biomass in stream reaches adjacent to small patch clear-cuts (4–20 ha) relative to upstream reference reaches. This result was observed despite removal of large wood and reduced pool area in harvested reaches. Given an increase in trout biomass concurrent with reduced large wood and percent pool area in harvested reaches, Murphy and Hall (1981) concluded that changes in trout biomass were likely attributed to greater primary production leading to increased invertebrate prey availability. These findings, along with other Pacific Northwest studies (e.g., Aho 1976; Gregory 1980; Murphy et al. 1981; Hawkins et al. 1983), were used to help develop early conceptual models of the temporal responses of resident salmonids following riparian harvest (Sedell and Swanson 1984; Gregory et al. 1987). These models suggest that fish biomass will be elevated for 10– 20 years after harvest, but that biomass will return to preharvest conditions within 40 years. The potential for biomass levels to fall below preharvest conditions are included if or when second-growth forests had lower light levels than preharvest conditions. Updates of this conceptual framework also ascribe high importance to stream light as a potential driver of long-term trends in salmonid abundance in headwater streams (Mellina and Hinch 2009), but acknowledge the potential for substantial variation in long-term stand development trajectories that may affect changes in canopy cover (Warren et al. 2016). To date, empirical support for the long-term trends is limited, especially on streams where the initial responses to harvest have been quantified.

In this study, we revisited five of the six fish-bearing stream reach pairs originally surveyed by Murphy and Hall (1981) to determine how stream conditions, benthic biofilms, invertebrate predators, and ultimately resident coastal cutthroat trout have responded to nearly four decades of riparian forest regeneration. Using the upstream reference reaches identified by Murphy (1979), which were bordered by old-growth riparian forests, this design is similar to a before–after, control–impact (BACI) study with riparian regeneration as the treatment. We hypothesized that canopy closure associated with stand regeneration would correspond with declines in chlorophyll a (hereinafter chl a) standing stocks, predatory invertebrate biomass, and cutthroat trout biomass. These long-term responses have important implications for stream function across North America where riparian forest recovery is an ongoing and widespread process (Richardson et al. 2012).

Methods

Study system

The five streams evaluated in this study are located within the H.J. Andrews Experimental Forest (hereinafter HJA) and the sur- rounding Willamette National Forest in the western Cascade Mountains of Oregon (Figure 4.1). This region is characterized by a Mediterranean climate of wet winters and dry, warm summers. Stream reaches ranged in elevation from 630 to 940 m and were relatively high gradient (4%–10%; Table 4.1) with boulder-dominated substrates. Before forest management began in the HJA in the 1950s and 1960s, the area was dominated by a mix of old-growth (dominant trees >400 years of age) and mature (100–150 years old) forests. Today, the HJA remains dominated by late-succession – old-growth forests, but patches of younger forest occur regularly in the system, reflecting the legacy of past experimental forest management. This patchy forest management within the larger basin created areas where a single stream could have some sections that were heavily impacted by logging and others that were largely unaffected. In this study, we assessed stand regeneration effects on established reach pairs that utilized this patchy management history. Each reach pair in a stream consisted of a stream reach bordered by old-growth riparian forest (hereinafter referred to as old-growth reaches) and a reach bordered by previously harvested and currently regenerating riparian forest (hereinafter referred to as previously harvested reaches). Streamside harvesting of the relatively small patch clear-cuts (4–20 ha) evaluated in this study occurred between 1953 and 1971 (Table 4.1). Harvesting occurred on both stream banks in Mack Creek and Cook Creek, but only on one stream bank at cutblock MR404 on McRae Creek and cutblocks LO701 and LO703 on Lookout Creek. In all cases trees were removed to the stream edge with no buffers, and wood was removed from streams during harvest operations, in accordance with standard forest management practices at that time. Stands were planted with Douglas-fir (*Pseudotsuga menziesii*) within 5 years of harvest in the management areas, with the exception of Mack Creek, which was allowed to naturally regenerate. Following harvest or disturbance, red alder (*Alnus rubra*) commonly occupies riparian zones in this region (Summers 1982; Van Pelt et al. 2006; Villarin et al. 2009) and was a dominant canopy species over the stream along the previously harvested reaches of LO701, Cook, and MR404. Very few alder were present at LO703, where dense vine maple (*Acer circinatum*) was instead the dominant hardwood species directly adjacent to the stream. Forests adjacent to old-growth, reference reaches were dominated by Douglas-fir, western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). In these reaches, alder was present but provided notably less direct over-stream canopy cover.

Detailed explanations of where previous reach pair study sites were established are provided in the appendix of the thesis of Murphy (1979), and we were therefore able to identify the locations of both impacted and reference reaches used in the initial surveys. In the initial study (Murphy and Hall 1981), six fish-bearing paired reaches were surveyed. We could no longer access one of these streams due to road closures. The reaches surveyed in Murphy and Hall (1981) were 30– 50 m in length except for Mack Creek, which had a study reach 200 m in length. We increased reach lengths in the 2014 study to a minimum of 10 times bank-full width (range 90–200 m; Table 4.1) to encompass a wider variety of habitats and account for more spatial variability in fish abundance and biomass. However, lengthening the reaches slightly altered current assessment relative to the initial study. To evaluate whether the use of longer reaches affected the outcome of the stand-regeneration analysis relative to the previous surveys at these sites, we subdivided each individual reach into two sections: (*i*) a 30–40 m reach that corresponded directly to the reach surveyed in Murphy and Hall (1981) and (*ii*) the additional stream section (ranging from 50 to 70 m). Results from the shorter (30–40 m) reaches were similar to results from the entire reach that included the shorter reaches. More specifically, the ratios between the harvested reach and the old-growth reach in each reach pair were similar between the shorter reaches and the full reaches, and in every case, the ratio did not affect which reach had greater trout biomass (i.e., if the ratio was greater than 1 for the longer reach, it was also greater than 1 for the shorter survey). Because longer reaches encompass more habitat units and align more with contemporary survey methods, we present results from the full survey reaches in this manuscript. The distances between the downstream impacted sites and the upstream reference sites in reach pairs within a stream ranged from 135 to 325 m.

Resident coastal cutthroat trout were the dominant fish species at all sites, with sculpin (*Cottus* spp.) present in just one site (MR404). Coastal giant salamanders (*Dicamptodon tenebrosus*) were present at all surveyed reaches and were a substantial component of total vertebrate biomass (>50% in some streams).

Field sampling

We collected data on a suite of abiotic and biotic variables that matched those assessed by Murphy and Hall (1981) to evaluate reach-pair changes over time. All of the initial surveys were conducted in summer during the low-flow period between July and September of 1976, with the exception of Mack Creek fish surveys, which occurred during the summer of 1975. Hereinafter, we refer to the sampling by Murphy and Hall (1981) as “1976 surveys”. In the summer of 2014, sampling also occurred during summer low-flow conditions. Physical habitat variables included canopy cover, bank-full width, wetted width, pool area, large wood abundance and volume, mean daily mean temperature, and stream gradient. Canopy cover was quantified in this study using a spherical densitometer with measurements taken in each cardinal direction (n = 4) at 11 locations in each reach. Murphy and Hall (1981) visually assessed canopy openness, and while there is potential for these methods to yield different estimates, all analyses are based on a comparison of changes in the differences within reach pairs (old-growth versus harvested) during each sampling period. Thus, methodology is internally consistent within the two periods, and we focus on the change in ratios between reference and regenerated sites over time (rather than comparing the change in reference over time with the change in regenerated sites over time). Bank-full and wetted widths were measured at regularly spaced intervals, and reach area (for subsequent percent pool area and per unit area standardization of invertebrate and fish assessments) were calculated as reach length multiplied by mean wetted width. We followed the methods of Murphy and Hall (1981) in identifying and characterizing pools, which were identified during summer low-flow conditions as slow-velocity habitat units with minimal turbulence. Pool area was calculated using the length and width of each pool, and percent pool area was calculated as the total pool area divided by total wetted reach area. We counted all large wood pieces — dead wood greater than 10 cm in diameter and 1 m in length — within the bank-full channel. For each piece of large wood, we measured the total length within the stream channel and the diameter of the log at both ends. The mean of the two diameter measurements was used with length of wood in the bank-full channel to calculate wood volume. Total channel area (mean bank-full width multiplied by reach length) was used to calculate large wood volume per unit area. Temperature loggers (HOBO Pro v2; Onset Computer Corporation, Bourne, Massachusetts) were deployed for a 2-week period during midsummer to evaluate relative temperature among streams and differences between paired reaches. Owing to a limitation in the number of sensors, temperature data were collected during the same time period (8–24 August) for all streams except Cook Creek, where temperature sensors were deployed from 20 July to 3 August. Temperature data were not collected in Murphy and Hall (1981), and therefore it was not possible to assess long-term changes in temperature.

Periphyton chl *a* accrual was quantified in the current study on 15 cm × 15 cm ceramic tiles (225 cm^2) deployed in July and incubated for 6 weeks in riffle sections of the stream ($n = 10$ per reach). Ten tiles were placed in the stream thalweg at regular intervals along each study reach. Tiles were scraped using a wire brush in the field, and slurries containing periphyton and stream water for each tile were placed in a cooler and brought back to the lab. Samples were vacuum-filtered using Whatman 47 mm GF/F glass fiber filters, and filters were frozen for 24–48 h prior to extraction of chl *a* with 15 mL of 90% acetone. Samples were stored in the dark for 2–4 h, brought to room temperature, and shaken twice prior to measurements.

Chl *a* concentrations were assessed using fluorometric methods and phaeophytin correction outlined in EPA method 445.0 (Arar and Collins 1997); however, samples were not centrifuged prior to analysis (Turner Designs Chlorophyll Application Guide, p. 4). Chl *a* accrual on tiles was also quantified by Murphy and Hall (1981), but they deployed two ceramic tiles for approximately 4 weeks and analyzed chl *a* concentration using methods outlined in Wetzel and Westlake (1969). We increased sample sizes in this study to provide a more rigorous quantification of differences in periphyton accrual on tiles between reaches in a pair that accounts for potential variability in local periphyton standing stocks.

Predatory invertebrates were quantified in the original study by Murphy and Hall (1981), and we therefore evaluated predatory invertebrate biomass in 2014 to evaluate this response over time. Between August and September of 1976, Murphy and Hall (1981) collected three benthic samples from riffle habitats and pooled these into a single sample for each study reach. The 2014 macroinvertebrate sampling was conducted during low flow in late July, and both reaches of a reach pair were always sampled on the same day. In each sampling event, six Surber samples (363 µm, 0.0625 m^2) were collected from riffle habitats at regular intervals along each reach. Substrate within the Surber sample quadrate was disturbed to a depth of 10 cm for approximately 30 s. Samples were stored in 90% alcohol until processing. In the laboratory, the contents of each of the six Surber samples from each reach were combined into a single pooled sample. This pooled sample was then subsampled using a plankton splitter until a minimum of 500 individuals were picked from the subsample. Murphy and Hall (1981) picked predatory invertebrates from their samples in the field, which clearly biases the final sample composition toward large-bodied individuals. We therefore conducted a 60 s visual search of the remaining sample (less the subsample) to collect large-bodied individuals and more effectively match the initial study. Invertebrates were identified to family or genus (Merritt et al. 2008) and individually measured using an ocular micrometer mounted on a dissecting microscope. Invertebrate length was converted to biomass using length–mass relationships from published studies (Sample et al. 1993; Sabo et al. 2002) and personal data (M. Wipfli, unpublished data). Subsample abundance and biomass was extrapolated (subsample abundance or biomass divided by subsample proportion multiplied by Surber sample area) and combined with the 60 s sample to estimate total abundance and total biomass for each stream reach.

In 2014, fish were collected using a backpack electroshocker (Smith-Root model LR-20B). Block nets were set at the upper and lower ends of each reach to prevent movement and close the system for the duration of the surveys (nets were left in place for the duration of the mark–recapture period). Fish were anesthetized using AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand), weighed, and measured (total length). For mark–recapture surveys, fish were marked with a small caudal clip. Fish were released and each reach was resurveyed after approximately 24 h. Mark–recapture population estimates were used in four streams (Cook, MR404, LO701, LO703), and abundance was estimated using the Lincoln–Peterson mark–recapture model, modified by Chapman (1951). Mark–recapture reach-scale biomass was estimated by multiplying abundance estimates by mean mass. Juvenile (0+) and adult (1+) cutthroat trout were analyzed separately. In 1976 surveys, mark–recapture methods were used at Cook Creek, MR404, and LO703, but multiple pass depletion methods were used at LO701.

In both 1976 and 2014, multiple pass depletion methods were used to estimate population abundance in Mack Creek. The long-term research project provided the 2014 electrosurvey data used in this study (S.V. Gregory, Oregon State University, Department of Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR 07331, USA, unpublished data). However, abiotic and other biotic variables were collected as part of this study, and thus, population estimates, which use reach area, may differ from those of S.V. Gregory.

Salamanders were also sampled during both the 1976 and 2014 survey events. Unfortunately, sparse data from the 1976 surveys (see Murphy 1979, his appendix G) limit our ability to rigorously assess differences in salamander biomass within reach pairs over time (e.g., numbers were too low to provide a robust population estimate in most streams). We therefore only quantitatively evaluate salamander biomass in 2014 and compare estimates of biomass in the harvested and old-growth reach of each reach pair with the other variables collected in this study in 2014. Salamanders were surveyed using the same methods as cutthroat trout. However, salamanders were marked with a visual elastomer tag (Northwest Marine Technology, Shaw Island, Washington) for mark–recapture surveys.

Statistical analysis

Our comparisons of 2014 results with those of Murphy and Hall (1981) are similar in design to a BACI study. This design has been commonly used to assess the short-term impacts of riparian harvest (and other large-scale perturbations) on an ecosystem using a control or reference reach and a treatment reach with data collected before and after a treatment (Stewart-Oaten et al. 1986). In this study, the Murphy and Hall (1981) data represent our pretreatment condition. Each reach pair (n = 5) consisted of an old-growth, reference reach and a previously harvested, treatment reach. The treatment, or “impact” in this case, is nearly four decades of recovery from riparian harvesting.

Methodology was consistent within sampling years but differed slightly between 1976 and 2014 for some metrics (e.g., chl *a*). We therefore focus on assessing changes in the ratios between reaches within each pair (previously harvested: old-growth) in 2014 relative to the 1976 surveys. We compare the ratios of response variables between previously harvested and old-growth reaches within years (1976 and 2014), and we evaluate the mean change in the ratios of each response variable between previously harvested and old-growth reaches before (1976) and after (2014) riparian forest stand regeneration. To statistically evaluate potential differences in response metrics within years, we conduct one-sample *t* tests of the natural-log-transformed ratios (previously harvested: old-growth) within each year. A mean of 0 in this analysis would indicate no difference in the response variable between paired previously harvested and old-growth reaches during that period (1976 or 2014). Because ratios are more easily interpreted, we provide back-transformed estimates of the mean ratio (previously harvested: old-growth), associated 95% confidence intervals, *t* statistics, and *p* values. To evaluate whether the mean ratios for previously harvested and old-growth reaches differed between sampling periods (1976 versus 2014), we conduct paired *t* tests of the difference in log-ratios from 1976 to 2014.

Results

In 1976, Murphy and Hall (1981) compared stream sections bordered by recent patch clear-cuts with paired old-growth reference sections on the same stream. During these initial surveys, percent pool area and large wood volume were lower in the harvested reach compared with the old-growth reach for all five reach pairs (Figs. 2A and 2B, respectively). In contrast, canopy openness, periphyton chl *a* (with one exception), predatory invertebrate biomass, and cutthroat trout biomass were greater in the harvested reach of each reach pair (Figs. 2C–2F). After nearly four decades of riparian regeneration, the ratios (previously harvested : old-growth) of percent pool area and large wood volume largely persisted, while the ratios of canopy openness, chl *a*, predatory invertebrate biomass, and cutthroat trout biomass decreased, indicating a relative decline of the latter metrics in previously harvested reaches relative to paired old-growth reaches (Figure 4.3).

In 1976, percent pool area in harvested reaches averaged 0.71 times (95% CI: 0.50–1.00; back-transformed from log-ratio estimates) that of associated upstream old-growth reaches (one-sample *t* test of natural log-ratios; $T_{[4]} = –2.79$; $p = 0.049$). In 2014, percent pool area was still lower in previously harvested reaches and averaged 0.85 times (95% CI: 0.54–1.33) that of old-growth reaches, although these differences were no longer statistically significant ($T_{[4]} = –1.02$, $p = 0.363$). In 1976, large wood, which had been removed during harvesting operations, was substantially lower in the harvested reach of each pair and averaged only 6% (95% CI: 1%–81%) of wood volume in old-growth reaches ($T_{[3]} = –3.44$; $p = 0.041$). Large wood volume in one previously harvested reach was reported as zero (versus 0.9 $m^3 \cdot 100\ m^{-2}$ in the paired old-growth reach), and therefore the ratio of this reach pair could not be evaluated. Four decades later, large wood volume was still substantially lower in previously harvested reaches, averaging 16% (95% CI: 5%–54%) of wood volume in paired old-growth reaches ($T_{[4]} = –4.17$; $p = 0.014$). In contrast with percent pool area and large wood volume, changes in the ratio of canopy cover between paired previously harvested and old-growth reaches changed substantially over the four-decade time interval. In 1976, canopy openness was on average 2.46 times (95% CI: 1.62–3.72) greater in the harvested reach compared with paired old-growth reaches ($T_{[4]} = 6.02$; $p = 0.004$).

However, in 2014, canopy openness in previously harvested reaches was on average 0.76 times (95% CI: 0.26–2.20) the canopy openness in paired old-growth reaches ($T_{[4]}$ = –0.72; p = 0.510).

Mean ratios of chl *a*, predatory invertebrate biomass, and cutthroat trout biomass between previously harvested reaches and paired old-growth reaches generally reflected canopy openness results from 1976 and 2014. In 1976, chl *a* was on average 1.86 times (95% CI: 1.21–2.86) greater in the harvested reach of each pair ($T_{[4]}$ = 2.15; p = 0.098) relative to the old-growth reach. In 2014, chl *a* in previously harvested reaches was on average 0.81 times (95% CI: 0.59–1.09) that of paired old-growth reaches ($T_{[4]}$ = –1.96; p = 0.121). Predatory invertebrate biomass was quantified in four reach pairs in 1976 but was not collected in LO703. Predatory invertebrate biomass was on average 2.27 times (95% CI: 1.06–4.87) greater in previously harvested reaches compared with paired old-growth reaches during this initial survey period ($T_{[3]}$ = 3.41; p = 0.042). In 2014, predatory invertebrate biomass was quantified at all five reach pairs, and predatory invertebrate biomass in previously harvested reaches averaged 0.72 times (95% CI: 0.44–1.17) the biomass of paired old-growth reaches ($T_{[4]}$ = –1.88; p = 0.134). Lastly, in 1976, cutthroat trout biomass was on average 1.86 times (95% CI: 1.21–2.85) greater in previously harvested reaches compared with paired old-growth reaches ($T_{[4]}$ = 4.00; p = 0.016). Four decades later, cutthroat trout biomass in previously harvested reaches was on average 0.96 times (95% CI: 0.64–1.45) that of paired old-growth reaches ($T_{[4]}$ = –0.26; p = 0.809).

Differences in ratios of paired previously harvested and old-growth reaches between 1976 and 2014 were evaluated using log-ratios (Figure 4.3). The mean difference in log-ratios of percent pool area (paired *t*-test of natural-log-ratios; 95% CI: –0.62–0.28; $T_{[4]}$ = –1.07; p = 0.344) and large wood volume (95% CI: –4.01–1.33; $T_{[3]}$ = –1.60; p = 0.209) were not significantly different between 1976 and 2014. However, the mean difference of log-ratios between 1976 and

2014 were significantly different for canopy openness (95% CI: 0.15–2.20; $T_{[4]} = 3.19$; $p = 0.033$), chl *a* (95% CI: 0.18–1.46; $T_{[4]} = 3.47$; $p = 0.023$), and predatory invertebrate biomass (95% CI: 0.70–1.78; $T_{[3]} = 7.28$; $p = 0.005$). While the mean log-ratio of cutthroat trout biomass was substantially lower in 2014 compared with 1976, the mean difference in log-ratios was not significant at $\alpha = 0.05$ (95% CI: –0.04–1.36; $T_{[4]} = 2.62$; $p = 0.059$).

Although on average across the five reach pairs, forest regeneration resulted in a decline in canopy openness, chl *a*, predatory invertebrate biomass, and ultimately cutthroat trout biomass, this result was not universal. In 2014, canopy openness was still substantially greater in the previously harvested reach of LO703 relative to the old-growth reach (54% versus 34%) despite four decades of stand regeneration. While the canopy did not close over this time interval as we expected, the lack of canopy closure at this site was fortuitous in that it allowed us to more explicitly evaluate the role of light regulating bottom-up controls on stream biota. In 1976, canopy openness, chl *a*, and cutthroat trout biomass in LO703 were greater in the harvested reach (predatory invertebrates were not collected at this site during initial surveys). In 2014, contrary to expectations, mean chl *a* and predatory invertebrate biomass were relatively similar between the previously harvested and old-growth reaches. However, consistent with expectations, cutthroat trout biomass remained greater in the previously harvested reach relative to the more shaded old-growth reach (8.01 versus 5.13 g m^{-2}).

We were not able to rigorously compare estimates of salamander biomass between 1976 and 2014. However, results from 2014 alone are consistent with those observed for cutthroat trout biomass (Figure A4.1). Estimates of salamander biomass were similar between the harvested reach and the old-growth reach for MR404, Mack Creek, and LO701. In Cook Creek, where estimates of canopy openness and cutthroat trout biomass were lower in the harvested reach, salamander biomass was just over half the estimated biomass in the old-growth reach (4.41 versus 8.1 $g \cdot m^{-2}$). In LO703, estimated salamander biomass was substantially greater in the harvested reach compared with the old-growth reach (14.95 versus 9.82 $g \cdot m^{-2}$), a result that is also consistent with canopy openness and trout biomass.

Discussion

After nearly four decades of riparian regeneration, mean canopy openness, chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout biomass declined in harvested reaches relative to paired old-growth reference reaches, which provides empirical data supporting conceptual models of stream abiotic and biotic responses to riparian stand regeneration over time in forested ecosystems. In the sites evaluated in this study, mean chl *a*, predatory invertebrate biomass, and cutthroat trout biomass were initially greater in harvested reaches where canopies were more open relative to paired, old-growth reaches 5–23 years after riparian harvest occurred (Murphy and Hall 1981). These results were observed despite the removal of large wood and lower percent pool area in harvested reaches compared with paired old-growth reaches. In 2014, large wood volume was still substantially lower in previously harvested reaches but percent pool area was similar between paired previously harvested and old-growth reaches. Consistent with the hypothesis that stream light availability can be an important bottom-up driver of the biomass of periphyton and biota in headwater streams, declines in canopy openness in previously harvested reaches relative to paired old-growth reaches over this time interval were accompanied by similar declines in periphyton chl *a*, predatory invertebrate biomass, and cutthroat trout biomass in four of five streams. Overall results from four of the five sites were consistent with trajectories of change portrayed in conceptual models where bottom-up processes strongly influence top predator biomass (usually salmonids), with increases in predator biomass shortly after riparian forest harvest and declines in the biomass of stream predators following stand regeneration when canopies close back over the stream (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009; Warren et al. 2016).

In contrast with our expectations, trout biomass remained substantially greater in the previously harvested reach relative to the reference, old-growth reach at site LO703. While the trend at this site did not fit the classic hypothesized trajectory of biomass over time (e.g., reduced biomass), this result ultimately provides support for the importance of light as a driver of trout biomass in these forested headwater streams. The LO703 site experienced little change in canopy cover from 1976 to 2014, with greater canopy openness in the previously harvested reach during both survey periods. Therefore, the absence of a relative decline in trout biomass following stand regeneration from 1976 to 2014 is consistent with the hypothesized mechanism of changes in canopy cover exerting controls on consumers through bottom-up processes. However, in 2014, chl *a* and the biomass of predatory invertebrates were similar between reaches within this pair despite differences in canopy cover. We speculate that the similarity in chl *a* may be attributed to greater grazing pressure in the previously harvested reach because total invertebrate biomass (not just predatory invertebrates) was approximately 40% greater in the previously harvested reach in 2014 compared with the old-growth reach (Kaylor and Warren 2017), and other studies have found that the effects of changing light on periphyton standing stocks can be missed when macroinvertebrate consumption is high (Kiffney et al. 2004). Additionally, salamander biomass at this site was 1.5 times greater in the previously harvested reach in 2014. The previously harvested reach of LO703 was the only previously harvested reach in which vine maple (rather than alder) dominated the riparian tree community. The results from this reach pair therefore also highlight the importance of considering multiple riparian development trajectories when assessing and projecting forest recovery influences on streams and the biota therein (Warren et al. 2016).

While changes in light over time appear to be the dominant driver of the trout biomass in our study streams, variables not quantified in this study may have also influenced trout biomass over time. Nutrient inputs to streams, particularly nitrogen, often increase in response to riparian harvest (Feller 2005; Kreutzweiser et al. 2008), and increased nutrient inputs have been linked to increased predator production through bottom-up pathways (Johnston et al. 1990; Deegan and Peterson 1992; Peterson et al. 1993; Cross et al. 2006). However, stream nutrient responses to riparian harvest typically depend on the amount of the basin harvested (Tiedemann et al. 1988; Feller 2005), and the size of harvest units in this study were small (<20 ha) within a surrounding basin of unharvested forest. Similarly, temperature may have increased following riparian harvest, which could have altered stream productivity and fish growth rates. In the 1970s, temperature was only monitored at one of the five sites (Mack Creek), and mean weekly temperatures did not exceed 1.0 °C greater in the harvested reach compared with the upstream reference reach (Aho 1976). Given the small sizes of the harvest units and the cool background temperatures of the streams in this study, we do not invoke temperature changes as a major driver of the response in predatory invertebrate or trout biomass. Lastly, because fish are visual feeders, changes in light may have led to changes in fish biomass by altering fish feeding efficiency (Wilzbach and Hall 1985). While decreasing light could lead to reduced feeding efficiency, we do not believe that it was a dominant driver of the responses observed here because it would not account for the changes in chl *a* or predatory invertebrates that we observed.

A limited number of studies have empirically evaluated resident fish responses to timber harvest on the same streams over time scales greater than 10 years (Bisson et al. 2008). These studies reveal the potential for drastically different short- and long-term trajectories from those observed in this study. In the Alsea Watershed study located in the Oregon Coast Range, clear-cut harvesting of the entire 71 ha Needle Branch watershed resulted in a short-term reduction in resident cutthroat trout biomass and abundance (Hall and Lantz 1969). After 25–30 years post-harvest, cutthroat trout biomass had not recovered and remained below preharvest levels (Gregory et al. 2008). Short-term effects of increased temperature, longer-term effects of habitat degradation, and interactions with other salmonid species were identified as possible explanations of continued suppression (Gregory et al. 2008). In East Creek, British Columbia, cutthroat biomass was lower relative to a reference reach following clear-cut harvesting and stream wood removal (Young et al. 1999). Temperatures exceeded 30 °C shortly after harvesting, which likely resulted in high short-term mortality. Approximately a decade later, temperature in the harvested reach had substantially decreased, pool area had increased, and trout abundance was similar to that of the reference reach. Pool area increased again over the next decade, and trout abundance in the previously impacted reach was nearly double that of the reference reach. While this initially appears to contrast with hypothesized trajectories associated with stand recovery and canopy closure, both riparian thinning and habitat restoration occurred in this stream between the second and third sampling events, which confound interpretation of habitat changes alone as the mechanism driving long-term recovery trends (Young et al. 1999).

Our current study along with the two earlier long-term studies and studies quantifying responses over shorter time frames highlight the potential for fish recovery to progress along multiple alternative trajectories that are affected directly and indirectly by trajectories of change in the riparian forest (Hall and Lantz 1969; Young et al. 1999; Gregory et al. 2008; Mellina and Hinch 2009). Long-term recovery from forest management is also a result of how stream habitat and food webs are initially affected by management. In the short term, resident salmonid biomass may substantially decrease when increases in temperature exceed thermal limits or when habitat, particularly loss of pools, is substantially degraded (reviewed in Mellina and Hinch 2009). Populations may recover relatively quickly (<10 years) as temperature recovers or when restoration efforts can enhance the recovery of key habitat elements such as pool structure (Young et al. 1999). However, natural recovery of pool-forming large wood operates on decadal and centennial time scales (Benda et al. 2003; Gregory et al. 2003; Warren et al. 2009), and it is likely that fish populations affected by the loss of large wood structure will remained suppressed for a long period of time (Connolly and Hall 1999). In high-gradient, boulder-dominated systems where large rocks are functioning as key pool-forming agents during summer, changes or differences in large wood volume may be more likely to yield equivocal results since habitat is not limiting (Warren and Kraft 2003). In these systems, changes in light availability and primary production are likely to be the dominant drivers of consumer biomass over time. To illustrate how trajectories of change over time for resident salmonids following riparian harvest can vary depending on the type, degree impact, and trajectories of recovery in the riparian forest, we suggest six dominant alternative trajectories a resident trout population may follow after riparian harvest (Figure 4.4). The set of six alternative trajectories is not exhaustive but demonstrates the complexity of potential resident salmonid responses based on food web and habitat impacts associated with riparian harvest. Greater detail on each trajectory is provided in Appendix B.

In light-limited systems that exhibit trajectories similar to those observed in this study (Figure 4.4, trajectory 1), the timing of canopy closure and duration of a closed canopy will ultimately influence long-term responses to timber harvest and subsequent regeneration. If canopies close quickly (<20 years) and are followed by a long period (>50 years) of low light associated with stands in the mid-seral stages of stand development, harvesting may result in a net reduction in benthic biofilms, aquatic macroinvertebrates, and total trout biomass over decadal time scales, even if an initial increase in biomass was observed in the years shortly after canopy removal. In Douglas-fir dominated regions of the Pacific Northwest, canopy closure over headwater streams typically occurs within 30 years after riparian harvest, and canopies remain more closed than preharvest, old-growth conditions from 30 to 100 years (Kaylor et al. 2017). This has important implications considering riparian harvest has been advocated as a potential tool for increasing fish productivity in Pacific Northwest streams (Newton and Ice 2016) with relatively little consideration of long-term responses and alternative trajectories.

Broadly, this study highlights that changes in stream light availability over time, whether associated with forest recovery or in response to other riparian forest changes, can influence consumers through bottom-up pathways in forested headwater streams. Riparian forest recovery from historical harvest is a widespread process that affects light availability in forested streams across North America (Keeton et al. 2007; Kaylor et al. 2017). Results from this study provide support for the hypothesis that decreasing light availability associated with canopy closure is likely to be accompanied by reductions in consumer biomass in light-limited streams (when habitat degradation has been minimal). However, many forest recovery trajectories exist, and these stand development processes will interact with stream conditions and the physiological constraints of stream biota to allow for multiple trajectories of change over time. Understanding long-term responses of stream habitat, productivity, and consumer populations to riparian harvest and recovery will improve our ability to contextualize and project ongoing changes to stream ecosystem function and stream biota in the future.

Acknowledgements

We thank Brian VerWey, Kate Pospisil, Emily Heaston, Chris Kopet, and Emily Purvis for their work in the field and the H.J. Andrews staff for logistical support. Stanley Gregory and Randy Wildman provided unpublished 2014 fish and salamander survey data from Mack Creek. Judy Li, William Gerth, Dave Lytle, and Rich Van Driesche provided lab space and expertise for invertebrate sorting and identification. Matthew Sloat provided feedback and suggestions on alternative trajectories salmonid populations may take following riparian harvest. Data and facilities were provided by the H.J. Andrews Experimental Forest and Long Term Ecological Research program, administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest. This material is based upon work supported by the National Science Foundation under Grant No. DEB-1440409. Additional funding was provided by Oregon's Fish and Wildlife Habitat in Managed Forests Research Program and by the National Science Foundation's Graduate Research Fellowship Program (Grant No. 1314109-DGE). All surveying efforts were in compliance with Oregon State University's Animal Care and Use Committee (permit No. 4439).

Literature cited

Aho, R.S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. Oregon State University. Available from https://ir.library.oregonstate.edu/xmlui/handle/1957/21777.

Ambrose, H.E., Wilzbach, M.A., and Cummins, K.W. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. North Am. Benthol. Soc. **23**(4): 701–712. doi:doi/10.1899/0887-3593(2004)023<0701:PRTILA>2.0.CO;2.

Arar, E.J., and Collins, G.B. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. *In* US Environmental Protection Agency Method 445.0 Revision 1.2. Cincinnati, Ohio.

Baldigo, B.P., Murdoch, P.S., and Burns, D.A. 2005. Stream acidification and mortality of brook trout (Salvelinus fontinalis) in response to timber harvest in Catskill Mountain watersheds, New York, USA. Can. J. Fish. Aquat. Sci. **62**: 1168–1183. doi:10.1139/F05-022.

Benda, L., Miller, D., Sias, J., Martin, D., Bilby, R., Veldhuisen, C., and Dunne, T. 2003. Wood recruitment processes and wood budgeting. Am. Fish. Soc. Symp. **37**: 49–73.

Beschta, R.L., Bilby, R.E., Brown, G.W., Holtby, L.B., and Hofstra, T.D. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. *In* Streamside management: Forestry and fishery interactions, vol. 57. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Institute of Forest Resources, Seattle, Washington. pp. 191–232.

Bilby, R.E., and Bisson, P.A. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. **49**: 540–551. doi:10.1139/f92-064.

Bilby, R.E., and Ward, J.W. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. **48**: 2499–2508. doi:10.1139/f91-291.

Bisson, P.A., Gregory, S. V., Nickelson, T.E., and Hall, J.D. 2008. The Alsea Watershed Study: A comparison with other multi-year investigations in the Pacific Northwest. *In* Hydrological and Biological Responses to Forest Practices. *Edited by* J.D. Stednick. Springer. pp. 259–289.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution, with applications to zoological sample censuses. Univ. Calif. Publ. Stat. **1**: 131–160.

Connolly, P.J., and Hall, J.D. 1999. Biomass of Coastal Cutthroat Trout in unlogged and previously clear-cut basins in the central Coast Range of Oregon. Trans. Am. Fish. Soc. **128**: 890–899. doi:10.1577/1548-8659(1999)128<0890.

Croke, J.C., and Hairsine, P.B. 2006. Sediment delivery in managed forests: a review. Environ. Rev. **14**: 59–87. doi:10.1139/A05-016.

Cross, W.F., Wallace, J.B., Rosemond, A.D., and Eggert, S.L. 2006. Whole-system nutrient enrichment increases secondary production in a detrital-based ecosystem. Ecology **87**(6): 1556–1565. doi:10.1890/0012-9658(2006)87[1556:WNEISP]2.0.CO;2.

Deegan, L. a, and Peterson, B.J. 1992. Whole-river fertilization stimulates fish production in an arctic tundra river. Can. J. Fish. Aquat. Sci. **49**: 1890–1901.

Feller, M.C. 2005. Forest harvesting and streamwater inorganic chemistry in western North America: A review. J. Am. Water Resour. Assoc. **41**(4): 785–811. doi:10.1111/j.1752-1688.2005.tb03771.x.

Gregory, S.V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. Oregon State University. Available from http://ir.library.oregonstate.edu/xmlui/handle/1957/17914.

Gregory, S.V., Lamberti, G.A., Erman, D.C., Koski, K. V., Murphy, M.L., and Sedell, J.R. 1987. Influences of forest practices on aquatic production. *In* Streamside Management: Forestry and Fishery Interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Institute of Forest Resources, Seattle, Washington. pp. 233–255.

Gregory, S.V., Meleason, M., and Sobota, D. 2003. Modeling the dynamics of wood in streams and rivers. Am. Fish. Soc. Symp. **37**: 315–335.

Gregory, S.V, Schwartz, J.S., Hall, J.D., Wildman, R.C., and Bisson, P.A. 2008. Long-term trends in habitat and fish populations in the Alsea Basin. *In* Hydrological and Biological Responses to Forest Practices. *Edited by* J.D. Stednick. Springer. pp. 237–257. Available from http://www.springerlink.com/index/G011704122L53704.pdf.

Groom, J.D., Dent, L., Madsen, L.J., and Fleuret, J. 2011. Response of western Oregon (USA) stream temperatures to contemporary forest management. For. Ecol. Manage. **262**(8): 1618–1629. doi:10.1016/j.foreco.2011.07.012.

Hall, J.D., and Lantz, R.L. 1969. Effects of Logging on the habitat of coho salmon and cutthroat trout in coastal streams. *In* Symposium on Salmon and trout in streams. *Edited by* T.G. Northcote. H.R. MacMillan Lectures in Fisheries, University of British Columbia. pp. 355–375.

Hawkins, C.P., Murphy, M.L., Anderson, N., and Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Can. J. Fish. Aquat. Sci. **40**(8): 1173–1185. doi:10.1139/f83-134.

Johnston, N.T., Perrin, C.J., Slaney, P.A., and Ward, B.R. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. **47**: 862–872. doi:10.1139/f90-099.

Kaylor, M.J., Warren, D.R., and Kiffney, P.M. 2017. Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams. Freshw. Sci. **36**(1). doi:10.1086/690624.

Kaylor, M.J., and Warren, D.R. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere, 8(6): e01845. doi:10.1002/ecs2.1845.

Keeton, W.S., Kraft, C.E., and Warren, D.R. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecol. Appl. **17**(3): 852–68. Available from http://www.ncbi.nlm.nih.gov/pubmed/17494402.

Kiffney, P.M., Richardson, J.S., and Bull, J.P. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. J. North Am. Benthol. Soc. **23**(3): 542–555.

Kreutzweiser, D.P., and Capell, S.S. 2001. Fine sediment deposition in streams after selective forest harvesting without riparian buffers. Can. J. For. Res. **31**: 2134–2142. doi:10.1139/cjfr-31-12-2134.

Kreutzweiser, D.P., Hazlett, P.W., and Gunn, J.M. 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. Environ. Rev. **16**(NA): 157–179. doi:10.1139/A08-006.

Mellina, E., and Hinch, S.G. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Can. J. For. Res. **39**(7): 1280–1301. doi:10.1139/X09-037.

Merritt, R.W., Cummins, K.W., and Berg, M.B. (*Editors*). 2008. An introduction to the aquatic insects of North America. Kendell Hunt Publishing Company.

Moore, R.D., Spittlehouse, D.L., and Story, A. 2006. Riparian microclimate and stream temperature response to forest harvesting: A review. J. Am. Water Resour. Assoc. **41**(4): 813–834. doi:10.1111/j.1752-1688.2005.tb03772.x.

Murphy, M.L. 1979. Predator assemblages in old-growth and logged sections of small cascade streams. Oregon State University. Available from http://andrewsforest.oregonstate.edu/pubs/pdf/pub1933.pdf.

Murphy, M.L., and Hall, J.D. 1981. Vaired effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. **38**: 137–145. doi:10.1139/f81-018.

Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. **110**(4): 469–478. doi:10.1577/1548-8659(1981)110<469.

Murphy, M.L., Heifetz, J., Johnson, S.W., Koski, K. V, and Thedinga, J.F. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. **43**: 1521–1533. doi:10.1139/f86-190.

Nakano, S., Miyasaka, H., and Naotoshi, K. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology **80**(7): 2435–2441. doi:10.2307/176923.

Newton, M., and Ice, G. 2015. Regulating riparian forests for aquatic productivity in the Pacific Northwest, USA: addressing a paradox. Environ. Sci. Pollut. Res.: 1–9. doi:10.1007/s11356-015-5814-7.

Pan, Y., Chen, J.M., Birdsey, R., McCullough, K., He, L., and Deng, F. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences **8**(3): 715–732. doi:10.5194/bg-8-715-2011.

Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., Hiltner, A., Kipphut, G., Lock, M.A., Fiebig, D.M., Mckinley, V., Miller, M.C., Vestal, J.R., Ventullo, R., Ecology, S., and Apr, N. 1993. Biological responses of a tundra river to fertilization. Ecology **74**(3): 653–672. Available from http://www.jstor.org/stable/1940794.

Ralph, S.C., Poole, G.C., Conquest, L.L., and Naiman, R.J. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. Can. J. Fish. Aquat. Sci. **51**: 37–51. doi:10.1139/f94-006.

Richardson, J.S., Naiman, R.J., and Bisson, P.A. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshw. Sci. **31**(1): 232–238. doi:10.1899/11-031.1.

Sabo, J.L., Bastow, J.L., and Power, M.E. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. North Am. Bentholocial Soc. **21**(2): 336–343. doi:10.2307/1468420.

Sample, B.E., Cooper, R.J., Greer, R.D., and Whitmore, R.C. 1993. Estimation of insect biomass by length and width. Am. Midl. Nat. **129**(2): 234–240. doi:10.2307/2426503.

Sedell, J.R., and Swanson, F.J. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. *In* Fish and Wwldlife relationships in old-growth forests. *Edited by* W.R. Meehan, T.R. Merrell, and T.A. Hanley. Juneau, Alaska. pp. 9–16.

Stewart-Oaten, A., Murdoch, W.W., and Parker, K.R. 1986. Environmental impact assessment: “pseudoreplication” in time? Ecology **67**(4): 929–940. doi:10.2307/1939815.

Summers, R.P. 1982. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. Oregon State University. Available from http://ir.library.oregonstate.edu/xmlui/handle/1957/9877.

Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, L.A., Newbold, J.D., Standley, L.J., Hession, W.C., and Horwitz, R.J. 2004. Riparian deforestation , stream narrowing , and loss of stream ecosystem services. Proc. Natl. Acad. Sci. **101**(39): 14132–14137. doi:10.1073/pnas.0405895101.

Tiedemann, A.R., Quigley, T.M., and Anderson, T.D. 1988. Effects of timber harvest on stream chemistry and dissolved nutrient losses in northeast Oregon. For. Sci. **34**(2): 344–358.

Van Pelt, R., O’Keefe, T.C., Latterell, J.J., and Naiman, R.J. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecol. Monogr.

76(2): 277–298. Available from http://www.jstor.org/stable/27646041.

Villarin, L.A., Chapin, D.M., and Jones, J.E. 2009. Riparian forest structure and succession in second-growth stands of the central Cascade Mountains, Washington, USA. For. Ecol. Manage. **257**(5): 1375–1385. doi:10.1016/j.foreco.2008.12.007.

Wallace, J.B. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science (80-.). **277**(5322): 102–104. doi:10.1126/science.277.5322.102.

Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecol. Monogr. **69**(4): 409–442. doi:10.2307/2657224.

Warren, D.R., Keeton, W.S., Kiffney, P.M., Kaylor, M.J., Bechtold, H.A., and Magee, J. 2016. Changing forests - changing streams: riparian forest stand development and ecosystem function in temperate headwaters. Ecosphere **7**(8): e01435. doi:10.1002/ecs2.1435.

Warren, D.R., and Kraft, C.E. 2003. Brook trout (Salvelinus fontinalis) response to wood removal from high-gradient streams of the Adirondack Mountains (N. Y., U. S. A.). Can. J. Fish. Aquat. Sci. **60**: 379–389. doi:10.1139/F03-031.

Warren, D.R., Kraft, C.E., Keeton, W.S., Nunery, J.S., and Likens, G.E. 2009. Dynamics of wood recruitment in streams of the northeastern US. For. Ecol. Manage. **258**(5): 804–813. doi:10.1016/j.foreco.2009.05.020.

Wetzel, R.G., and Westlake, D.F. 1969. Estimating quantity and quality of biomass - periphyton. *In* A manual on methods for measuring primary production in the aquatic environment. *Edited by* R.A. Voflenweider. Davis Co, Philadelphia. pp. 33–40.

Wilzbach, M.A., and Hall, J.D. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. Verhandlungen Int. Verein Limnol. **22**: 2516–2522.

Wilzbach, M.A., Harvey, B.C., White, J.L., and Nakamoto, R.J. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. Can. J. Fish. Aquat. Sci. **62**: 58–67. doi:10.1139/F04-177.

Wootton, J.T. 2012. River food web response to large-scale riparian zone manipulations. PLoS One **7**(12): 1–9. doi:10.1371/journal.pone.0051839.

Young, K.A., Hinch, S.G., and Northcote, T.G. 1999. Status of resident Coastal Cutthroat Trout and their habitat twenty-five years after riparian logging. North Am. J. Fish. Manag. **19**: 901–911.

Table 4.1: Physical attributes of stream reach pairs in summer 2014. OG =bordered by old-growth riparian forest and PH = bordered by previously harvested riparian forest on at least one stream bank. Temperature is the mean daily mean temperature for a two-week period in July, 2014.

Site	Riparian type	Harvest Year	Area Harvested (ha)	Bankfull Width (m)	Canopy Openness (%)	Gradient (%)	Wood Volume (m^3 100 m^{-2})	Pool Area (%)	Elevation (m)	Temp (°C)
LO703	OG	-	-	7.8	34.0	6.4	2.0	16.8	940	9.1
	PH	1960	7	7.4	53.8	6.4	0.7	15.4	900	9.3
Mack	OG	-	-	9.8	23.9	9.5	6.0	27.0	800	12.4
	PH	1965	4	9.3	32.2	9.9	1.5	21.4	750	12.7
LO701	OG	-	-	9.9	20.2	7.1	2.7	40.2	810	9.9
	PH	1959	12	9.0	10.5	6.0	0.9	42.4	750	10.3
Cook	OG	-	-	10.55	23.8	4.6	6.6	17.5	700	13.8
	PH	1971	7	8.6	4.8	4	0.6	21.2	650	13.9
MR404	OG	-	-	10.4	29.0	7.6	6.8	41.0	660	13.7
	PH	1953	20	8.6	32.7	4.0	0.3	19.2	630	13.6

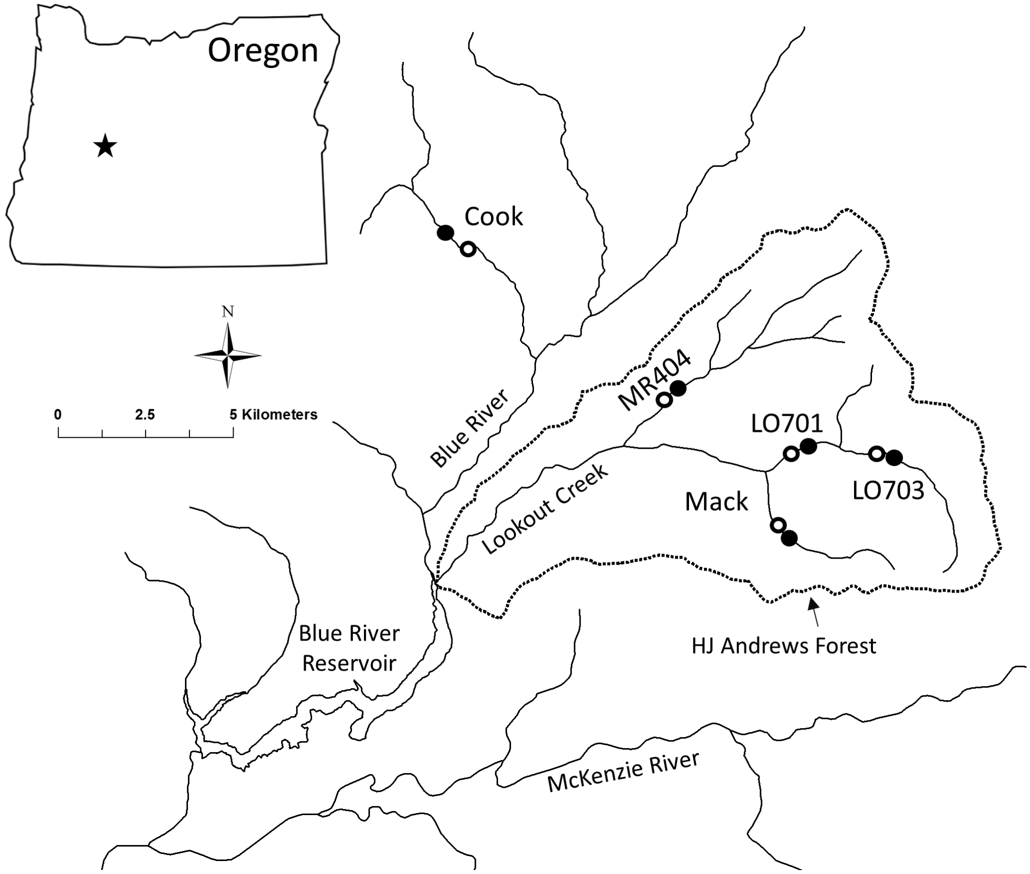
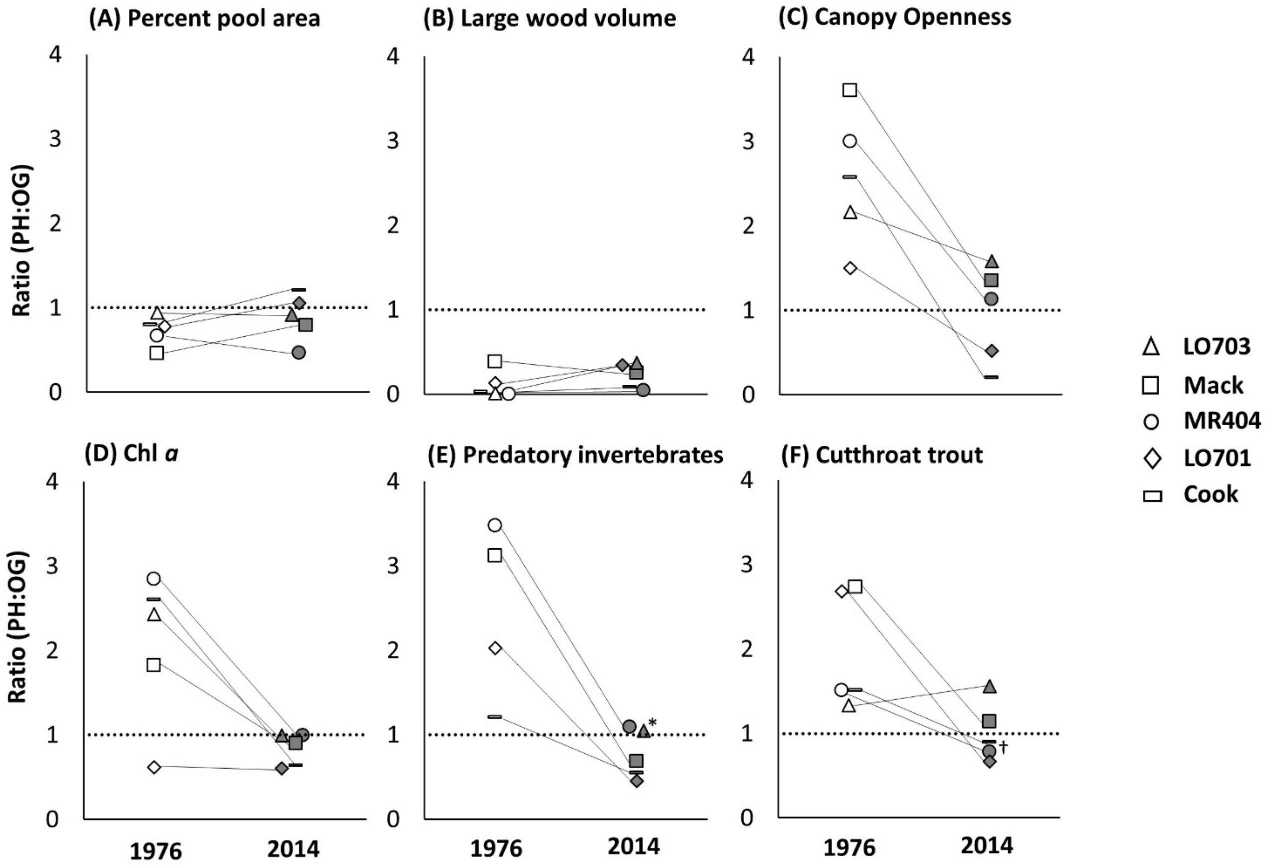


Figure 4.1: Blue River drainage, a tributary of the McKenzie River, and sampling sites. Filled circles indicate upstream old-growth, reference reaches and open circles indicate previously harvested reaches of each reach pair.



* No macroinvertebrate sampling in 1976.

† For MR404, the ratio in 2014 is 1.13 when sculpin are included.

Figure 4.2: Ratios of previously harvested to old-growth values for percent pool area (A; %), large wood volume (B; $m^3 \cdot 100\ m^{-2}$), canopy openness (C; %), chl *a* (D; $\mu g \cdot cm^{-2}$), predatory invertebrate biomass (E; $g \cdot m^{-2}$) and cutthroat trout biomass (F; $g \cdot m^{-2}$) in five reach pairs in the 1970s (open shapes) and in 2014 (filled shapes) after four decades of riparian regeneration.

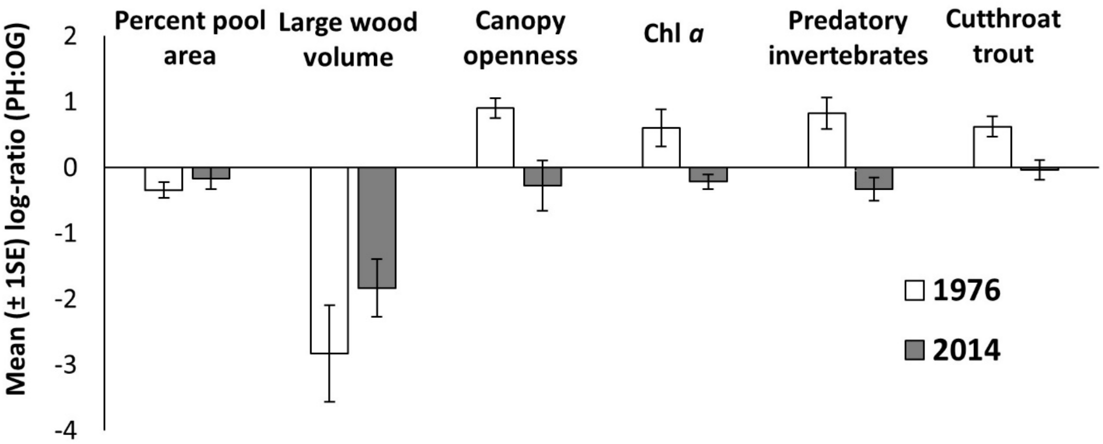


Figure 4.3: Mean log-ratios (previously harvested: old-growth; ±1SE) of five reach pairs for the suite of abiotic and biotic variables in the 1970s (open bars) and in 2014 (filled bars) after four decades of riparian regeneration. A value of zero indicates no difference between reaches within a reach pair.

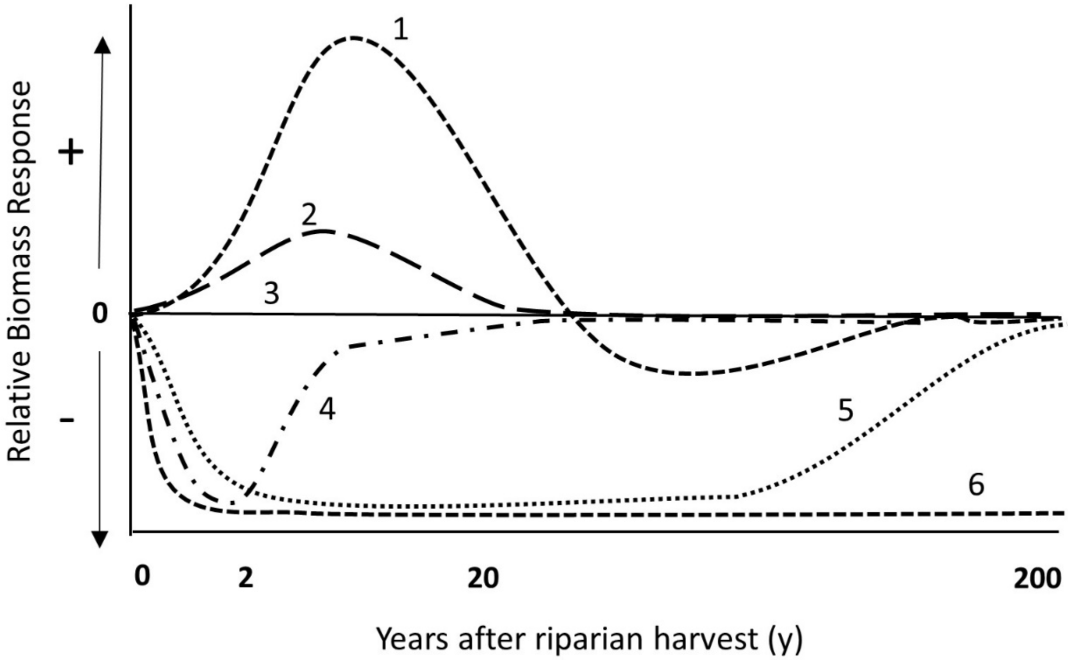


Figure 4.4: A suite of potential long-term responses of a resident trout population to riparian timber harvest: 1) Changes in canopy cover drive primary and secondary production; 2) Smaller changes in canopy cover such as those from thinning with a riparian buffer promote smaller magnitude and shorter duration changes in primary and secondary production; 3) Harvesting results in minimal changes in habitat and production; 4) Short-term negative response (e.g. temperature or sedimentation) that quickly recovers; 5) Long-term negative response associated with habitat degradation from the loss of large wood; 6) Alternative steady state in which both habitat and populations do not recover on these time scales (e.g. historic splash dams scouring stream substrate to bedrock). See Appendix B for more detailed explanations of trajectories.

CHAPTER 5: RELATING SPATIAL PATTERNS OF STREAM METABOLISM TO DISTRIBUTIONS OF JUVENILE SALMONIDS AT THE RIVER NETWORK SCALE

Matthew J. Kaylor, Seth M. White, W. Carl Saunders, and Dana R. Warren

Abstract

Understanding the factors that drive spatial patterns in stream ecosystem processes and the distribution of aquatic biota is important to effective management of these systems and the conservation of biota at the network scale. In this study we conducted field surveys throughout an extensive river network in NE Oregon that supports diminishing populations of wild salmonids. We collected data on physical habitat, nutrient concentrations, biofilm standing stocks, stream metabolism (gross primary production (GPP) and ecosystem respiration (ER)), and ESA-listed juvenile salmonid density from approximately 50 sites across two sub-basins. Our goals were to 1) to evaluate network patterns in these metrics, and 2) determine network-scale linkages among these metrics, thus providing inference of processes driving observed patterns.

Ambient nitrate-N and phosphate-P concentrations were low across both sub-basins (< 40 μg/L). Nitrate-N decreased with watershed area in both sub-basins, but phosphate-P only decreased in one sub-basin. These spatial patterns suggest co-limitation in one sub-basin but N limitation in the other; experimental results using nutrient diffusing substrates across both sub-basins supported these predictions. Solar exposure, temperature, GPP, ER, and GPP:ER increased with watershed areas, but biofilm Chl *a* and ash-free dry mass (AFDM) did not. Spatial statistical network (SSN) models explained between 70 and 75% of the total variation in biofilm Chl *a,* AFDM, and GPP, but only 21% of the variation in ER. Temperature and nutrient concentrations were the most supported predictors of Chl *a* and AFDM standing stocks, but these

variables explained little of the total variation compared to spatial autocorrelation. In contrast, solar exposure and temperature were the most supported variables explaining GPP, and these variables explained far more variation than autocorrelation. Solar exposure, temperature, and nutrient concentrations explained almost none of the variation in ER. Juvenile salmonids – a key management focus in these sub-basins - were most abundant in cool stream sections where rates of GPP were low, suggesting temperature constraints on these species limit their distribution to oligotrophic areas where energy production at the base of the food web may be limited.

Introduction

Analysis of spatial patterns can provide insights into ecological processes that may not be apparent through traditional sampling and statistical techniques (Jeltsch et al. 1999; McIntire and Fajardo 2009). This is particularly evident in stream and river ecosystems where evaluation of inherent network structure helps elucidate processes that can be missed in assessments at smaller spatial scales (Fausch et al. 2002). Spatially-explicit data have recently been used to infer processes regulating network-scale stream temperatures (Isaak et al. 2017b), stream water chemistry (McGuire et al. 2014), hydrologic processes (Segura et al. *in press*), the distribution of biota (Filipa et al. 2017; Isaak et al. 2017a; Saunders et al. 2018), and stream metabolism (Rodriguez-Castillo et al. 2018). The processes of primary production and ecosystem respiration (collectively referred to as stream metabolism) are integral in determining community structure of aquatic biota and ecosystem function through controls on nutrient dynamics, biogeochemical cycling, and energy flow to consumers (Bernhardt et al. 2017). Gross primary production (GPP) and ecosystem respiration (ER) are processes of particular interest in stream and river environments because they integrate physical patterns in watershed structure with ecosystem processes throughout river networks, while at the same time acting as a driver of biotic organization across the landscape (Bernhardt et al. 2017). Given these linkages, determining spatial patterns of stream metabolism can improve our understanding how stream communities are assembled and can aid in the management of these ecosystems. In this study we use spatially-explicit data throughout a stream network to evaluate relationships between nutrient dynamics, biofilm standing stocks, stream metabolism, and the distribution of two native fish species of high interest to managers (Chinook salmon, *Oncorhynchus tshawytscha*; Steelhead, *O. mykiss*) in a large Columbia River Basin tributary.

Localized experimental and observational studies have found GPP to be regulated by light availability (Bilby and Bisson 1992; Roberts et al. 2007), nutrient loading (Peterson et al. 1993), and temperature (Demars et al. 2011). Stream reach-scale GPP is also often closely related to standing stocks of benthic periphyton (Morin et al. 1999; Dodds 2006; Bernot et al. 2010); however, this is not always the case as the strength of the relationship between GPP and periphyton standing stocks may be affected by grazing pressure, self-shading, and time since disturbance (Uehlinger 2006; Roberts et al. 2007). Regional studies exploring relationships between GPP and abiotic stream characteristics have found that GPP is most closely associated with light flux (Mulholland et al. 2001; Bernot et al. 2010; Finlay 2011). Conversely, attempts to correlate nutrient concentrations with rates of GPP in observational field studies rarely find significant positive relationships in riverine systems (see Bernhardt et al. 2017), despite nutrient availability being clearly identified as limiting factors in reach-scale experimental nutrient additions and localized bioassays (Peterson et al. 1993; Tank and Dodds 2003; Johnson et al. 2009). This disconnect may in part be attributed to the interaction between metabolism and nutrient concentrations; through their influence on nutrient uptake and retention, these ecosystem processes both affect, and are affected by, stream nutrient concentrations (Finlay et al. 2011;

Tank et al. 2017a). In river reaches with high rates of GPP and ER, high nutrient demand can lead to a reduction in the availability and concentration of limiting nutrients (Tank et al. 2017). Given the longitudinal connectivity of streams, localized areas of high uptake in one area can result in reduced supply downstream, which can in-turn create periodicity in the longitudinal patterns of nutrient concentrations (Finlay et al. 2011; Dong et al. 2017). Exploring, network patterns of stream GPP and ER (collectively stream metabolism) together with patterns of stream nutrient concentrations could reconcile the disconnect between local GPP and local stream nutrient availability.

In addition to the importance of stream GPP and stream ER on patterns in stream chemical attributes throughout a watershed, these metabolic processes integrate energy flow of linked aquatic-terrestrial food webs, and spatial variability in metabolism rates have the potential to drive the distribution and productivity of stream biota. At broad spatial scales, the ratio of GPP to ER (hereafter GPP:ER) in streams has been correlated with aquatic macroinvertebrate production in streams (Marcarelli et al. 2011). More recently, Saunders et al. (2018) found that rates of GPP throughout a stream network were positively correlated with juvenile Chinook salmon (*Oncorhynchus tshawytscha)* and steelhead (*O. mykiss*) density in a NE Oregon basin. At the stream reach scale (e.g. 100-1000 m), experimental increases in GPP and ER have been linked with increased secondary production of invertebrates and fish (Bilby and Bisson 1992; Peterson et al. 1993; Cross et al. 2006). Given these linkages, understanding spatial variation in stream metabolism is necessary for understanding how ecosystems are structured and to effectively manage land use practices at large spatial scales (Naiman et al. 2012). However, our understanding of stream metabolism across stream networks is limited, especially regarding processes driving large-scale spatial patterns.

Recent research in the analysis of stream networks has suggested that the inclusion of spatial autocorrelation functions can account for non-independence of samples and improve understanding of how explanatory variables are related to response variables (Isaak et al. 2014). These spatial stream network (SSN) modeling techniques have been developed to apply autocorrelation functions that are specific to the unique spatial structures of streams (e.g. connected by flow paths). SSN models have been applied to a number of stream physical metrics (Isaak et al. 2017b; Scown et al. 2017), and they are increasingly being applied to biological data (Frieden et al. 2014; Filipa et al. 2017; Isaak et al. 2017a), but their use in application to integrated ecosystem processes such as GPP or ER has been limited (but see Rodriguez-Castillo et al. 2018). In addition to assessing potential factors influencing GPP and ER, the use of SSN models allows for prediction of GPP and ER at unsampled locations, thereby increasing spatial resolution across stream networks. Quantifying GPP and ER is logistically taxing, and accurate prediction of these metrics at unsampled locations may be particularly useful for managers and researchers interested in guiding management actions.

We evaluated and analyzed spatially-explicit data to explore patterns of stream temperature, solar radiation, nutrient availability, biofilm standing stocks, stream metabolism, and the distribution of juvenile salmonids (*O. tshawytscha; O. mykiss*) at approximately 50 sites throughout two sub-basins of the Grande Ronde River in NE Oregon, USA. Our goals were to 1) evaluate network patterns in these metrics, and 2) determine network-scale linkages among these metrics, thus providing inference of processes driving observed patterns. To accomplish these goals, we first evaluated relationships between watershed area and all variables to determine broad patterns associated with increasing stream size. This approach has been utilized in a number of studies evaluating stream nutrient dynamics, GPP, and ER (Finlay 2011; Finlay et al.

2011; Hoellein et al. 2013). We then evaluated relationships among explanatory variables (i.e. nutrients, light, and temperature) and response variables (i.e. periphyton biomass, GPP and ER) using SSN models and further determined how the spatial patterns of explanatory variables and how the underlying network structure of the response variables (spatial autocorrelation) could account for these processes across the watershed (Rodriguez-Castillo et al. 2018). We expected light, nutrients, and temperature to all be important factors accounting for periphyton standing stocks and GPP estimates, and we expected temperature and nutrients to be important factors predicting ER (Acuna et al. 2008; Demars et al. 2011). In addition, we expected spatial autocorrelation to be an important additional predictor variable for periphyton standings stocks, GPP, and ER as this metric can encompass a wide range of potential unmeasured factors that may not be clearly associated with the abiotic predictor variables that we selected.

This high-resolution network-scale analysis provided an opportunity to evaluate predictions of how nutrients, primary producers, and stream metabolism are spatially structured within a stream network. During periods of low-flow, nutrient demand is expected to be highest and nutrient supply lowest, increasing the potential for biotic controls on nutrient concentrations (Wollheim et al. 2018). We therefore expected limiting nutrient concentrations to decrease with watershed area due to biological uptake and depletion of nutrients as has been observed in other study systems during low-flow conditions (Finlay et al. 2011). In contrast, light availability and temperature are expected to increase with watershed area as streams widen, and the River Continuum Concept (Vannote et al. 1980) evokes these changes along a continuum of increasing stream size as drivers of increasing biofilm standing stocks, GPP and GPP:ER. However, others have postulated that local conditions within a watershed (e.g. geomorphology, lithology, and climate) and anthropogenic modifications to stream and riparian ecosystems disrupt processes along this continuum (Minshall et al. 1983, 1985; Ward and Stanford 1983; Finlay 2011). In this study with a full network perspective of 50 sites, we can evaluate these frameworks. In addition, by quantifying light, nutrients and temperature across this network, we gain insight into mechanisms driving patterns in periphyton standing stocks and metabolism at the network scale.

We also explored relationships between stream productivity and key biota in this river system (i.e., ESA-listed salmonid fish) in a comparison of spatial patterns in GPP with the spatial patterns of juvenile salmon and steelhead throughout the network. In this analysis we sought to determine whether the areas with high densities of juvenile salmonids overlapped with areas of low versus high background productivity. In some systems areas of high productivity coincide with high fish abundance (Saunders et al. 2018), but if that is not the case, this could help to identify opportunities for enhancing the effectiveness of stream management.

Methods

Study sites

The study was conducted in two large sub-basins of the upper Grande Ronde River in NE Oregon: the upper Grande Ronde River mainstem system (hereafter UGR), and Catherine Creek (hereafter CC). The Grande Ronde River flows north from its headwaters in the Blue Mountains into the Snake River, which then flows into the Columbia River. The climate in this region is characterized by cold, moist winters and warm, dry summers with mean daily air temperatures near the city of La Grande average -0.42 °C in January and 21 °C in July. Average annual precipitation across the basin ranges from 36 cm in the valleys to 152 cm in the mountains, with most of the precipitation in the mountains falling as snow (McCullough et al. 2016). Annual streamflow runoff is therefore mostly reliant on winter snowpack, with peak flows typically occurring in the spring and minimum flows occurring in the late summer prior to the onset of winter precipitation (Kelly and White 2016).

A total of 54 sites were sampled in the summer of 2016 across the two sub-basins (Figure 5.1). All sites were associated with the Columbia Habitat Monitoring Program (CHaMP 2016), a program characterizing tributary spawning and rearing habitat of Columbia River salmonids. CHaMP sites were selected based on a spatially balanced design (generalized random tessellation stratified [GRTS]; Stevens and Olsen 2004) throughout current, historical, and potential habitat for Chinook Salmon and Steelhead. Sites sampled in 2016 ranged from first order tributaries to mainstem sections; therefore, sites in this study represent the variety of habitats within these sub-basins. CHaMP site reach lengths were approximately 20 x the bankfull stream width, ranging from 120-600 m.

Physical variables

Estimates for physical variables demonstrated to directly or indirectly influence periphyton standing stocks, GPP, and ER based on previous research (i.e., solar access and stream temperature; see Larned 2010; Bernhardt et al. 2017) were obtained for each site using the procedures outlined in CHaMP (CHaMP 2016). Solar access – the percentage of sunlight reaching a stream surface after accounting for sun angle, topographic shading, and vegetative shading – was estimated using a SunEye (Solmetric Corporation; Sebastopol, CA). To obtain comparable temperature values for all sites, we used 2002-2011 August mean temperature estimates from the NorWeST stream temperature model (Isaak et al. 2017b). To evaluate NorWeST model predictions, we also empirically quantified temperature at 30 of the 54 sites in summer 2016 at 1-hr intervals and found a high degree of correlation ($R^2 = 0.985$; $p < 0.001$).

Watershed area for each site was obtained using the STARs package (v2.0.4; Peterson and Hoef 2014) in ArcGIS (v10.3.1).

Nutrient concentration

Nutrient concentrations were sampled throughout each basin during mid-August (8/6-8/9). Nutrients were collected from all 2016 CHaMP sites (n = 54) as well as additional sites (n = 27) such as tributary junctions and unsampled tributaries to increase spatial resolution of nutrient concentrations. At each site, three replicate samples were taken from flowing water using a 60 ml syringe. Water was filtered through 25 mm Whatman GF/F filters into 15 ml plastic vials. Samples were stored on ice and frozen within 10 hours. Samples were kept frozen until May 2017, when they were analyzed using a Dionex 1500 Ion Chromatograph (detection limit = 2 $\mu g\ L^{-1}$) for nitrate-N and phosphate-P. Check standards were run along with samples to ensure machine accuracy. Nutrient samples were also collected from a subset of sites in mid-June to determine whether spatial patterns in nutrients differed as flows decreased through summer. Patterns were generally consistent between sampling events, although concentrations were slightly greater in mid-June. Given this consistency and the greater number of sites sampled in August, we focus analyses on August nutrient concentrations but provide June concentrations in the Appendix (Figure A5.1).

Nutrient limitation

Nutrient limitation was assessed using nutrient diffusing substrate (NDS) bioassays. Five sites were selected across each sub-basin (n = 10 total) to capture a range of temperature and landscape positions (Figure 5.1). However, the NDS arrays at one site in UGR were tampered with, resulting in a total of four sites in UGR. At each site, a metal L-bar containing 12 poly-con cups comprised of different nutrient treatments was placed in a rifle at the downstream end of each site (Tank et al. 2017b). Cups were filled with 2% agar and one of four potential treatments; control (unamended), nitrogen addition (1 M N; NH_4Cl), phosphorus addition (1 M P; KH_2PO4), and nitrogen and phosphorus combined (1 M N, 1 M P). Glass fritted discs were placed on top of agar and lids with 25 mm diameter holes were closed so that the disc was firmly attached. NDS bioassays were deployed for 21 days. Upon retrieval, chlorophyll *a* (Chl *a*) on each glass fritted disc was measured using an *in situ* fluorometer (bbe-moldaenke BenthoTorch; Schwentinental, Germany). Prior to measurement, cups were positioned in a plastic container filled with stream water and placed in the shade for a 30 min minimum acclimation period to account for light effects on fluorometric Chl *a* estimation (Kaylor et al. 2018). For each 12-cup array, the three cups of each treatment were averaged to obtain mean treatment values.

Periphyton Standing Stocks

Standing stocks of periphyton Chl *a* and ash-free dry mass (AFDM) were quantified at 50 sites following methods outlined in Kaylor et al. (2018). At each site, 11 evenly spaced transects were established and a single rock was collected from each transect, except for transect 11, where two rocks were gathered for a total of 12 rocks. Rocks were collected from the 25th, 50th or 75th percentile of stream wetted width and this location was altered systematically at each successive transect. The surveyor walked to the approximate stream location and then without looking down, grabbed the first rock they touched that was between 10-25 cm in width. A 7 cm diameter PVC pipe section was used to define a circular area to scape periphyton from the top of each rock. Periphyton from four rocks was rinsed into a single container and Chl *a* and AFDM sub-samples were drawn from the pooled sample using a modified 60 ml syringe. This resulted in three replicates of Chl *a* and AFDM per site. The subsample was filtered in the field through 47 mm Whatman GF/F filters using a handheld vacuum pump. Filters were folded in aluminum foil and either flash frozen using dry ice or put on ice and frozen within 6 hr. Chl *a* was quantified using acetone extraction and fluorometric analysis (Arar and Collins 1997). AFDM samples were dried at 60 ºC for 24 hrs, and then weighed to the nearest mg. Samples were then combusted at 500 ºC for 2 h and reweighed. The difference between dried mass and ashed mass was divided by the proportional area sampled to obtain AFDM (g m^{-2}).

Gross primary production and ecosystem respiration

Stream metabolism was estimated using single-station, open-channel methods (Grace and Imberger 2006) which utilize diurnal changes in stream dissolved oxygen to estimate rates at which oxygen is contributed to (i.e., GPP), and consumed from (i.e., ER) streams. MiniDOT optical dissolved oxygen and temperature sensors (Precision Measurement Engineering, Vista, California, U.S.A.) were deployed at summer baseflow conditions in a total of 49 sites – 32 in UGR and 17 in CC – during 22 July - 26 August 2016. There was limited cloud cover during the summer and no substantial precipitation events occurred during the sampling period. All sensors were placed at the downstream end of each CHaMP site in stream sections with flowing but non-turbulent water (Siders et al. 2017).

Because of limitations on the number of available loggers (n = 11), sensors were rotated throughout the 49 sites by deploying them for a minimum of three cloudless 24-hr periods, and then moving them to new locations. This approach is consistent with Castillo et al. (2018), in which GPP was similarly quantified at the network scale by collecting DO data at each site for three days. Consequently, metabolism was estimated at sites over slightly different time intervals. To describe temporal trends over the sampling interval, three longer-term stations were established to monitor metabolism throughout the duration of sampling other sites (n = 2 in UGR and n = 1 in CC; see Figure A5.2). At each of these stations, photosynthetically active radiation (hereafter PAR; Odyssey sensors, Dataflow Systems, Christchurch, New Zealand) and barometric pressure (Extech RHT50 sensors, FLIR Commercial Systems Inc., Nashua, NH, USA) were measured at 5-min intervals.

Metabolism was estimated using a Bayesian single-station estimation program (BASE v3.0; Grace et al. 2015) in the program R (R Core Team 2015). The BASE program simultaneously estimates gross primary production (GPP), ecosystem respiration (ER), and the reaeration coefficient (K) through an iterative process using a Markov Chain Monte Carlo (MCMC) method. Additional parameters for light saturation (p) and temperature dependence (θ) can optionally be estimated by the model. Five-parameter models, in which estimates of GPP, ER, K, p, and θ were derived, always out performed (i.e., lower AIC values) 3-parameter models where values for p and θ were fixed. Therefore, 5-parameter models were used for all metabolism estimates (Grace et al. 2015). We used default model priors for GPP, ER, p and θ. The prior for K for each site was derived from nighttime regression utilizing diurnal DO concentrations and DO saturation (Hall and Hotchkiss 2017). We applied a standard deviation of the K prior distributions that allowed for deviation from the nighttime regression estimate but reduced extreme daily K estimate outliers and improved consistency among days at each site. The default model priors for BASE restrict daily K values to be less than 40 day^{-1}. However, some sites in this study were high gradient with K values that may exceed this value. We therefore set the maximum K to 60 day^{-1}, so we did not force K to be lower than expected based on nighttime regression.

Model input requirements include light flux (PAR µmol m^{-2} s^{-1}), dissolved oxygen concentration (mg L^{-1}), temperature (ºC), barometric pressure (ATM), and salinity (ppt). Dissolved oxygen and temperature were obtained empirically at each site. Due to limited sensors, PAR could not be recorded at all stations; PAR was continuously recorded at permanent stations and extra sensors (*n* = 3) were deployed at additional sites. When PAR was not empirically recorded at a site, data from the nearest site (< 5 km) were used. Barometric pressure was recorded at each of the three permanent stations and data were modeled for other sites based on differences in elevation. Salinity was assumed to be zero for all sites.

All models were run with 20,000 MCMC iterations (10,000 burn-in iterations). For each day, model performance was assessed using criteria outlined in Grace et al. (2015). Only models with all R-hats < 1.1, posterior predictive checks between 0.1 and 0.9, and r^2 of predicted DO values versus measured DO values > 0.7 were included in subsequent analysis. We excluded sites where model-estimated K exceeded 45 day^{-1} (*n* = 4) as high K values make it difficult to obtain reliable GPP and ER estimates (Hall and Hotchkiss 2017; Appling et al. 2018). Model estimates of GPP and ER for multiple days at each site were averaged to obtain mean values per site. These values were multiplied by mean stream depth to obtain aerial rates of GPP and ER (g O_2 m^{-2} d^{-1}).

Juvenile Salmonid Surveys

Abundance of salmonids was estimated at CHaMP sites during the period of summer low flow as described in Justice et al. (2017). Depending on stream size, one or two snorkelers moved in an upstream direction the length of each reach while enumerating fish and communicating with each other their observations to avoid double counting. Snorkel counts at each site were expanded to abundance estimates using a correction factor (Jonasson et al. 2015) developed from paired mark-recapture and snorkel survey data to account for fish that were not observed by snorkelers; the correction factor was specific to habitat type (pools, riffles, runs). Aerial density of salmonids (fish m^{-2}) was calculated by dividing the corrected abundance estimates by the total surface area within the reach as determined from reach metrics collected during from CHaMP surveys.

Statistical Analysis

To examine how explanatory and response variables relate to stream size, we first plotted watershed area (km^2) against each variable. This follows an established approach to infer ecological processes (e.g. nutrient dynamics) from spatial patterns in response variables plotted against watershed area, and to identify thresholds marking drastic shifts in measured variables (Finlay et al. 2011).

We assessed nutrient limitation on nutrient diffusing substrates at each site using one-way analysis of variance (ANOVA) to compare Chl *a* accrual across the four treatments (C, N, P, N+P). We then applied Tukey's post hoc test to determine significant differences among treatments. These differences were used to assess the type of nutrient limitation at each site, and more broadly to determine the dominant nutrient(s) limiting periphyton accrual in each sub-basin (i.e. N limitation, P limitation, primarily N limited and secondarily P limited, primarily P limited and secondarily N limited, or co-limited by both N and P).

We used SSN models (Isaak et al. 2014) to evaluate potential factors influencing periphyton standing stocks, GPP and ER at the network scale. Prior to SSN model formulation, spatial data was formatted and processed using the STARs package (v2.0.4; Peterson and Hoef 2014) in ArcGIS (v10.3.1). A preconditioned stream network layer (e.g. continuous stream network with all stream segments flow-oriented towards a single drainage point) was downloaded from the National Stream Inventory (https://www.fs.fed.us/rm/boise/AWAE/projects/NationalStreamInternet). Spatial processing to produce an SSN object was conducted following procedures outlined in Ver Hoef et al. (2014).

SSN models are based on the multiple linear regression model framework, with fixed-effect predictors (e.g. habitat or landscape covariates) and spatial autocovariance functions as random effects. Variation is partitioned into fixed effects, spatial covariance, and residual variation known as the "nugget". There are three potential covariance structures for SSN models. Tail-up covariance (TU) accounts for covariance with points upstream of the designated location within the stream network, tail-down covariance (TD) accounts for spatial autocorrelation with points downstream of the designated location within the stream network, and Euclidean covariance represents autocorrelation based on linear distances not associated with a stream network. Although including multiple covariance structures (e.g. tail-up and tail-down in same model) can improve model predictions (Garreta et al. 2010), each additional covariance structure is associated with additional costs in terms of parameter estimation ($n \geq 2$ parameters per covariance structure). Given our low-sample size (~50), we restricted models to tail-up covariance structures, as this autocorrelation structure was expected to best represent the processes evaluated (e.g. GPP should be influenced by upstream processes). Covariance structures can be modeled with exponential, spherical, Mariah, or linear-with-sill forms (Peterson and Ver Hoef 2010). Preliminary comparisons of models with different covariance forms (e.g., exponential, spherical) revealed little differences in root mean square prediction error (RMSPE) among models relative to differences observed between spatial and non-spatial models. We therefore used the spherical form for all covariance structures.

We used four fixed-effect variables - solar access, nitrate-N concentration, phosphate-P concentration, and stream temperature – to predict biofilm biomass, GPP and ER, as mechanisms for their control over response variables are well-established. All correlations of the four explanatory variables were evaluated for collinearity and exhibited Pearson's correlation coefficients < 0.6. For each response variable (Chl *a,* AFDM, GPP and ER), we formulated a set of candidate models based on all combinations of the four explanatory variables (15 total model structures for each response variable). To achieve assumptions of normality, nitrate-N, phosphate-P and all response variables were natural-log transformed. Visual inspection of plotted data did not provide evidence for nonlinearity among covariates or inflated variance with increasing mean of dependent variables and the analysis proceeded incorporating only linear relationships. Similarly, there was no evidence of either increasing or decreasing variance as values of the x-variable increased. Next, all candidate models were fit and model assumptions of normality and constant variance were checked using model residuals.

Candidate models were ranked with Akaike's Information Criterion (AIC) adjusted for small sample size (AICc) (Hurvich and Tsai 1989). To evaluate the potential importance of fixed-effect variables in explaining variation in response variables, we calculated the relative importance of each variable based on the sum of Aikaike weights for all models containing each variable (Burnham and Anderson 2004). We present the three top ranked models (lowest AICc values).

In summer 2016, we obtained reliable data from 45-50 CHaMP sites for each response variable; however, the usage of SSN models allows for prediction at unsampled locations as long as the fixed effect explanatory variables in each model are also available at each prediction location. We therefore predicted each response variable at 52 unsampled CHaMP sites, where explanatory covariates were available. For each response variable, the model with the lowest AICc value from the set of candidate models was used to predict values at unsampled locations.

Results

Physical attributes

The UGR drains a larger area than CC and therefore sites within UGR encompassed a greater range of watershed areas (22-285 km^2 vs 38-1405 km^2). Despite differences in watershed area, discharge at the farthest downstream site in CC was 0.85 m^3 s^{-1} whereas discharge at the farthest downstream site in UGR was 1.34 m^3 s^{-1}. Solar exposure and temperature increased with watershed area in both sub-basins (Figure 5.2a,b), but solar exposure and temperature were typically lower for a given watershed area in CC compared to UGR. Solar exposure ranged from 34% to 83% (mean = 57%; SD = 12.8) and from 31% to 98% (mean = 68%; SD = 16.8) in CC and UGR, respectively. Mean August temperature ranged from 10.5°C to 16.6°C (mean = 13.5°C; SD = 1.9) and from 11.8°C to 19.8°C (mean = 15.8°C; SD = 2.4) in CC and UGR, respectively.

Nutrient spatial patterns

Spatial patterns in nutrient concentrations differed between UGR and CC (Figure 5.2c-d). In UGR, phosphate-P concentrations were generally higher (> 10 μg/L) in sites with watershed areas of less than 100 km^2 compared to sites with watersheds greater than 100 km^2 where concentrations were less than 10 μg/L. Nitrate-N concentrations were low throughout UGR but were elevated in some sites with watershed area less than 100 km^2. Although the nitrate-N:phosphate-P ratios were always < 16, the very low nutrient concentrations and decreasing trend of both nutrients would suggest co-limitation of N and P in UGR, especially in sites with watershed areas greater than 100 km^2. In CC, nitrate-N decreased with watershed area whereas phosphate-P remained elevated across sites independent of watershed area, suggesting greater relative demand for N and therefore potential N-limitation. Elevated phosphate-P concentrations in CC may be indicative of younger, more erodible basalts compared to older, more weathered underlying geology in UGR.

Nutrient diffusing substrates

Nutrient diffusing substrates were used to test predictions of nutrient limitation inferred from spatial patterns of nitrate-N and phosphate-P throughout the stream network. In UGR, we observed shifts from N limitation in the upper reaches to co-limitation and then primary N limitation with secondary P limitation in sites with the largest watershed area (Figure 5.3a). At site 1 in UGR, which had the smallest drainage area (63 km^2), Chl *a* accrual on N-amended and N+P-amended substrates were significantly different (Tukey's post hoc comparisons, $p < 0.05$) from C-amended and P-amended substrates but were not different from each other ($p > 0.05$), indicating N limitation. At site 2 (356 km^2), Chl *a* on N-amended substrates was greater than C-amended and P-amended substrates, but this was not significant at $\alpha = 0.05$. N+P amended substrates were significantly different then C, N, and P-amended substrates indicating co-limitation. At sites 3 (512 km^2) and 4 (1005 km^2), Chl *a* on N-amended substrates was significantly greater than C-amended substrates ($p < 0.05$) and N+P-amended substrates were significantly greater than N-amended substrates indicating primary N limitation and secondary co-limitation.

In Catherine Creek, NDS responses to treatments consistently demonstrated N limitation (Figure 5.3b). At every site (ranging in watershed area from 24 to 279 km^2) Chl *a* accrual on N-amended substrates was significantly greater than control substrates ($p < 0.05$), and Chl *a* accrual on N+P amended substrates were significantly greater than controls at 4 of the 5 sites, but were not significantly different from N-amended substrates at any of the sites. P-amended substrates were not significantly ($p > 0.05$) different from control substrates at any site.

Periphyton Standing Stocks

Chl *a* and AFDM were positively correlated ($r^2 = 0.73$) and exhibited similar spatial patterns (Figure 5.2e,f; Figure 5.4a,b). Chl *a* ranged from 0.4 to 13.1 µg cm^{-2} and AFDM ranged from 5.1 to 48.1 g m^{-2}; however, Chl *a* and AFDM were considerably lower in CC with maximum values of 2.5 µg cm^{-2} and 17.6 g m^{-2}, respectively. Across both sub-basins there were no consistent trends between watershed area and Chl *a* or AFDM (Figure 5.2e,f). However, we were able to predict 70-73% of the variation in Chl *a* and AFDM across this stream network using spatial autocorrelation, temperature, and nutrient concentrations (Table 5.1). Of this variation, the proportion attributed to fixed effects (e.g. temperature and nutrients) was only 0.16-0.20 and 0.24-0.30 while the proportion attributed to autocovariance was 0.60-0.63 and 0.44-0.45 for Chl *a* and AFDM, respectively. Relative variable importance averaged across all models indicated that temperature (0.55), nitrate-N (0.26), and phosphate-P (0.17) were the most important fixed-effect variables explaining Chl *a* (Table 5.2). Temperature was also the highest ranked fixed-effect explaining AFDM (0.59), followed by phosphate-P (0.32) and nitrate-N (0.09)(Table 5.2).

Gross primary production and ecosystem respiration

Reliable model performance statistics (Grace et al. 2015) were achieved for at least two full days in 45 of the 49 sites where dissolved oxygen sensors were deployed. GPP estimates ranged from 0.03 – 6.56 g O_2 m^{-2} d^{-1} and mean ER ranged from 0.36 – 6.87 g O_2 m^{-2} d^{-1} (Figure 5.2g,h; Figure 5.4c,d); however, GPP was generally greater in UGR compared to CC (Figure 5.2g). GPP increased with watershed area (Figure 5.2g) in both UGR and CC, but for a given watershed area, GPP was greater on average in UGR. ER increased with watershed area in UGR but in CC, ER peaked at sites with watershed area near 100 km^2 with lower estimated ER in sites with smaller and larger watershed areas (Figure 5.2h). The ratio of GPP to ER (GPP:ER) increased with watershed area in both basins, but for a given watershed area was greater on average in UGR (Figure 5.2j). Surprisingly, Chl *a* explained little variation in GPP in both UGR ($r^2 = 0.01$) and CC ($r^2 = 0.11$).

The top three ranked models predicting GPP explained between 71-73% of variation across this stream network (Table 5.1). The proportion of this variation attributed to fixed effects was much greater for GPP than of for either of the standing-stock estimates (Chl *a* and AFMD). Fixed effects accounted for 0.71-0.73 of the variation while the proportion of variation explained by autocorrelation was minimal (< 0.02). Relative variable importance averaged across all models indicated that temperature (0.37) and solar access (0.36) were the most important fixed-effect predictors of GPP, followed by nitrate-N (0.16) and phosphate-P (0.11)(Table 5.2).

In contrast to models predicting GPP, models were poor at predicting ER. The top three ranked models predicting ER only explained between 0.17 and 0.21 of the variance, and the proportion of this variance attributed to fixed effects was less than 0.10 (Table 5.1), indicating little predictive power of ER using the four fixed-effects used in this study. Phosphate-P was the most important fixed-effect based on relative variable importance averaged across all models (0.38) followed by temperature (0.31), nitrate-N (0.23), and solar access (0.09).

Metabolism data (GPP and ER) were collected continuously at three stations to identify any temporal trends occurring throughout the 6-week duration of the study. At these three stations (1 in CC and 2 in UGR), we observed some temporal variation, but variation within sites was generally small and changes over time were less than variation among sites (Figure A5.2). Consequently, we concluded that any variation in measurements due to temporal changes over our 6-week sampling interval was likely overshadowed by spatial differences.

Juvenile salmonid spatial patterns

Juvenile salmonid density ranged from 0.001 individuals m^{-2} to 1.492 individuals m^{-2} across the 43 sites in the two basins (Figure 5.4e). In both UGR and CC, juvenile densities were greatest in headwater sections where GPP was very low, and there was a negative relationship between GPP and salmonid density across UGR ($r^2 = 0.35$; $p = 0.001$) and CC ($r^2 = 0.10$; $p = 0.28$). Similar to other studies in nearby basins (Tait et al. 1994, Li et al. 1994), salmonid density was negatively correlated with temperature in UGR ($r^2 = 0.74$, $p < 0.001$). However, in CC this relationship was not evident ($r^2 = 0.01$, $p = 0.680$).

Discussion

High-resolution sampling throughout the river network, combined with multiple analytical approaches allowed us to quantify spatial patterns of nutrient concentrations, periphyton standing stocks, GPP, ER, and the distribution of biota that are of management concern. Models were effective in explaining 70-75% of the variation in periphyton standing stocks and GPP using a mixed-effects modeling approach that accounted for spatial autocorrelation (e.g. SSN), which allowed for accurate prediction of these variables at unsampled locations where explanatory covariates were also collected (Figures A5.3 and A5.4). Temperature, light availability, GPP and GPP:ER increased with watershed area, and while there were outliers, these trends were generally consistent with predictions outlined in the River Continuum Concept (Vannote et al. 1980). However, differences in rates of GPP between sub-basins for a given watershed area suggest that local factors within these watersheds control the nature of these relationships (Minshall et al. 1983, 1985). Salmonids were most abundant in cool stream sections where rates of GPP were low, a result that contrasts observations from a nearby basin where salmonid density was positively correlated with GPP (Saunders et al. 2018). The opposing relationships between these studies potentially reflects different landscape filters that regulate the distribution of salmonids between these basins (Poff 1997). In the sub-basins evaluated in our study, temperature has been shown to influence spawning locations and limit the distribution of juvenile salmonids (White et al. 2017; Justice et al. 2017), which may restrict juvenile salmonids to cool, oligotrophic areas where low rates of primary production may be limiting energy flow to the food web.

Nutrients

Nutrient concentrations were not strong predictors of biofilm standing stocks or GPP in our study sites. Nutrient concentrations within a river are typically poorly correlated with GPP (see Bernhardt et al. 2017). However, experimental nutrient additions to stream ecosystems have resulted in enhanced GPP, ER, and secondary production (Peterson et al. 1993; Slavik et al. 2004; Cross et al. 2006), providing evidence that nutrient supply, rather than concentration, often limits GPP, ER, and bottom-up drivers of secondary production. Results from our nutrient diffusing substrate experiment demonstrate that periphyton Chl *a* accrual in UGR was primarily limited by nitrogen and secondarily co-limited by nitrogen and phosphorous, while CC was primarily limited by nitrogen alone. Detecting a nutrient response in the NDS experiment but not the statistical modeling approach could be the result of different periphyton communities colonizing artificial substrates versus natural substrates or differences in grazing rates (Cattaneo and Amireault 1992). Alternatively, we suggest that low nutrient concentrations across both sub-basins and a small range in nutrient concentrations throughout the watershed created conditions in which nutrients would fail to emerge as strong correlates in a linear mixed-model analysis.

While there was limited evidence for a relationship between nutrient concentrations and GPP at individual points, spatial patterns suggested interactions between nutrients concentrations, productivity, and associated nutrient demand. During periods of low-flow, nutrient demand is expected to be highest and nutrient supply lowest, increasing the potential for biotic controls on nutrient concentrations (Wollheim et al. 2018). Rates of production during these low-flow periods may increase demand and further drive spatial patterns (Finlay et al. 2011). For example, nitrogen uptake (Tank et al. 2017a) and nutrient retention efficiency (Sabater et al. 2000), which affect longitudinal patterns of nutrient concentrations, were greater in streams with open canopies where autotrophic demand would be higher, compared to more shaded streams. Light availability and GPP increased with watershed area in both UGR and CC, which may indicate greater cumulative demand with downstream distance that resulted in depleted nutrients. Both nitrate-N and phosphate-P concentrations were elevated in shaded headwaters of UGR but decreased with watershed area. Conversely, nitrate-N concentrations in CC decreased with watershed area while phosphate-P concentrations remained relatively uniform. This suggests that demand for both nitrate and phosphate is high throughout UGR, but in CC demand is high for nitrate, but not phosphate. These spatial nutrient patterns along with the NDS results suggest that during summer low-flow periods, in-stream demand for nutrients in UGR and CC exceeds supply and therefore exerts control on nutrient concentrations (Wollheim et al. 2018).

Patterns and predictors of GPP and ER

Due to historic difficulty quantifying stream GPP, researchers have measured periphyton Chl *a* and ash-free dry mass (AFDM) as proxies for GPP. However, periphyton Chl *a* and AFDM were poorly correlated with reach-scale GPP in our study. Although this contrasts with studies that report positive associations between Chl *a* and GPP (Morin et al. 1999; Dodds 2006; Rodriguez-Castillo et al. 2018), it is consistent with other studies (Velasco et al. 2003; Izagirre et al. 2008). We quantified periphyton Chl *a* on benthic substrates, but this assessment did not include aquatic macrophytes. Macrophytes were generally uncommon throughout the basin but were observed in some headwaters (as bryophytes) and warm, mainstem sites (as vascular plants as well as filamentous algae), which could lead to discrepancies if macrophytes contribute substantially to whole-reach GPP (Kaenel et al. 2000). Additionally, standing stocks reflect accrual of periphyton after grazing by organisms, and spatial differences in grazing rates may result in a decoupling of standing stocks and GPP. Regardless of the drivers of this decoupling, our results suggest that using standing stocks as a proxy for GPP could lead to inaccurate conclusions about local and network-scale primary production across our study region.

Solar access (potential light exposure) and temperature emerged as the best predictors of GPP in this system. Metrics of solar radiation potential have been positively correlated with GPP in a number of studies encompassing a wide geographic area (Mulholland et al. 2001; Bernot et al. 2010; Finlay 2011; Hoellein et al. 2013; Tank et al. 2017a; Rodriguez-Castillo et al. 2018; Saunders et al. 2018). As streams widen, solar radiation reaching stream channels is expected to increase due to the decreased ability of riparian vegetation to shade streams (Vannote et al. 1980). However, for a given stream size, we found that solar radiation was variable, which may be attributed to historic and ongoing land-use within these sub-basins (Justice et al. 2017). This heterogeneity resulted in a decoupling of the relationship between solar radiation and temperature and allowed us to include both these covariates as predictors of GPP, improving model predictions of GPP at the network scale.

GPP and ER were well correlated in UGR (GPP explained 72% of the variation in ER), but not in CC (GPP only explained 5% of the variation in ER). ER represents the combined carbon consumption by autotrophs and heterotrophs, and ER and GPP may be coupled through autotrophic respiration (Hall and Beaulieu 2013). GPP:ER was greater in UGR (mean = 0.67) compared to CC (mean = 0.17), increasing the potential for autotrophic respiration to influence ER in UGR. Alternatively, GPP an ER in UGR may be linked but not truly coupled if carbon fixed by autotrophs is released as dissolved organic carbon, which then acts as a key source of organic matter fueling adjacent heterotrophs (Hotchkiss and Hall 2015). Lastly, GPP and ER may be largely functioning independently but are controlled by similar factors in UGR (Hall and Beaulieu 2013). For example, increasing temperature with watershed area in UGR may have increased rates of both GPP and ER independently. Ultimately, the decoupling of GPP and ER in CC may explain why factors associated with GPP across both basins did not emerge as strong predictors of ER across both basins.

Fixed-effect covariates — temperature, solar radiation, and nutrient concentrations — explained very little variation in ER across these two sub-basins. Further, the combination of fixed effects and autocovariance were only able to explain approximately 21% of the variation in ER. This contrasts with Rodriguez-Castillo et al. (2018) in which SSN models that included GPP and temperature as fixed-effects explained up to 67% of the variation in ER across a stream network. Other factors, such as the availability of dissolved, fine, and particulate organic carbon may have been more associated with ER rates in CC (Roberts et al. 2007). Identification of additional covariates that drive spatial structure and stream metabolism at the network scale will allow ecologists to gain a deeper mechanistic understanding and predictive ability.

Evaluation of RCC predictions

The high-resolution analysis in the present study allows us to evaluate how key abiotic factors expected to change throughout a river network may affect ecosystem processes. The River Continuum Concept (RCC, Vannote et al. 1980) proposes increasing light availability as streams widen to drive increased GPP and GPP:ER until streams become large enough where light attenuation and turbidity reduce benthic primary production. Our results generally support RCC predictions for low-to-mid order streams, as solar radiation, GPP, and GPP:ER increased with drainage area across both sub-basins. These spatial patterns are consistent with a growing body of research demonstrating increasing GPP and GPP:ER as a function of stream size within mid-order streams (Meyer and Edwards 1990; McTammany et al. 2003; Ortiz-Zayas et al. 2005; Finlay 2011; Finlay et al. 2011; Hoellein et al. 2013; Rodriguez-Castillo et al. 2018). However, our results also support predictions that local conditions within a watershed, whether natural (e.g. meadows) or anthropogenic (e.g. land-use practices), may dictate the relationship between watershed area and metabolism within a network leading to outliers in GPP:ER that deviate from RCC predictions (Minshall et al. 1983, 1985). For example, GPP and GPP:ER were greater for a given watershed area in UGR, where temperature and solar radiation were greater, compared to CC, which was cooler and more shaded on average. Finlay et al. (2011) found a non-linear relationship between watershed area and light availability with an abrupt transition occurring near 100 km^2 in which light and GPP rapidly increased. We did not detect abrupt changes in light as a function of watershed area in UGR or CC potentially because riparian communities and land-use legacies in these sub-basins have led to reduced riparian cover (Justice et al. 2017; White et al. 2017). These effects would be greatest in the smallest streams where canopies can close over streams resulting in little light penetration. It is unclear whether restoring vegetation and shading within these sub-basins would manifest in abrupt transitions in light and GPP, as observed in Finlay et al. (2011). Ultimately, when considering many points throughout a network we simultaneously find support for the RCC in the general trends of light, GPP, and GPP:ER, but also support for the idea that there may be deviations from the RCC model at multiple points along a river network and between watersheds.

Spatial patterns of GPP and Salmonids

In UGR and CC, juvenile Chinook and steelhead densities (individuals m^{-2}) in 2016 were greatest in areas that corresponded to low rates of GPP, resulting in a negative relationship between GPP and salmonid density. This contrasts with Saunders et al. (2018) in which GPP was positively correlated with juvenile salmonid density (individuals m^{-1}) in the nearby John Day River basin in NE Oregon. However, Saunders et al. (2018) explicitly sampled within a geographic extent exhibiting temperatures suitable to support salmonids. Sampling within a broader geographic extent within the same basin as Saunders et al. (2018), previous studies evaluating fewer sites ($n = 7$), but a wider range of temperatures, reported negative relationships between salmonid density and stream temperature as well as proxies for primary production (periphyton biomass) and prey availability (invertebrate density) (Li et al. 1994; Tait et al. 1994). Thus, across broad geographic extents, temperature, including thermal refugia (Ebersole et al. 2003), may exert greater control on salmonid spawning and rearing distributions (Justice et al. 2017), but within habitat exhibiting suitable temperatures, spatial patterns in GPP may influence the energy available for higher trophic levels and the distribution of juvenile salmonids (Saunders et al. 2018).

Fish and overall river management in the basins evaluated in this study are primarily focused on juvenile salmonids, but constraining our assessment of management needs to juvenile salmonid density, rather than total fish density or biomass, limits our ability to consider relationships between GPP and higher trophic levels. In cooler, headwater sections of UGR and CC, fish species composition is dominated by salmonids but warm water species increase with distance downstream (Jonasson et al. 2015). The inclusion of total fish biomass as a response variable may have resulted in a positive relationship with GPP, as has been observed in other studies evaluating metrics of productivity or invertebrate prey biomass and top predator biomass (Hawkins et al. 1983; Kaylor and Warren 2017). Nonetheless, river sections with high salmonid densities but low primary production may provide managers with targeted areas where actions can be taken to enhance primary production or food availability (Naiman et al. 2012).

SSN usage and implications

The inclusion of spatial autocorrelation can improve prediction of response variables at unsampled locations across a stream network (Isaak et al. 2014). However a trade-off is that covariates used to predict response variables need to be available at both sampled and unsampled locations, often limiting covariates to broad geographic descriptors (e.g. elevation, drainage area, etc.). While this approach can increase predictive power throughout a network, mechanistic linkage may be lost. We were able to maintain mechanistic linkage by utilizing an extensive monitoring program — the Columbia Habitat Monitoring Program (CHaMP) — to sample a subset of sites and then predict response metrics at unsampled sites where mechanistic covariates were explicitly measured (e.g. solar exposure) rather than proxies to represent variables of interest (e.g. stream order as a proxy for light reaching streams). As a result of including these sites, we were able to use the most commonly associated explanatory variables of GPP (i.e. nutrients, light, and temperature) to predict response variables at unsampled locations (Figures A5.3 and A5.4), and these covariates explained far more variation in GPP than autocorrelation. Using broad geographic covariates would have likely decreased the proportion of variation explained by covariates and increased the proportion explained by autocorrelation. Data from CHaMP surveys are available across other sub-basins of the Columbia River, and there are a number of other large scale monitoring efforts across this region (e.g. the Aquatic and Riparian Effectiveness Monitoring Program), making this kind of analysis broadly available. Our results indicate that at unsampled sites, ecosystem processes can be predicted along with scaled estimates of error, which increases spatial resolution within a basin.

Conclusions

In this study we explored linkages among ecosystem properties and metabolic processes, and we compared those patterns to the distribution of aquatic biota throughout a river network. Resolving linkages between abiotic conditions and biotic responses in GPP and ER is one incremental step in the larger task of understanding the complex patterns of metabolic regimes (Bernhardt et al. 2017) and the role of spatial patterns in rivers. Further, in our comparison of stream metabolism patterns with those of an endangered native fish, we take a first step in meeting the need for a spatially explicit understanding of the river network that considers the relationships between food webs, nutrients, and aquatic biota to better inform our understanding of streams at the networks scale and ultimately stream management (Fausch et al. 2002; Naiman et al. 2012; Saunders et al. 2018). Our approach provides a framework that is applicable to large portions of the Columbia River basin as well as other areas where habitat monitoring is conducted at a comparable spatial scale.

Acknowledgements

Gavin Jones and Jeremiah Newell assisted in field sampling. This research was supported by a National Science Foundation Graduate Research Fellowship (Grant No. 1314109-DGE awarded to MJ Kaylor), the US Department of Agriculture National Institute of Food and Agriculture McIntire Stennis program (award 1009738), and the Bonneville Power Administration (Project # 2009-004-00).

Literature cited

Acuna, V., A. Wolf, U. U., and K. Tockner. 2008. Temperature dependence of stream benthic respiration in an Alpine river network under global warming. Freshwater Biology 53:2076–2088.

Appling, A. P., R. O. J. Hall, C. B. Yackulic, and M. Arroita. 2018. Overcoming equifinality: leveraging long time series for stream metabolism estimation. Journal of Geophysical Research: Biogeosciences 123:624–645.

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. Page US Environmental Protection Agency Method 445.0 Revision 1.2. Cincinnati, Ohio.

Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, M. Arroita, A. P. Appling, M. J. Cohen, W. H. McDowell, R. O. J. Hall, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic. 2017. The metabolic regimes of flowing waters. Limnology and Oceanography (00).

Bernot, M. J., D. J. Sobota, R. O. Hall, P. J. Mulholland, W. K. Dodds, J. R. Webster, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, W. H. Mcdowell, J. L. Meyer, B. Peterson, G. C. Poole, H. M. Valett, C. Arango, J. J. Beaulieu, A. J. Burgin, C. Crenshaw, A. M. Helton, L. Johnson, J. Merriam, B. R. Niederlehner, J. M. O’Brien, J. D. Potter, R. W. Sheibley, S. M. Thomas, and K. Wilson. 2010. Inter-regional comparison of land-use effects on stream metabolism. Freshwater Biology 55(9):1874–1890.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33(2):261–304.

Cattaneo, A., and M. C. Amireault. 1992. How artificial are artificial substrata for periphyton? Journal of the North American Benthological Society 11(2):244–256.

CHaMP, (Columbia Habitat Monitoring Program). 2016. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detrital-based ecosystem. Ecology 87(6):1556–1565.

Demars, B. O. L., J. R. Manson, J. S. Ólafsson, and G. M. Gíslason. 2011. Stream hydraulics and temperature determine the metabolism of geothermal Icelandic streams. Knowledge and Management of Aquatic Ecosystems 402(05):1–17.

Dodds, W. K. 2006. Eutrophication and trophic state in rivers and streams. Limnology and Oceanography 51(1):671–680.

Dong, X., A. Ruhí, and N. B. Grimm. 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proceedings of the National Academy of Sciences (6):201617571.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 60(10):1266–1280.

Fausch, K. D., C. E. Torgersen, C. V Baxter, and H. W. Ll. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6):483–498.

Filipa, A., F. Lorenzo, Q. Ma, P. Beja, and M. F. Magalha. 2017. Geostatistical distribution modelling of two invasive crayfish across dendritic stream networks:2899–2912.

Finlay, J. C. 2011. Stream size and human influences on ecosystem production in river networks. Ecosphere 2(8):1–21.

Finlay, J. C., J. M. Hood, M. P. Limm, M. E. Power, J. D. Schade, and J. R. Welter. 2011. Light-mediated thresholds in stream-water nutrient composition in a river network. Ecology 92(1):140–50.

Frieden, J. C., E. E. Peterson, J. Angus Webb, and P. M. Negus. 2014. Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. Environmental Modelling and Software 60:320–330. Elsevier Ltd.

Garreta, V., P. Monestiez, and J. M. Ver Hoef. 2010. Spatial modelling and prediction on river networks: up model, down model or hybrid? Environmetrics 21:439–456.

Grace, M., and S. Imberger. 2006. Stream metabolism: performing & interpreting measurements. New South Wales Department of Environmental Conservation Stream metabolism workshop May 31(September):204.

Grace, M. R., D. P. Giling, S. Hladyz, V. Caron, R. M. Thompson, and R. Mac Nally. 2015. Fast processing of diel oxygen curves: Estimating stream metabolism with BASE (BAyesian Single-station Estimation). Limnology and Oceanography: Methods 13:103–114.

Hall, R. O. J., and J. J. Beaulieu. 2013. Estimating autotrophic respiration in streams using daily metabolism data. Freshwater Science 32(2):507–516.

Hall, R. O. J., and E. R. Hotchkiss. 2017. Stream metabolism. Page *in* G. A. Lamberti and F. R. Hauer, editors. Methods in Stream Ecology, 3rd edition. Academic Press.

Hawkins, C. P., M. L. Murphy, N. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40(8):1173–1185.

Hoellein, T. J., D. A. Bruesewitz, and D. C. Richardson. 2013. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. Limnology and Oceanography 58(6):2089–2100.

Hotchkiss, E. R., and R. O. J. Hall. 2015. Whole-stream 13C tracer addition reveals distinct fates of newly fixed carbon. Ecology 96(2):403–416.

Hurvich, C., and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76(2):297–307.

Isaak, D. J., J. M. Ver Hoef, E. E. Peterson, D. L. Horan, and D. E. Nagel. 2017a. Scalable population estimates using spatial-stream-network (SSN) models, fish density surveys, and national geospatial database frameworks for streams. Canadian Journal of Fisheries and Aquatic Sciences 74:147–156.

Isaak, D. J., E. E. Peterson, J. M. Ver Hoef, S. J. Wenger, J. A. Falke, C. E. Torgersen, C. Sowder, E. A. Steel, M.-J. Fortin, C. E. Jordan, A. S. Ruesch, N. Som, and P. Monestiez. 2014. Applications of spatial statistical network models to stream data. WIREs Water 1(June):277–294.

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, D. E. Nagel, C. H. Luce, S. W. Hostetler, J. B. Dunham, B. B. Roper, S. P. Wollrab, G. L. Chandler, D. L. Horan, and S. Parkes-payne. 2017b. The NorWeST summer stream temperature model and scenarios for the western U.S.: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Water Resources Research 53:1–25.

Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi. 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society 27(2):252–268.

Jeltsch, F., K. Moloney, and S. J. Milton. 1999. Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. Oikos 85(3):451–466.

Johnson, L. T., J. L. Tank, and W. K. Dodds. 2009. The influence of land use on stream biofilm nutrient limitation across eight North American ecoregions. Canadian Journal of Fisheries and Aquatic Sciences 66(7):1081–1094.

Jonasson, B. C., E. R. Sedell, S. K. Tattam, A. B. Garner, C. D. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, J. M. Hay, G. A. McMichael, B. C. Power, O. C. Davos, and J. R. Ruzycki. 2015. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. La Grande, Oregon.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management 188:212–227.

Kaenel, B. R., H. Buehrer, and U. Uehlinger. 2000. Effects of aquatic plant management on stream. Freshwater Biology 45:85–95.

Kaylor, M. J., A. Argerich, S. M. White, B. J. Verwey, and I. Arismendi. 2018. A cautionary tale for in situ fluorometric measurement of stream chlorophyll a: influences of light and periphyton biomass. Freshwater Science 37(2):287–295.

Kaylor, M. J., and D. R. Warren. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere 8(6):e01845.

Kelly, V. J., and S. White. 2016. A method for characterizing late-season low-flow regime in the upper Grand Ronde River Basin, Oregon. Page Scientific Investigations Report 2016-5041.

Larned, S. T. 2010. A prospectus for periphyton: recent and future ecological research. Journal of the North American Benthological Society 29(1):182–206.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123(4):627–640.

Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall, Jr. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92(6):1215–1225.

McCullough, D. A., S. White, C. Justice, M. Blanchard, R. Lessard, D. Kelsey, and J. Nowinski. 2016. Assessing the status and trends of spring Chinook habitat in the upper Grande Ronde River and Catherine Creek.

McGuire, K. J., C. E. Torgersen, G. E. Likens, D. C. Buso, W. H. Lowe, and S. W. Bailey. 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proceedings of the National Academy of Sciences of the United States of America 111(19):7030–5.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90(1):46–56.

McTammany, M. E., J. R. Webster, E. F. Benfield, and M. A. Neatrour. 2003. Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society 22(3):359–370.

Meyer, J. L., and R. T. Edwards. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology 71(2):668–677.

Minshall, G. W., W. Kenneth, R. C. Petersen, and D. A. Bruns. 1985. Developments in Stream Ecosystem Theory. Canadian Journal of Fisheries and Aquatic Sciences 42:1045–1055.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, R. L. Vannote, R. C. Petersen, T. L. Bott, and C. E. Cushing. 1983. Interbiome Comparison of Stream Ecosystem Dynamics. Ecological Monographs 53(1):1–25.

Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. Journal of the North American Benthological Society 18(3):299–307.

Mulholland, P. J., C. S. Fellows, J. L. Tank, N. B. Grimm, J. R. Webster, S. K. Hamilton, E. Marti, L. R. Ashkenas, W. B. Bowden, W. K. Dodds, W. H. McDowell, M. J. Paul, and B. J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46:1503–1517.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109(52):21201–7.

Ortiz-Zayas, J. R., W. M. J. Lewis, J. F. I. Saunders, J. H. J. McCutchan, and F. N. Scatena. 2005. Metabolism of a tropical rainforest stream. Journal of the North American Benthological Society 24(4):769–783.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. Mckinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74(3):653–672.

Peterson, E. E., and J. M. Ver Hoef. 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks 91(3):644–651.

Peterson, E. E., and J. M. Ver Hoef. 2014. STARS: An ArcGIS toolset used to calculate the statistical models to stream network data. Journal of Statistical Software 56(2):1:17.

Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10(4):588–606.

Rodriguez-Castillo, T., E. Estevez, A. M. Gonzalez-Ferreras, and J. Barquin. 2018. Estimating Ecosystem Metabolism to Entire River Networks. Ecosystems

Sabater, F., A. Butturini, E. MartÍ, I. Muñoz, A. Romani, W. Joanne, and S. Sabater. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. Journal of the North American Benthological Society 19(4):609–620.

Saunders, W. C., N. Bouwes, P. McHugh, and C. E. Jordan. 2018. A network model for primary production highlights linkages between salmonid populations and autochthonous resources. Ecosphere 9(3):e02131.

Scown, M. W., M. G. Mcmanus, J. H. Carson, and C. T. Nietch. 2017. Improving predictive models of in-stream phosphorus concentration based on nationally-available spatial data coverages. Jounral of the American Water Resources Association 53(4):944–960.

Siders, A. C., D. M. Larson, J. Ruegg, and W. K. Dodds. 2017. Probing whole-stream metabolism: influence of spatial heterogeneity on rate estimates. Freshwater Biology 62:711–723.

Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of Kuparuk River ecosystem to phosphorus fertilization. Ecology 85(4):939–954.

Stevens, D. L., and A. R. Olsen. 2004. Spatially Balanced Sampling of Natural Resources. Journal of the American Statistical Association 99(465):262–278.

Tait, C. K., J. L. Li, G. A. Lamberti, T. N. Pearsons, and H. W. Li. 1994. Relationships between riparian cover and the Community structure of high desert streams. Journal of the North American Benthological Society 13(1):45–56.

Tank, J. L., and W. K. Dodds. 2003. Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. Freshwater Biology 48:1031–1049.

Tank, J. L., E. Marti, T. Riis, D. von Schiller, A. J. Reisinger, W. K. Dodds, M. R. Whiles, L. R. Ashkenas, W. B. Bowden, S. M. Collins, C. L. Crenshaw, T. A. Crowl, N. A. Griffiths, N. B. Grimm, S. K. Hamilton, S. L. Johnson, W. H. McDowell, B. M. Norman, E. J. Rosi, K. S. Simon, S. A. Thomas, and J. R. Webster. 2017a. Partitioning assimilatory nitrogen uptake in streams: an analysis of stable isotope tracer additions across continents. Ecological Monographs 0(0):1–19.

Tank, J. L., A. J. Reisinger, and E. J. Rosi. 2017b. Nutrient limitation and uptake. Pages 147–171 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology, 3rd edition. Academic Press.

Team, R. C. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Uehlinger, U. 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. Freshwater Biology 51:938–950.

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Velasco, J., A. Millan, M. L. Suarez, C. Guerrero, and M. Ortega. 2003. Macrophytic, epipelic and epilithic primary production in a semiarid Mediterranean stream. Freshwater Biology 48:1408–1420.

Ver Hoef, J. M., E. E. Peterson, D. Clifford, and R. Shah. 2014. SSN: An R package for spatial statistical modeling on stream networks. Journal of Statistical Software 56(3):1–45.

Ward, J. V, and J. a Stanford. 1983. Serial Discontinuity Concept of Lotic Ecosystems.

White, S. M., C. Justice, D. A. Kelsey, D. A. McCullough, and T. Smith. 2017. Legacies of stream channel modification revealed using General Land Office surveys, with implications for water temperature and aquatic life. Elem Sci Anth 5(0):3.

Wollheim, W. M., S. Bernal, D. A. Burns, J. A. Czuba, C. T. Driscoll, A. T. Hansen, R. T. Hensley, J. D. Hosen, S. Inamdar, S. S. Kaushal, L. E. Koenig, Y. H. Lu, A. Marzahri, P. A. Raymond, D. Scott, R. J. Stewart, P. G. Vidon, and E. Wohl. 2018. River network saturation concept : factors influencing the balance of biogeochemical supply and demand of river networks. biogeochemistry.

Table 5.1: The top three models for each response variable based on AICc weights. RMSPE is the root mean squared prediction error. LOOCV is the squared residuals between observed and predicted values through leave-one-out cross validation. Correlation composition is the proportion the explained variance partitioned into fixed-effects, spatial autocorrelation, and the residual "nugget".

								Correlation composition		
Response variable	Model rank	Fixed effect(s)	Fixed effect *p*-value	RMSPE	Δ AICc	Weight	LOOCV r^2	Fixed-effects	Spatial correlation	Nugget
Chl a	1	Temp	**0.004**	0.488	0.00	0.36	0.71	0.16	0.63	0.21
	2	Temp + NO3	**0.004** 0.123	0.481	0.61	0.27	0.72	0.20	0.60	0.20
	3	Temp + PO4	**0.003** 0.438	0.489	1.80	0.15	0.71	0.18	0.60	0.22
AFDM	1	Temp + PO4	**<0.001** 0.070	0.355	0.00	0.46	0.73	0.30	0.44	0.26
	2	Temp	**<0.001**	0.372	0.42	0.37	0.70	0.24	0.50	0.26
	3	Temp + PO4 + NO3	**<0.001** 0.086 0.870	0.366	3.51	0.08	0.71	0.30	0.45	0.25
GPP	1	Temp + Solar Access	**<0.001** **<0.001**	0.698	0.00	0.40	0.73	0.75	0.01	0.24
	2	Temp + Solar Access + NO3	**<0.001** **<0.001** 0.187	0.695	0.55	0.30	0.73	0.77	0.01	0.22
	3	Temp + Solar Access + PO4	**<0.001** **<0.001** 0.910	0.721	1.92	0.15	0.71	0.76	0.02	0.22
ER	1	PO4	0.270	0.647	0.00	0.22	0.21	0.03	0.56	0.41
	2	Temp	0.096	0.665	0.25	0.19	0.17	0.06	0.40	0.54
	3	Temp + PO4	0.096 0.250	0.664	0.88	0.14	0.18	0.08	0.47	0.45

Table 5.2: Relative variable importance of each explanatory variable for each response variable.

Response variable	Temperature	Solar access	Nitrate-N	Phosphate-P
Chl *a*	0.55	0.03	0.26	0.17
AFDM	0.59	0.00	0.09	0.32
GPP	0.37	0.36	0.16	0.11
ER†	0.31	0.09	0.23	0.38

† Note that these fixed-effect variables explained very little variation in ER relative to autocorrelation and should be interpreted with caution.

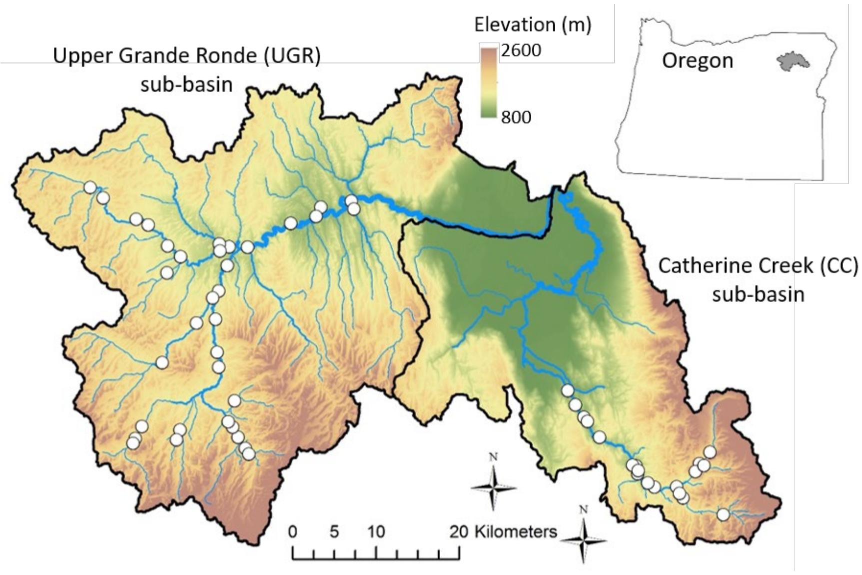


Figure 5.1: Sites sampled within the upper Grande Ronde and Catherine Creek sub-basins.

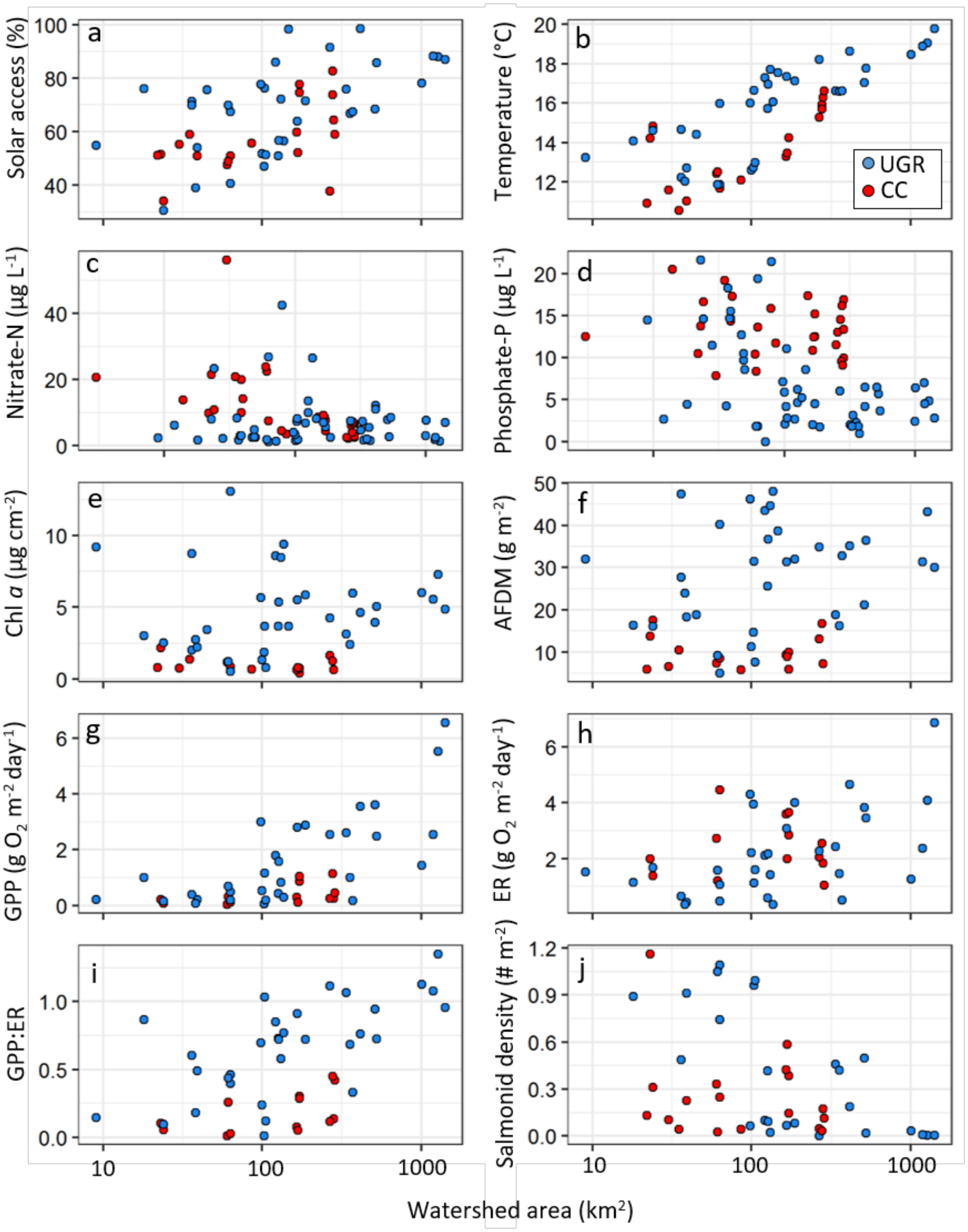


Figure 5.2: Relationships between watershed area (km2) and (a) solar access (% of full sun or open canopy), (b) mean August temperature (°C), (c) nitrate-N concentrations (µg L^{-1}), (d) phosphate-P concentrations (µg/L), (e) biofilm chlorophyll *a* (µg/cm^2), (f) biofilm ash-free dry mass (g/m^2), (g) gross primary production (mg $O_2 \cdot m^{-2} \cdot d^{-1}$), (h) ecosystem respiration (mg $O_2 \cdot m^{-2} \cdot d^{-1}$), (i) the ratio of gross primary production to ecosystem respiration, and (j) salmonid density (#/m^2). Red points indicate sites from Catherine Creek and blue points indicate sites from the upper Grande Ronde River.

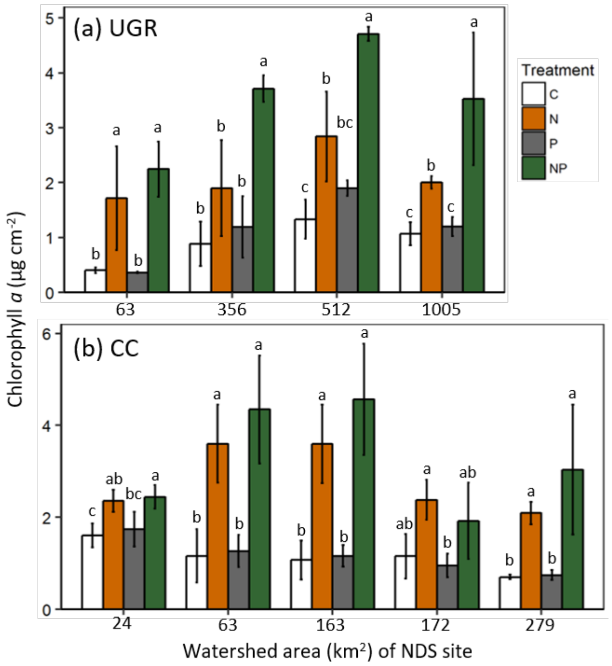


Figure 5.3: Mean Chl *a* accrual on nutrient diffusing substrates with four treatments (C, N, P, N+P) from upper Grande Ronde (a) and Catherine Creek (b). Error bars indicated 95% confidence intervals. Bars with the same lowercase letters are not significantly different from each other.

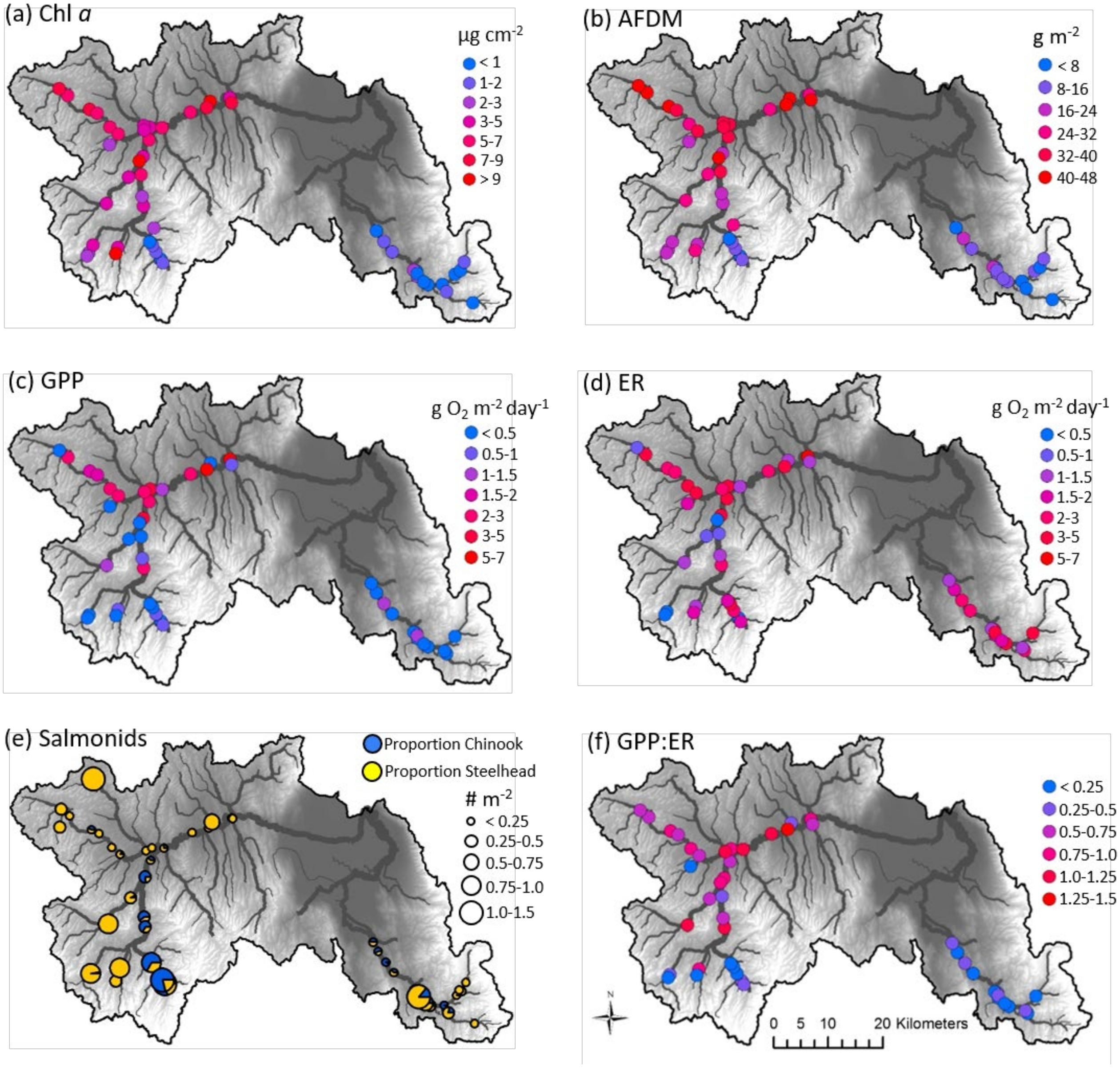


Figure 5.4: Spatial patterns in (a) biofilm chlorophyll *a,* (b) biofilm ash-free dry mass, (c) gross primary production rates, (d) ecosystem respiration rates, (e) juvenile salmonid densities, and (f) the ratio of gross primary production to ecosystem respiration.

CHAPTER 6: CARCASS ADDITIONS INCREASE JUVENILE SALMONID GROWTH, CONDITION, AND SIZE IN AN INTERIOR COLUMBIA BASIN TRIBUTARY

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Abstract

The number of returning adult salmon and steelhead to Columbia River tributaries has declined precipitously compared to historical runs and the loss of these subsidies has been suggested as a key factor affecting recovery of juvenile salmon production in headwater streams. Managers commonly add salmon carcasses to streams to supplement the loss of nutrients delivered from naturally spawning salmon. The focus of these management efforts is often on stimulating food web productivity through autotrophic pathways with less consideration of how direct consumption of eggs and carcass tissue may impact target species (e.g. juvenile salmonids). We added steelhead carcasses to three paired study reaches in a tributary to the Snake River, and evaluated impacts on juvenile Chinook and steelhead growth, body condition, size, and diet. Chinook and steelhead consumed an abundance of eggs and carcass tissue and this consumption markedly increased energy rations of diets within 4 weeks of adding carcasses. Between one and three weeks after adding carcasses, steelhead and Chinook growth rates were 6-23 times and 1.1-5 times greater in the treatment reaches relative to control reaches, respectively. Across all three pairs, mean body condition increased in the treatment reach relative to the control after carcass additions for both species. Effects on growth and condition were smallest and least persistent in the coldest upstream pair where scavengers removed the majority of carcasses within 3 weeks. The greatest effects were observed in the middle pair where scavenging was minimal and Chinook and steelhead body condition remained elevated 7 weeks after carcass additions and Chinook weighed 33% more and were 6 mm longer than in treatment reaches relative control at the conclusion of the study. Fall-migrant Chinook from the treatment reach of the middle pair were captured at a downstream trap and were significantly larger than fall-migrants from control reaches. We used 18 years of tagging and detection data from this system to demonstrate a positive relationship between juvenile Chinook size and emigration survival for two life histories of juvenile Chinook. This positive relationship suggests that the increased growth of juvenile Chinook resulting from this management action can enhance survival.

Introduction

Over the last century, human activities such as over-harvest, dam construction, and habitat degradation have led to a marked decline in naturally spawning salmon and steelhead across the Pacific Northwest (Gresh et al. 2000). In addition to the cultural and economic impacts of reduced fishery resources, the diminished abundance of anadromous salmon may have ecological impacts on tributary streams that historically supported high numbers of spawning salmon. Returning adult salmon and steelhead transport large amounts of carbon and nutrients upstream from the ocean, and these subsidies can fuel stream food webs by promoting algal growth (Verspoor et al. 2011) and enhancing invertebrate (Minakawa et al. 2002) and fish production (Bilby et al. 1998; Bentley et al. 2012; Collins et al. 2016). With fewer spawning adults and reduced marine-derived resource subsidies, the growth rates and production of juvenile salmonids may be lower now than historically. Effects on juvenile growth and production are particularly important because increased juvenile size has been linked to greater rearing survival and emigration survival (Zabel and Achord 2004; Ebersole et al. 2006; Monzyk et al. 2009; Pess et al. 2011), potentially stimulating a positive feedback loop resulting in more returning adult salmon.

Salmon subsidies can influence stream food webs through complex direct and indirect pathways (Collins et al. 2016), and the pathway through which subsidies are received may affect the magnitude and timing of juvenile salmonid responses. Nutrients released from carcasses (or salmon carcass analogs) can be assimilated by biofilms, stimulating primary production and thereby providing bottom-up increases in the productivity of invertebrates and fish (Kohler et al. 2008, 2012; Wipfli et al. 2010; Morley et al. 2016). Alternatively, biota can directly consume carcass eggs and flesh (Bilby et al. 1998; Armstrong and Bond 2013; Collins et al. 2016), or indirectly predate upon organisms that directly consumed eggs and carcass flesh (Collins et al. 2016). Energy is lost with each trophic level transfer and, therefore, the direct consumption pathway is a more efficient transfer of energy to fish compared to bottom-up processes through multiple trophic levels. Additionally, the timing and persistence of bottom-up effects and direct consumption may differ. For example, juvenile salmonid growth responses to pulsed subsidies of eggs and tissue can be immediate, but these effects may be ephemeral and not persist after these resources are gone (Armstrong et al. 2010; Bentley et al. 2012). On the other hand, there is typically a lag between bottom-up effects of salmon subsidies on each successive trophic level (Nelson and Reynolds 2014), but bottom-up effects may be detected over a longer duration (Verspoor et al. 2011).

Management actions aiming to increase production of suppressed salmon stocks often focus on improving physical habitat with less focus on stream food webs and productivity (Naiman et al. 2012). An important exception to this has been the addition of adult salmon and steelhead carcasses or salmon carcass analogs (SCA) to streams to compensate for the loss of naturally spawning salmon subsidies and to thereby promote enhanced stream and juvenile salmonid productivity (Collins et al. 2015). However, the efficacy of this practice has been debated (Collins et al. 2015), especially given substantial effort and cost associated with obtaining, storing, and ultimately distributing carcasses or SCA along a stream. While studies have found increased juvenile salmonid growth rates, body condition, abundance, and assimilation of salmon-derived nutrients following the addition of these resources in some streams (Bilby et al. 1998; Kohler et al. 2012; Collins et al. 2016), results from a recent meta-analysis (Janetski et al. 2009) and review (Collins et al. 2015) indicate that responses are highly variable, with other studies finding little to no response to carcass additions (Wilzbach et al. 2005; Harvey and Wilzbach 2010). This highlights that responses to added salmon subsides are context dependent, varying by region, geomorphology, species being evaluated, and carcass loading, among other factors (Janetski et al. 2009). Therefore, it cannot be assumed that adding carcasses to any given stream will yield positive desired effects (i.e. increased juvenile salmonid growth and survival).

While a number of studies have been conducted on salmon carcass addition effects along coastal stream ecosystems, few studies have evaluated effects of carcass additions in interior Columbia Basin tributaries (see Collins et al. 2016 for carcass effects on resident salmonids and Kohler et al. 2008, 2012 for effects of salmon carcass analogs on juvenile salmonids), a region where the current number of salmon is estimated to be just 1.3% of historic numbers (Gresh et al. 2000). In upper Columbia River tributaries species composition, seasonal hydrology, climate, disturbance, and notably the timing of spawning salmon may differ substantially from coastal drainages of the Pacific Northwest and Alaska where the majority of carcass addition studies have been conducted (Janetski et al. 2009). In the upper Columbia River region encompassing eastern Oregon, eastern Washington and western Idaho, Spring Chinook salmon (*Oncorhynchus tshawytscha*) spawn in mid-to-late summer – a period coinciding with annual low flows and maximum temperatures. Thus, natural adult salmon subsidies are available to rearing juvenile salmonids within a critical growth period during the relatively short time they spend rearing in streams. Beyond this seasonal context for salmon carcass subsidies, local context associated with stream network may also influence subsidy effects due to differences in temperature and temperature-associated species assemblage shifts. This question of network context is particularly under-explored as even in coastal stream systems where most carcass subsidy work has been done, assessments focus on a single site, in replicate artificial channels or on replicate sites that are set up to be comparable in size and condition (Janetski et al. 2009; Collins et al. 2015). Few studies consider how the role of carcasses may change in different locations along a stream network. Yet this is an important consideration as, salmonids spawn and ultimately rear throughout many parts of a river network, and within this range large temperature changes can occur within relatively short distances and/or timeframes due to limited shading (Justice et al. 2017).

Given the numerous factors limiting salmonid production, the recovery of salmonid populations within the Columbia Basin requires an integrated approach involving management actions that consider food webs in addition to physical habitat availability (Naiman et al. 2012). This study evaluates a potential management action to enhance juvenile salmonid productivity in interior Columbia Basin streams. We added carcasses in late-summer to three locations positioned along a temperature gradient of the Grande Ronde River of NE Oregon, a tributary of the Snake River. We quantified juvenile Chinook salmon and steelhead (*O. mykiss*) growth rates, body condition, size, and diet responses to carcass additions. To contextualize effects of carcass additions on size and survival, we additionally use a long-term dataset to evaluate relationships between juvenile Chinook size and rearing/emigration survival. This study differed from many other carcass addition management actions in two key ways. First, we made a point of adding gravid females. The direct consumption of eggs in particular has been shown to be a vital resource for resident fish and juvenile anadromous fish in Alaskan streams (Armstrong et al. 2010; Ruff et al. 2011; Bentley et al. 2012), but eggs are often removed before carcass additions due to hatchery operations. Second, we deployed carcasses at a relatively low density. This lower density decreased the likelihood of detecting responses but was intended to reflect the density of carcasses that can be added as a large extent management action rather than as an experimental study.

Methods

The study was conducted on the Grande Ronde River which flows from the Blue Mountains of NE Oregon northward to the confluence with the Snake River. All study sites were located upstream of the town of La Grande on the Upper Grande Ronde River (hereafter UGR) which drains approximately 1896 km^2. The UGR is a snowmelt-driven system with peak flows occurring during the spring and annual low-flow occurring in late summer after a period in which little precipitation typically occurs. Winters are cold with much of the study area covered in ice, while summers are hot and dry. Historically, this system supported multiple anadromous salmonid species and evolutionary life histories but due to a range of factors leading to suppressed salmonid stocks, only spring Chinook and summer steelhead currently have viable populations in the UGR (ODFW 1990; Nehlsen et al. 1991).

Using a BACI study design, sampling was conducted before and after the addition of carcasses in three paired reaches at different locations along the UGR mainstem (Figure 6.1). The treatment (carcass additions) and reference (i.e. control – no carcass addition) reaches of each of the three study pairs were located within sites associated with the Columbia River

Habitat Monitoring Program (CHaMP), a program characterizing tributary spawning and rearing habitat of Columbia River salmonids. The upstream and middle pairs were located on U.S. Forest Service land while the downstream pair was located on private land. Due to temperature and habitat differences, the fish communities in each pair differed. The upstream pair was dominated primarily by juvenile Chinook and steelhead, but also contained lower abundances of sculpin (*Cottus* spp.), bull trout (*Salvelinus confluentus*), and brook trout (*Salvelinus fontinalis*). The community in the middle pair was dominated by juvenile Chinook and steelhead as well as increased numbers of sculpin, longnose dace (*Rhinichthys cataractae*) and speckled dace (*Rhinichthys osculus*). In the downstream pair, the fish community was dominated by northern pikeminnow (*Ptychocheilus oregonensis*), bridgelip sucker (*Catostomus columbianus*), and redside shiner (*Richardsonius balteatus*). Steelhead were common, but Chinook were rare (< 20) and we were not able to quantify growth rates or diets for juvenile Chinook in this reach. Both juvenile steelhead and resident *O. mykiss* occupy these stream pairs and we refer to the population collectively as steelhead due to the dominance of this life history in this basin (Ruzycki et al. 2003).

Due to their position within the river network, reaches differed in discharge, temperature, stream width, and length surveyed (Table 6.1). Our goal was to add carcasses at similar areal densities in each treatment reach, and due to differences in wetted width of each pair, different amounts of carcasses were added to each pair. Approximately 86, 123, and 163 steelhead carcasses were added to treatment reaches of the upstream, middle and downstream pairs, respectively. The average weight of male and female carcasses was 2.68 and 2.89 kg, respectively. This translated to stocking densities of 0.27 kg/m^2, 0.18 kg/m^2, and 0.19 kg/m^2 in the upstream, middle, and downstream pairs, respectively. Approximately 55% of carcasses were female and the majority of females contained eggs (eggs from approximately 30 females were removed for hatchery operations). All steelhead were sourced from within the Grande Ronde Basin to avoid potential spread of out-of-basin pathogens. Steelhead carcasses were collected in spring 2017, immediately frozen, and remained frozen until deployment in August 2017. Although steelhead carcasses were used, the timing of carcass additions were in accordance with Spring Chinook spawning in mid-August. To limit movement of carcasses out of study reaches, carcasses were secured within treatment reaches using a piece of rebar that was pounded into the streambed with a two meter piece of paracord was attached to the rebar. The piece of paracord contained four loops and one steelhead was attached to each of these loops with a ziptie that was inserted into a slit cut between the jaw of each individual. To evaluate any potential scavenging of carcasses, we positioned trail cameras (Model BTC-5HD-850, Browning Trail Cameras, Morgan, UT) at three locations within each treatment reach.

Salmonid growth

Each treatment and control site was sampled five to six times over the summer; two to three sampling events before carcass addition and three events after the addition of carcasses to obtain growth rates for at least one interval before and two intervals after carcass addition. Fish were captured using herding methods in which fish were herded by a snorkeler into a seine net equipped with a 1 m^3 bag (Tattam et al. 2017). Occasionally an electrofisher (Smith-Root 12-B, Vancouver, WA) was used to capture fish when herding methods were not efficient (e.g. higher flows and colder temperatures). Fish were anesthetized using AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand), weighed, and measured (fork length). During all sampling events (except the last event) all steelhead > 65 mm were tagged with 9 or 12 mm PIT-tags (9 mm tags were used on fish < 80 mm and 12 mm tags were used on fish > 80 mm). Juvenile Chinook were PIT-tagged in mid-August around the time carcasses were added. Chinook were too small (< 60 mm) during early sampling events, which precluded pre-treatment tagging of Chinook. The first Chinook tags were applied in mid-August, shortly after carcass additions. Juvenile salmonid individual growth rates between sampling events were obtained by recapturing and re-measuring individuals. Growth rates were calculated as percent change in mass per day:

$$Growth = \frac{W_t - W_{t-1}}{W_{t-1}} * \frac{1}{\Delta T} * 100$$

Where W_t is the mass (g) when the fish was recaptured, W_{t-1} is the mass of the fish when measured during the previous sampling event, and ΔT is the number of days between capture events. Fulton's body condition (K) of individuals during each event was calculated as:

$$K = \frac{W}{L^3} * 100$$

Where W is wet weight (g) and L is fork length (cm) of each fish.

Because Chinook growth data is not available prior to carcass addition, we also use changes in mean weight and length among sampling events to evaluate overall change in the size of juvenile Chinook in a reach in responses to carcass additions. During each sampling event, we measured a minimum of 75 Chinook to obtain mean weight and length.

At the downstream reach pair, which had a more diverse fish community, we PIT-tagged not only salmonids, but also northern pikeminnow (*n* = 359), bridgelip sucker (*n* = 154) and redside shiner (*n* = 165). Recapture of non-salmonids was very low (< 2%) in the second sampling event. With such poor recapture rates, we could not determine individual growth rates for any of these species and tagging for these taxa was subsequently abandoned.

Salmonid density

In previous studies, the addition of salmon carcasses subsidies has resulted in increased juvenile salmonid densities relative to control sites (Bilby et al. 1998). Therefore effects of increased food availability on growth may be negated by, or confounded by, changes in densities and associated impacts of density dependence. We estimated salmonid densities in each reach twice: once before carcass addition (early August) and once two weeks after carcass addition (8/29 – 8/31). A third survey was planned for late September but abnormally low stream temperatures and the onset of precipitation triggered salmonid winter concealment behavior in which fish seek shelter during the day and become more active at night (Van Dyke et al. 2009). This switch in behavior precluded accurate comparison of densities among events during the planned September event.

Abundance of salmonids was estimated using established snorkel count methods (Justice et al. 2017). Snorkel counts were expanded using a correction factor from Jonasson et al. (2015) developed from paired mark-recapture and snorkel survey data in the Grande Ronde itself to account for fish that were not observed by snorkelers; the correction factor was specific to habitat type (pools, riffles, runs). Aerial density of salmonids (fish m^{-2}) were calculated for each reach by dividing fish counts by the total reach surface area as estimated from CHaMP surveys in the summer of 2017.

Salmonid diets

We collected diets of juvenile salmonids to assess invertebrate prey and the direct consumption of carcass eggs and tissue that would allow us to fully account for carcass addition effects on energy intake. We sampled stomach contents of juvenile Chinook salmon and steelhead at four events; approximately two weeks before carcass addition and one, three, and seven weeks after carcass addition. For each event, we sampled stomach contents of 10-12 individuals per species in control reaches and approximately 25 individuals (~ 10 during pre-carcass addition event) in treatment reaches. Salmonid stomach contents were sampled using non-lethal gastric lavage methods (Meehan and Miller 1978; Kamler and Pope 2001) and stomach contents were stored in 95% ethanol until laboratory analysis. We enumerated the number of eggs in the stomach contents of each fish and we recorded the presence or absence of carcass tissue.

To evaluate carcass addition effects on instantaneous energy rations of salmonid diets, we evaluated stomach contents of 10 individuals of each species two weeks prior to carcass additions and then three and seven weeks after carcass additions in both control and treatment reaches. Samples used to calculate energy rations were processed by a professional laboratory (Rhithron Associates, Inc., Missoula, MO). All invertebrates within stomach contents were identified and converted to dry weight using established length-mass relationships. The energy density of each invertebrate taxon was calculated from dry mass based on equations in Cummins and Waychuck (1971). Egg energy density was assumed to be 7.8 kj g^{-1} of egg wet weight (Cummins and Wuycheck 1971). We assumed that each egg in a diet weighed 0.05 g. The average wet weight of eggs is likely greater, however diets contained a combination of full, undigested eggs, partially broken eggs, and egg shells which contained no egg material. Therefore, egg counts contained eggs where egg material had been digested but the shell remained. The 0.05 g value was calculated by comparing the predicted stomach contents expressed as percent body mass based on different egg weights and comparing these values to published maximum observed consumption values (Armstrong et al. 2013). A value of 0.05

g/egg produced maximum consumption values consistent with published literature (Armstrong et al. 2013). We were not able to process diet samples from one week after carcass addition. We focused efforts on pretreatment to encapsulate any differences before carcass additions and then three and eight weeks after addition in which we anticipated egg and tissue consumption to be greatest. For the week one samples, we calculated the energy ration contribution of only eggs since eggs were enumerated (see above).

Fall-migrant Chinook sampling

Juvenile Chinook in UGR exhibit two common over-wintering life history strategies before emigration to the ocean in the spring; 1) fall emigration from headwater rearing sections to mainstem habitats where they over-winter (fall migrants), and 2) over-wintering within summer headwater rearing sections (spring migrants) before emigration in the spring. We captured fall-migrant Chinook from a screw trap located between the middle and downstream pairs to evaluate whether Chinook emigrating downstream to the mainstem Grande Ronde from treatment reaches were larger than those from control reaches. The trap was run from 9/21/17 to 11/29/17 and checked daily. All juvenile Chinook individuals captured in the trap were checked for PIT-tags, and all tagged fish were identified, measured and weighed (a subsample of untagged Chinook were also tagged at the trap and fish length and weight were recorded for assessments of juvenile Chinook survival between the UGR and downstream dams on the mainstem Snake and Columbia Rivers – see below). In this fall survey period, between 25 and 36 individual Chinook were captured from each of the four upstream study reaches. Chinook were captured throughout most of the survey period, with a median capture date of 11/1/2017 for Chinook from the upstream pair, and a median capture date for Chinook from middle pair of 10/23/17.

Size-survival relationships

To contextualize potential carcass addition effects on juvenile Chinook size and evaluate this assumption specifically for this system, we evaluated relationships between juvenile Chinook size and survival using a long-term tagging and detection dataset (1997-2015). Each year, two groups of juvenile Chinook were PIT-tagged within the UGR basin: 1) fall migrant Chinook captured at the screw trap during migration to mainstem over-wintering habitats as noted above, and 2) Chinook over-wintering in natal rearing sections and emigrating in the spring (see Sedell et al. 2018 for tagging details). Fall migrant Chinook were tagged between September 8th and December 2nd in each year (median tagging date = October 21st) and spring migrant Chinook were tagged between November 26th and December 30th of each year (median tagging date = December 6th). A total of 8,547 fall migrant Chinook and 5,637 spring migrant Chinook were tagged over the 18-year study interval. The following spring in each year, tagged Chinook migrating to the ocean were detected at Lower Granite Dam (LGD), the first dam encountered on the Snake River. Survival estimates in this study therefore focus on winter survival and subsequent survival though the first approximately 420 km of their migration, when mortality rates can be particularly high (Monzyk et al. 2009). From where they are tagged, fish travel downstream through the mainstem Grande Ronde, through to the middle section of the mainstem Snake River and ultimately through Lower Granite Reservoir and through the fish passage facility at Lower Granite Dam.

Data Analysis

We utilized a before-after, control-impact (BACI) design to evaluate carcass addition influences on salmonid growth rates (Chinook and steelhead), body condition (Chinook and steelhead), mean length (Chinook only), and mean weight (Chinook only) in each pair independently. Differences in response metrics in each pair and for each event were assessed using linear models in the program R (v3.2.2; Bates). The effect of the treatment (carcass addition), sampling event, and the interaction between the carcass addition treatment and sampling event on each response variable were tested using a linear model. The number of sampling events or sampling intervals (growth rates) varied for each response variable and pair. Using an example of a response variable with five sampling events, the following statistical model was used to describe the linear model estimating the response variable:

$$Y_t = \beta_0 + \beta_1 Treat_t + \beta_2 Event_2 + \beta_3 Event_3 + \beta_4 Event_4 + \beta_5 Event_5 + \beta_6 Event_2 * Treat_t + \beta_7 Event_3 * Treat_t + \beta_8 Event_4 * Treat_t + \beta_9 Event_5 * Treat_t + \varepsilon_t$$

Where β_0 is the estimate for the mean response variable (growth rate, body condition, weight or length) in the control reach during event 1; β_1 is the incremental estimated effect of the treatment on the mean response variable (1 for carcass addition and 0 for control); $\beta_{2\text{-}5}$ are the estimated incremental effect of event on the mean response variable in events 2-5, respectively; and $\beta_{6\text{-}9}$ is the further estimated incremental effect of carcass addition on the mean response variable for each event 2-5, respectively; and $\boldsymbol{\varepsilon_t}$ is the random error term for the t^{th} observation. All estimates of response variable differences and confidence intervals between treatment and control reaches for each event were estimated from combinations of this model using the function “estimable” from the “gmodels” package (v2.13.2) in program R. Assumptions of normality and constant variance of the residuals from each model were verified graphically. We were particularly interested in the interaction between each event and the treatment to evaluate whether the effect of carcass additions on response variables differed over time. Statistical significance between the control and treatment reach was assessed using the 95% confidence estimates of the difference between the mean response variable in the treatment reach and the mean response variable in the control reach, with significance defined as 95% confidence intervals of this difference not encompassing zero.

We assessed differences in length, weight, and body condition of PIT-tagged Chinook from control and treatment reaches that were captured in the screw trap during downstream emigration in the fall of 2017. For each pair and for each response metric, potential differences were evaluated using unpaired Welch's two sample t-tests. Although individually tagged steelhead were later recaptured in the screw trap, low number of recaptures precluded statistical evaluation of differences in these metrics between control and treatment reaches.

We analyzed size-survival relationships for fall migrant and spring migrant Chinook separately. For each year, Chinook were grouped into 5 mm bins from 55-100 mm. Survival for each bin was calculated as the number detected at Lower Granite Dam after correcting for annual detection efficiency (Fish Passage Center 2017) divided by the number originally tagged. We excluded size groups in which less than 50 Chinook were tagged for each year. We then calculated the mean survival of each size group over the 18 year study interval and evaluated the relationship between size and mean survival.

Results

Carcass treatment persistence

In the middle and downstream study pairs camera taps and field observations of carcasses indicated there was relatively little impact of terrestrial scavengers on carcasses and field observations confirmed that most carcasses decomposed within the stream. Due to warm water temperatures, carcasses decomposed rapidly and little carcass material remained after 8 weeks. Trail camera footage revealed that bald eagles (*Haliaeetus leucocephalus*) were the dominant terrestrial scavenger in these pairs but most consumption occurred within the stream and thus carcass material (eggs and tissue) were released to streams during scavenging. In contrast to the middle and downstream pairs, terrestrial scavengers did impact carcass persistence and potential carcass subsidies effects in the upstream reach pair. Camera traps revealed that black bears (*Ursus americanus*) eventually found and then removed carcasses from the stream, resulting in a rapid loss of carcasses from the treatment reach. After two weeks, only 44 of the original 86 carcasses remained in the upstream treatment reach, and after three weeks less than 10 carcasses remained. Due to cool water temperatures, carcasses in this reach decomposed very little before they were scavenged. However, during the three weeks in which carcasses were present, eggs were commonly observed being released from carcasses into the stream. Bears were not observed on trail cameras at the middle and downstream pairs.

Growth and body condition responses

Steelhead mean growth rates increased in the treatment reach of each pair relative to the control reach following the addition of carcasses (Figure 6.2A). Prior to the addition of carcasses, mean growth rates between control and treatment reaches in all three pairs were not significantly different (e.g. 95% confidence intervals of the mean difference encompassed 0; $p < 0.05$). In the treatment reach of the upstream pair growth rates were significantly greater between one and three weeks after additions relative to the upstream control reach (95% CI = 1.8 to 3.3 Δ % mass/day; $p < 0.001$). However, significant differences in growth rates in this upstream pair did not persist, and growth during the period between three and seven weeks after carcass additions was not significantly different between the two reaches ($p < 0.05$). In the middle pair, mean growth rates were significantly greater in the treatment reach compared to the control reach within one week after carcass additions (95% CI = 0.20 – 1.79 Δ % mass/day; $p = 0.002$) and in the period between one and three weeks (95% CI = 3.34 – 4.91 Δ % mass/day; $p < 0.001$), but not from the third interval from three to seven weeks after carcass additions ($p < 0.05$). In the downstream pair growth patterns were similar to the middle pair, with significantly greater growth rates in the treatment reach within one week (95% CI: 0.10 – 2.46 Δ % mass/day; $p = 0.007$) and between one and three weeks (95% CI: 0.99 – 2.90 Δ % mass/day; $p < 0.001$) after carcass additions. We were only able to recapture two previously tagged individuals from the control reach of the middle pair during the final sampling event in October, precluding quantification of growth rates during this period.

Carcass additions significantly affected steelhead body condition in the middle and downstream pairs but not the upstream pair (Figure 6.2B). Mean body condition was not significantly different between the control and treatment of the upstream pair during any sampling event ($p > 0.05$), despite increased growth rates in the treatment reach. In the middle pair, mean body condition was similar ($p > 0.05$) between the control and treatment reach before and one week after carcass additions but was significantly greater in the treatment reach three weeks (95% CI: 0.13 – 0.22; $p < 0.001$) and seven weeks (95% CI: 0.05 – 0.16; $p < 0.001$) after carcass additions. In the downstream pair, mean body condition of was significantly lower in the treatment reach during the first sampling event (95% CI: -0.13 – -0.02; $p = 0.005$), similar one week after carcass additions ($p > 0.05$), and then significantly greater three weeks (95% CI: 0.07 – 0.19; $p < 0.001$) and seven weeks (95% CI: 0.01 – 0.11; $p = 0.02$) after carcass additions.

Chinook responses to carcass additions were more variable than steelhead responses and were not consistent between the two pairs in which Chinook were abundant (Figure 6.3). All Chinook were tagged after the addition of carcasses and we were only able to quantify post-treatment growth rates. In the upstream pair, Chinook growth rates were greater in the treatment reach relative to the control between one and three weeks after carcass addition but from three to seven weeks growth rates were lower in the treatment reach; however, these differences were not statistically significant ($p > 0.05$). In the middle pair, Chinook mean growth rates were significantly greater in the treatment reach of the middle pair between one and three weeks (95% CI: 1.08 – 1.52 Δ % mass/day; $p < 0.001$). However, growth rates were similar between the control and treatment reach three and seven weeks after carcass additions ($p > 0.05$).

In the upstream pair of study sites, Chinook mean body condition (Figure 6.3B) was consistently lower in the treatment reach prior to the addition of carcasses (95% CI of differences: -0.056 – -0.004; $p = 0.02$, and 95% CI of differences -0.056 – -0.013; $p = 0.002$ for the first and second sampling events, respectively.). After the addition of carcasses, body condition increased in the treatment reach relative to control reach. Although in the three post-treatment sampling events body condition was not significantly different between the control and treatment reach ($p > 0.05$), the increase in condition relative to pre-treatment differences suggests a positive effect of carcass additions on Chinook condition in the treatment reach. In the middle pair, mean body condition was similar ($p > 0.05$) between the control and treatment reach before carcass additions and for the first week after carcass additions ($p > 0.05$). However, both three and seven weeks after carcass addition body condition of juvenile Chinook was significantly greater in the treatment reach (95% CI: 0.035 – 0.103; $p < 0.001$, and 95% CI: 0.034 – 0.114; $p < 0.001$ for weeks three and seven, respectively).

Because juvenile Chinook were too small to be tagged in early summer prior to carcass additions, we evaluated changes in mean weight (Figure 6.3C) and mean length (Figure 6.3D) over time as additional proxies for growth responses to carcass additions. Mean juvenile Chinook weight was similar between the control and treatment reach of the upstream pair during the first sampling event, but was significantly lower in the treatment reach during the next pretreatment sampling event (95% CI of difference: -0.54 – -0.05 g; $p = 0.02$) and was even lower during the last pretreatment sampling event (95% CI of difference: -0.74 – -0.21 g; $p < 0.001$), suggesting slower summer growth rates in the treatment reach before carcasses were added. After the addition of carcasses, mean weights of juvenile Chinook were no longer different between the control and treatment reaches ($p > 0.05$), suggesting greater growth rates in the treatment reach during the interval between the last pre-treatment sampling event and the first post-treatment sampling period (a period of approximately two weeks). In the first post-treatment sampling period, juvenile Chinook were large enough to tag, therefore individual growth could be quantified and compared for the periods after carcass addition. Trends in mean length of Chinook in the upstream pair were similar (Figure 6.3D). Just prior to the addition of carcasses, Chinook were on average 4.23 mm shorter in the treatment reach compared to the control (95% CI of difference: -6.09 – -2.37 mm; $p < 0.001$), but significant differences in length were no longer observed after the addition of carcasses ($p > 0.05$). At the conclusion of the study

(October; seven weeks after carcass additions) Chinook in the treatment reach were on average 0.15 g larger and 0.62 mm longer in the treatment reach compared to the control.

In the middle pair of study reaches, juvenile Chinook mean weight was significantly greater in the treatment reach just prior to the addition of carcasses (95% CI of difference: 0.23 – 0.88 g; $p < 0.001$). One week after carcass additions, Chinook mean weight was significantly greater in the treatment reach, but differences were comparable to the pre-treatment period (95% CI: 0.06 – 0.64 g; $p < 0.02$). However, differences increased over time and juvenile Chinook were substantially larger in the treatment reach three (95% CI: 0.86 – 1.96 g; $p < 0.001$) and seven (95% CI: 1.08 – 2.37 g; $p < 0.001$) weeks after carcass additions. Trends in length were also similar, with significantly greater mean length in the treatment reach prior to the addition of carcasses (95% CI: 1.66 – 5.21 mm; $p < 0.001$), but larger differences occurring three (95% CI: 2.54 – 8.81 mm; $p < 0.001$) and seven (95% CI: 2.12 – 9.52 mm; $p < 0.001$) weeks after addition. At the conclusion of the study (October), juvenile Chinook in the treatment reach of the middle pair were on average 1.7 g larger and 6 mm longer than Chinook in the control reach.

Differences in individual growth rates between control and treatment reaches in did not appear to be driven by movement or density. Only four PIT-tagged salmonids (all Chinook) were recaptured in a reach different from the initial reach in which they were tagged, and these individuals were removed from growth analysis. Density estimates of steelhead were greater in the treatment reach compared to the control reach of the middle and downstream pairs before and after the addition of carcasses (Table A6.1), so we would expect lower rather than higher growth and condition in the treatment reaches if density dependence alone were the driver of these factors at these sites. Steelhead densities in the treatment reach of the upstream pair were approximately half that of the control reach (0.10 vs. 0.19 ind. m^{-2}) before carcass addition but were similar after carcass addition (0.26 vs. 0.31 ind. m^{-2}). Chinook density in the treatment reach of the upstream pair was approximately half that of the control reach before (0.59 vs. 1.16 ind. m^{-2}) and after (0.80 vs. 1.84 ind. m^{-2}) carcass addition. In contrast Chinook density was greater in the treatment reach of the middle pair compared to the control reach both before (0.22 vs. 0.11 ind. m^{-2}) and after (0.22 vs. 0.34 ind. m^{-2}) carcass addition.

Diet responses

Stomach contents indicated that juvenile salmonids were consuming substantial amounts of eggs (Figure 6.4) and carcass tissue one and three weeks after carcass addition in the treatment reaches. In the upstream pair, egg and carcass tissue consumption in the treatment reach was greatest one week after carcass addition with 60% of steelhead and 32% of Chinook stomachs containing eggs. Carcass tissue was present in 30% of steelhead one week after carcass addition but was not observed in Chinook over this time period. Three weeks after carcass addition, eggs were present in 32% of steelhead diets but were not detected in Chinook diets, and tissue was not observed in either species. Eggs and tissue were absent from both steelhead and Chinook stomach contents seven weeks after addition. No eggs or carcass material were observed in the diets of steelhead and Chinook captured in the control reach of the upstream pair during any sampling event.

In the middle pair, egg consumption in the treatment reach was documented for juvenile Chinook one and three weeks after carcass additions and egg consumption was documented in all three all three post-treatment survey periods for juvenile Steelhead (Figure 6.4). One week after carcass addition, 54.2% of steelhead and 8.3% of Chinook stomachs contained eggs, but carcass tissue was absent from both species. Three weeks after carcass addition, 83.3% of steelhead and 57.7% of Chinook stomachs contained eggs and carcass material was present in 20.8% of steelhead stomachs and 3.8% of Chinook stomachs. Seven weeks after carcass addition, eggs were present in 10.7% of steelhead stomachs and carcass tissue was present in 17.9% of steelhead stomachs, but both eggs and carcass tissue were absent from Chinook stomachs.

In the downstream pair, steelhead consumption of eggs and carcass followed a similar pattern as in the middle pair (Figure 6.4). One week after addition, 24% of stomachs contained eggs but no carcass tissue was present; three weeks after addition, 88.9% of stomachs contained eggs and 25.9% contained carcass tissue; and seven weeks after addition, 4.3% of stomachs contained eggs and 17.4% contained carcass tissue. As in the other sites, no carcass tissue or egg material were found in the diets of steelhead in the control reach of the downstream pair.

Eggs were a particularly high value food resource for juvenile salmonids in this system. Consumption of eggs substantially increased steelhead and Chinook energy intake (Figure 6.5), expressed as instantaneous rations (IR). Although only the IR of eggs was quantified for the period one week after carcass addition, steelhead ration sizes of the egg category alone during this event exceeded the total IR of controls during any of the other sampling events for all three pairs. Similarly, IR of the egg category of Chinook in the upstream pair exceeded the IR of Chinook in control reaches during other events. In the middle pair Chinook egg consumption was low one week after carcass additions. Three weeks after carcass addition, eggs dominated the IR of steelhead in all three pairs as well as Chinook in the middle pair. Steelhead IRs were 2.8, 19.6 and 11.8 times greater in treatment reach compared to the control reach of the upstream, middle, and downstream pairs, respectively, during this sampling event period. Chinook IR was 29.1 times greater in the treatment reach of the middle pair compared to the control reach during the three week sampling event. In the upstream pair, where scavenging reduced carcass abundances, Chinook IR in the treatment reach of upstream pair was just 0.29

times that of the control reach during week three sampling, and eggs did not contribute to IR during this period. Seven weeks after carcass addition, eggs were rarely observed in stomach contents of both steelhead and Chinook (Figure 6.4) and did not contribute substantially to the IR of either species (Figure 6.5).

Fall migrant Chinook size

There were no significant differences in mean length, weight or condition between control and treatment fall emigrating Chinook from the upstream pair (t-test; $p > 0.05$). In contrast, length ($p = 0.005$) and weight ($p = 0.002$) were significantly greater for Chinook from the middle pair treatment reach compared to the middle pair control reach. Mean length Chinook from the treatment reach of the middle pair was 5.3 mm (or 7%) greater and mean weight was 1.17 g (or 26%) greater than control Chinook. Mean condition was not significantly different for control and treatment Chinook from the middle pair ($p = 0.124$).

Size-survival relationships

Considering Chinook tagged in the upper Grande Ronde over 18 years, estimated survival was positively correlated to length for both fall migrant ($r^2 = 0.86$; $p = 0.001$) and spring migrant ($r^2 = 0.89$; $p = 0.01$) Chinook (Figure 6.7). For fall migrant Chinook, the smallest fish (60 to 65 mm) had survival rates of 12 to 15% between UGR and lower granite dam. Survival rate for juvenile Chinook increased with size as fish migrating at 90 mm had a survival rate (37.2%) that was 2-3 times that of the smallest fish. Overall, survival was estimated to increase 3.7% for every 5 mm increase in length. For spring migrant Chinook estimated survival was lower for all lengths but the slope of the relationship was similar. For every 5 mm increase in Chinook length, survival increased by 5.1%.

We used these length-survival relationships to estimate potential effects of carcass additions on survival. Fall migrant Chinook from the upstream pair were similar in size and thus estimated survival was similar. In contrast, fall migrant Chinook from the treatment reach of the middle pair were 5.3 mm larger than Chinook from the control reach and survival was estimated to be 3.9% greater (27.1% vs 23.2%). We assumed that within study reaches the majority of Chinook measured in October were spring emigrants and we therefore used October mean size to evaluate potential effects on survival using the spring migrant length-survival relationship. Similar to fall-migrants, Chinook in the treatment reach of the upstream pair were similar in size to Chinook in the control and therefore estimated survival was similar. Chinook in the treatment reach of the middle pair were 5.8 mm larger on average than Chinook in the control reach, yielding an estimated increase in survival of 6.0% (24.5% vs 18.5%).

Discussion

Management activities implemented to promote growth and survival of juvenile Pacific salmon in headwater ecosystems often focus on the restoration of the resource subsidies that derive from the mortality of returning adult fish (e.g. carcasses and nutrients). The response of juvenile salmon to carcass and carcass analog additions have been variable (Janetski et al. 2009), which raises questions about its viability as a wide-spread strategy (Collins et al. 2015). Understanding the geographic context and local stream conditions that influence the magnitude of stream salmonid responses to carcass additions is therefore important to improve the efficacy of this management action. By applying carcass addition treatments at three separate locations in a stream network using a BACI study framework, we were able to explore how stream conditions could affect the response of juvenile Chinook salmon and steelhead. Further, in our assessment of fish diet through direct observations at multiple times through summer, we were able to link responses in growth to the direct consumption of eggs and carcass tissue. Lastly, we were able to link positive effects on juvenile Chinook growth and size to their survival in this system. Our study demonstrated that carcass additions clearly have the potential to enhance juvenile salmonid growth and that increases in growth likely increase the survival of these fish during their downstream migration. Diet analysis clearly indicated that direct consumption of eggs and carcass tissue by juvenile fish was critical to this positive response, even when carcasses were removed by scavengers well before they could provide subsidies through dissolved inorganic nutrient release that can promote bottom-up food web pathways. Overall, our results highlight the value and viability of adding complete carcasses to a stream, and in particular, the value of including carcasses that contain eggs.

The addition of carcasses generally enhanced growth rates and condition of juvenile Chinook and steelhead. Growth rates were often close to zero for steelhead in control reaches and, consequently, short-term effect sizes in treatment reaches in this study were large. The large effect sizes under comparable fish densities demonstrates clear food limitation and that growth potential in these stream reaches in summer is far greater than observed in the absence of carcass subsidies. Increased growth rates have been observed in response to carcass additions in a number of studies (Wipfli et al. 2003, 2004; Kiffney et al. 2014; Collins et al. 2016); however, other studies observed no such increases in growth rates (Wilzbach et al. 2005; Harvey and Wilzbach 2010; Cram et al. 2011), suggesting varying success of carcass additions under different conditions. One potential factor explaining the degree to which growth rates vary across studies is the density of carcasses added to stream systems, evidenced by a positive relationship between carcass loading density and salmonid response effect size (Janetski et al. 2009). However, based on the analysis in Janetski et al. (2009) our study presents the lowest carcass loading rates of any known studies but among the highest effect sizes on growth rates. The large effect sizes observed in the current study may be attributed to strong food limitation during late summer, warm temperatures allowing for high growth potential when food is abundant, and eggs being retained within carcasses which were rapidly consumed by juvenile salmonids.

Salmonid growth responses observed in this study appeared to be primarily fueled by direct consumption of eggs and carcass material. It is unlikely that changes in primary production and associated invertebrate production could have accounted for short-term growth responses (within three weeks), because there is typically a lag between periphyton responses and the responses of higher trophic levels (Nelson and Reynolds 2014). There could be a partially indirect/direct consumption pathway by which carcass material is consumed by invertebrates (Winder et al. 2005; Claeson et al. 2006; Walter et al. 2006; Collins et al. 2016), resulting in increased prey consumption by salmonids (Collins et al. 2016). While this is a possible pathway in the current study, we do not believe that this was a dominant pathway for resource subsidies. Macroinvertebrates were not observed on carcasses despite snorkeling each site four-to-five times following carcass additions. The exception was crayfish, which were occasionally observed feeding on carcasses; however, crayfish were rarely in the diets of steelhead and never in the diets of Chinook, and it would therefore be unlikely to contribute substantially to observed salmonid growth responses. Further, diet analysis did not indicate that salmonids were consuming greater invertebrate biomass in the treatment reaches after carcass additions.

Eggs are a particularly high energy food resource that can fuel rapid growth rates (Denton et al. 2009; Ruff et al. 2011). We found that not only were salmonids consuming eggs, but that eggs were fueling increased energy rations of diets – by up to 30 times in some instances.

Salmonids were also consuming carcass tissue, but we were not able to quantify contributions of carcass tissue to the energy ration of diets. Incorporation of these materials would have increased effects of carcass addition on energy rations, and therefore our estimates are conservative. Salmonid consumption of eggs and carcass material was short-lived, however, with consumption peaking one or three weeks after carcass addition but little egg or carcass material in diets after seven weeks. Although short in duration, pulses of salmon subsidies through direct consumption can be a dominant source contributing to the annual production of salmonids. For example, Collins et al. (2016) found that carcass tissue fueled 17% of annual trout production in streams treated with carcasses (eggs removed). Studies evaluating salmonid consumption of eggs and carcass tissue during natural spawning runs have found that salmonids can obtain the majority of their annual energy intake during sockeye salmon (*O. nerka*) spawning; a period approximately five weeks in duration (Scheuerell et al. 2007; Denton et al. 2009; Bentley et al. 2012; Armstrong and Bond 2013). These results provide support that direct consumption of eggs and carcass material can stimulate increased growth rates and annual production of salmonids. This work reinforces the conclusions of early field studies on the role of salmon carcass subsidies which found that even though carcasses were spawned prior to carcass additions, the small amount of eggs that remained in carcasses were key in stimulating greater coho salmon (*O. kisutch*) and steelhead growth rates (Bilby et al. 1996, 1998).

Our results suggest that carcass additions likely increased juvenile salmonid overwinter and emigration survival. The combination of larger size (middle pair Chinook) and improved body condition (steelhead in all pairs, and Chinook in the middle pair) of salmonids in treatment reaches in October suggest greater juvenile fitness prior to the onset of winter, a period characterized by low growth rates (Tattam et al. 2017). A number of studies have found that larger size and greater condition can increase overwinter survival rates of salmonids (Quinn and Peterson 1996; Zabel and Achord 2004; Ebersole et al. 2006). In addition, consumption of eggs and carcass material can increase the lipid content of juvenile salmonids (Wipfli et al. 2004; Samways et al. 2017), which provide fat stores during periods of limited resources and low growth. Further evidence for potentially increased survival is provided from the positive relationship between Chinook size during fall or winter tagging versus survival to the Lower Granite Dam, approximately 420 km away (Figure 6.7). Using this relationship, we estimated the fall migrant Chinook survival from the middle pair increased 3.9% greater (27.1% vs 23.2%) and spring migrant Chinook survival from the middle pair increased 6.0% (24.5% vs 18.5%). These combined findings reporting positive associations between size and survival suggest that management actions that enhance growth rates and ultimately size likely increase rearing and emigration survival.

Management implications

The ultimate goal of carcass additions is to increase the number of adult salmon, a premise hinging on the assumptions that carcass additions 1) increase juvenile growth rates, 2) increased growth rates and size lead to greater juvenile survival, and 3) greater juvenile survival increases the number of adult salmon (Collins et al. 2015). Although carcass additions have been evaluated and applied as a management tool to enhance juvenile salmon growth in a number of coastal stream systems across the Pacific Northwest, the effects of carcass additions on juvenile salmonids within the interior Columbia Basin has received less attention. We demonstrated that the addition of carcasses in mid-summer (at an ecologically relevant time period – spawning, and deployed at a density representative of potential management applications), resulted in increased growth rates and greater body condition of juvenile salmonids. Effects were greatest in the middle and downstream sections of our study, which is likely attributable to a combination of stream temperatures that are more favorable for growth in the mid-order stream sections, and the removal of carcasses by bears in the cooler upstream study site. Diet analysis indicated that observed growth and condition effects were primarily attributed to increased energy intake from direct consumption of eggs and, to a lesser extent, carcass tissue. These results, as well as results from other studies demonstrating the importance of eggs fueling growth responses (Bilby et al. 1996, 1998), suggest that eggs should be retained during carcass addition management efforts to maximize salmonid growth potential. Using a long-term dataset (1997-2015) we demonstrate the Chinook size is related to survival to the first dam encountered during downstream migration, which suggests that management actions resulting in greater Chinook growth and ultimately size likely increase survival rates.

Although food web responses may differ between naturally spawning salmon and artificial carcass additions (Janetski et al. 2009), our results suggest that the losses of spawning salmon and steelhead within this system have reduced energy available for juvenile salmonids with potential declines in growth and survival. However, it is important to acknowledge that this study focused on reach-scale effects and the viability of such management actions must consider population level responses. Future research evaluating effects of carcass additions, or salmon carcass analogs, should expand assessments to consider larger population or sub-population level responses and further consider effects on other aspects of the salmon life cycle such as rearing survival, emigration survival, and survival to adulthood (e.g. smolt-to-adult).

Acknowledgements

We thank C. Hayes, A. Sanders, J. Dowdy, the ODFW Early Life History crew, and the Bureau of Reclamation summer interns for their assistance in field work. J. Dowdy, A. Dutterer, S. Favrot, W. Morton, A. Simpson and staff of the Grande Ronde Model Watershed provided logistical assistance. B. Bilby, A. Kohler, and S. Collins provided feedback on initial experimental design. S. Johnson, W. Gerth and I. Arismendi provided laboratory space and assistance. Ruth Bowman provided access to sites located on their property. We thank JT Lemanksi for constructive comments on this manuscript. This research was supported by the Bonneville Power Administration as part of the Columbia Basin Fish Accords Agreement (Project # 2009-004-00), an Oregon Watershed Enhancement Board (OWEB) Focused Investment Partnership (Project # 216-8205-15449) and a National Science Foundation Graduate Research Fellowship (Grant No. 1314109-DGE).

Literature cited

Armstrong, J. B., and M. H. Bond. 2013. Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. Journal of Animal Ecology 82(5):966–975.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445–1454.

Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. T. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams : Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94(9):2066–2075.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, and P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):113.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Bilby, R. E., B. R. Fransen, and P. a Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53(1):164–173.

Claeson, S. M., J. L. Li, J. E. Compton, and P. A. Bisson. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. Canadian Journal of Fisheries and Aquatic Sciences 63:1230–1241.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):1–18.

Collins, S. F., A. M. Marcarelli, C. V Baxter, and M. S. Wipfli. 2015. A Critical Assessment of the Ecological Assumptions Underpinning Compensatory Mitigation of Salmon-Derived Nutrients. Environmental Management 56:571–586. Springer US.

Cram, J. M., P. M. Kiffney, R. Klett, and R. L. Edmonds. 2011. Do fall additions of salmon carcasses benefit food webs in experimental streams? Hydrobiologia 675:197–209.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric Equivalents for Inverstigations in Ecological Energetics. International Association of Theoretical and Applied Limnology 18:1–158.

Denton, K. P., H. B. Rich, and T. P. Quinn. 2009. Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. Transactions of the American Fisheries Society 138(6):1207–1219.

Ebersole, J. L., P. J. Wigington, J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansen, B. A.

Miller, H. R. La Vigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats. Transactions of the American Fisheries Society 135:1681–1697.

Fish passage center 2016 annual report. 2017. . Portland, Oregon.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem : Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. Fisheries Habitat 25(1):15–21.

Harvey, B. C., and M. A. Wilzbach. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth, or retention in six northwestern California streams. North American Journal of Fisheries Management 30:1445–1451.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.

Jonasson, B. C., E. R. Sedell, S. K. Tattam, A. B. Garner, C. D. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, J. M. Hay, G. A. McMichael, B. C. Power, O. C. Davos, and J. R. Ruzycki. 2015. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. La Grande, Oregon.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management 188:212–227.

Kamler, J. F., and K. L. Pope. 2001. Nonlethal Methods of Examining Fish Stomach Contents Nonlethal Methods of Examining Fish Stomach Contents. Nebraska Cooperative Fish and Wildlife Research Unit-Staff Publications 55.

Kiffney, P. M., E. R. Buhle, S. M. Naman, G. R. Pess, and R. S. Klett. 2014. Linking resource availability and habitat structure to stream organisms: an experimental and observational assessment. Ecosphere 5(4):1–27.

Kohler, A. E., T. N. Pearsons, J. S. Zendt, M. G. Mesa, C. L. Johnson, and P. J. Connolly. 2012. Nutrient Enrichment with Salmon Carcass Analogs in the Columbia River Basin, USA: A Stream Food Web Analysis. Transactions of the American Fisheries Society 141(September 2014):802–824.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53(3):446–460.

Meehan, W. R., and R. A. Miller. 1978. Stomach Flushing: Eftectiveness and Influence on Survival and Condition of Juvenile Salmonids. Journal of Fisheries Research of the Board of Canada 35:1359–1363.

Minakawa, N., R. I. Gara, and J. M. Honea. 2002. Increased individual growth rate and community biomass of stream insects associated with salmon carcasses. Journal of the North American Benthological Society 21(4):651–659.

Monzyk, F. R., B. C. Jonasson, T. L. Hoffnagle, P. J. Keniry, R. W. Carmichael, and P. J. Cleary. 2009. Migration Characteristics of Hatchery and Natural Spring Chinook Salmon

Smolts from the Grande Ronde River Basin, Oregon, to Lower Granite Dam on the Snake River. Transactions of the American Fisheries Society 138:1093–1108.

Morley, S. A., H. J. Coe, J. J. Duda, L. S. Dunphy, M. L. Mchenry, B. R. Beckman, M. Elofson, E. M. Sampson, and L. Ward. 2016. Seasonal variation exceeds effects of salmon carcass additions on benthic food webs in the Elwha River. Ecosphere 7(8).

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109(52):21201–7.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nelson, M. C., and J. D. Reynolds. 2014. Time-delayed subsidies: Interspecies population effects in salmon. PLoS ONE 9(6):1–9.

ODFW (Oregon Department of Fish and Wildlife). 1990. Grande Ronde River Subbasin Salmon and Steelhead Production Plan. Portland, OR.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The Influences of Body Size, Habitat Quality, and Competition on the Movement and Survival of Juvenile Coho Salmon during the Early Stages of Stream Recolonization. Transactions of the American Fisheries Society 140(4):883–897.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (Oncorhynchus kisutch) in Big Beef Creek , Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Ruff, C. P., D. E. Schindle, J. B. Armstrong, K. T. Bentle, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92(11):2073–2084.

Ruzycki, J. R., M. W. Flesher, R. W. Carmichael, and D. L. Eddy. 2003. Lower Snake River Compensation Plan: Oregon Evaluation Studies-Steelhead Life History, Genetics, and Kelt Reconditioning. Oregon Department of Fish and Wildlife, La Grande, OR.

Samways, K. M., T. J. Blair, M. A. Charest, and R. A. Cunjak. 2017. Effects of spawning Atlantic salmon (Salmo salar) on total lipid content and fatty acid composition of river food webs. Ecosphere 8(6).

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52(10):1944–1956.

Sedell, E. R., S. K. Tattam, A. B. Garner, C. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, G. A. McMichael, E. N. Branigan, B. C. Power, O. C. Davis, and J. R. Ruzycki. 2018. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. 2017 Annual Report. BPA Project #

1992-026-04.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of Oncorhynchus mykiss growth require year-round monitoring. Ecology of Freshwater Fish 26:434–443.

Van Dyke, E. S., D. L. Scarnecchia, B. C. Jonasson, and R. W. Carmichael. 2009. Ecology of Winter Concealment Behavior of Juvenile Spring Chinook Salmon in the Grande Ronde River Basin, Oregon. Northwest Science 84(1):9–19.

Verspoor, J. J., D. C. Braun, M. M. Stubbs, and J. D. Reynolds. 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. Ecosphere 2(February):1–17.

Walter, J. K., R. E. Bilby, and B. R. Fransen. 2006. Effects of Pacific salmon spawning and carcass availability on the caddisfly Ecclisomyia conspersa (Trichoptera: Limnephilidae). Freshwater Biology 51:1211–1218.

Wilzbach, M. A., B. C. Harvey, J. L. White, and R. J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:58–67.

Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Canadian Journal of Fisheries and Aquatic Sciences 62:2285–2293.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 2004. Restoring productivity of salmon-based food webs : contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. Transactions of the American Fisheries Society 133:1440–1454.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, N. L. Mitchell, J. L. Lessard, R. A. Heintz, and D. T. Chaloner. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic levels in streamside experimental channels. Transactions of the American Fisheries Society 139:824–839.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85(3):795–806.

Table 6.1: Site characteristics during the summer of 2017.

Pair	Treatment	Mean Aug. Temp. (°C)	Max Aug. Temp. (°C)	Q Sept. (m^3/s)	Reach Length (m)	Wetted width (m)	Carcasses added	Carcass density (kg/m^2)
Upstream	Control	12.3	16.1	0.28	190	5.1	0	0
	Treatment	13.1	19.2	0.28	180	4.9	86	0.27
Middle	Control	17.4	24.0	0.49	233	8.8	0	0
	Treatment	17.4	24.2	0.55	180	11.1	123	0.18
Downstream	Control	17.7	24.5	0.50	357	9.9	0	0
	Treatment	18.14	26.5	0.55	286	8.3	163	0.19

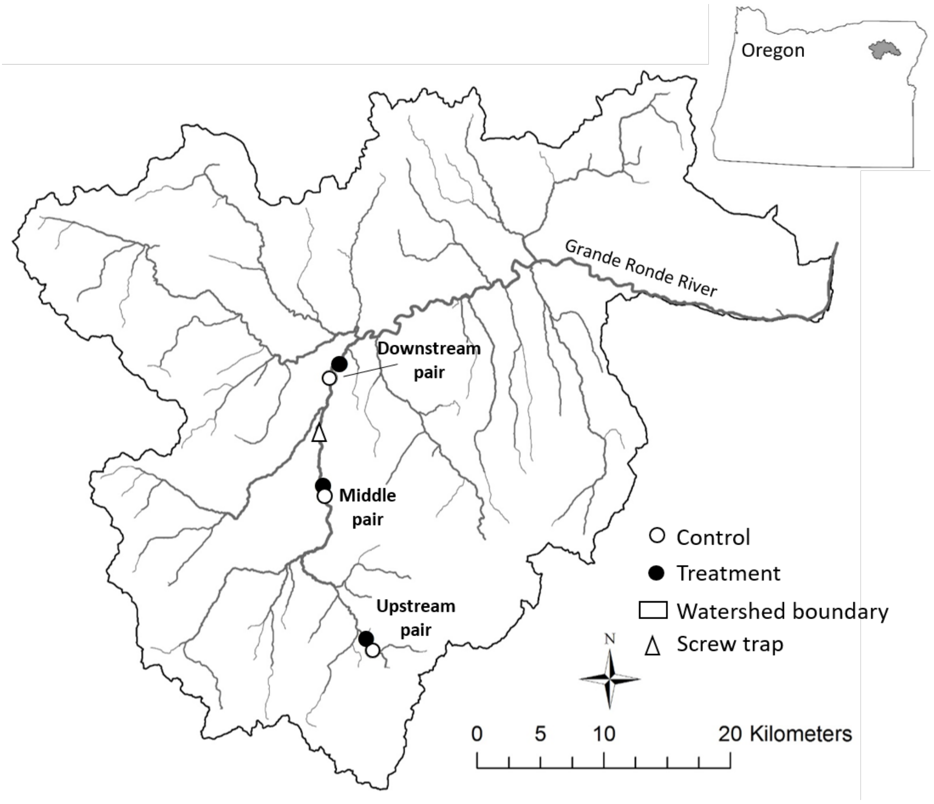


Figure 6.1: Map of the three study pairs each with an upstream control (open circles) and downstream treatment reach (filled circles) where carcasses were added. The distance between control and treatment sites within each pair ranged from 300-1000 m.

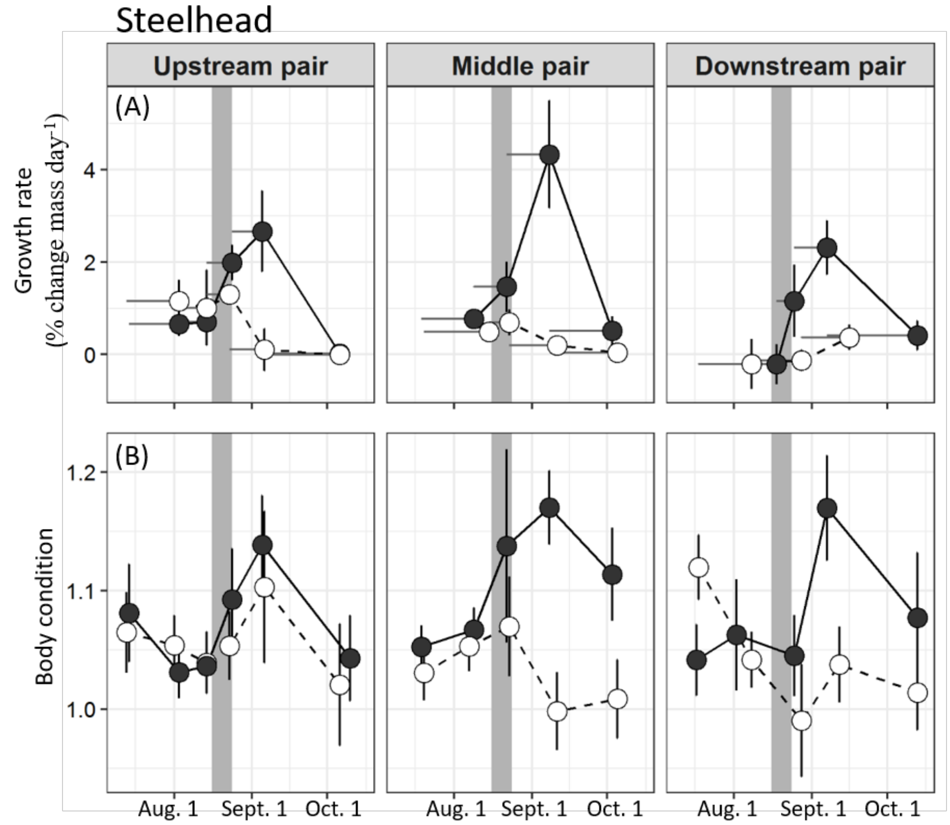


Figure 6.2: Juvenile steelhead mean instantaneous growth rate (A; % change mass/day) and mean body condition (B) over time. The shaded box indicates approximately when carcasses were added to streams. Vertical error bars indicate 95% confidence intervals. Horizontal error bars for growth indicate the duration growth rates were calculated for with the point representing the date of recapture for that interval.

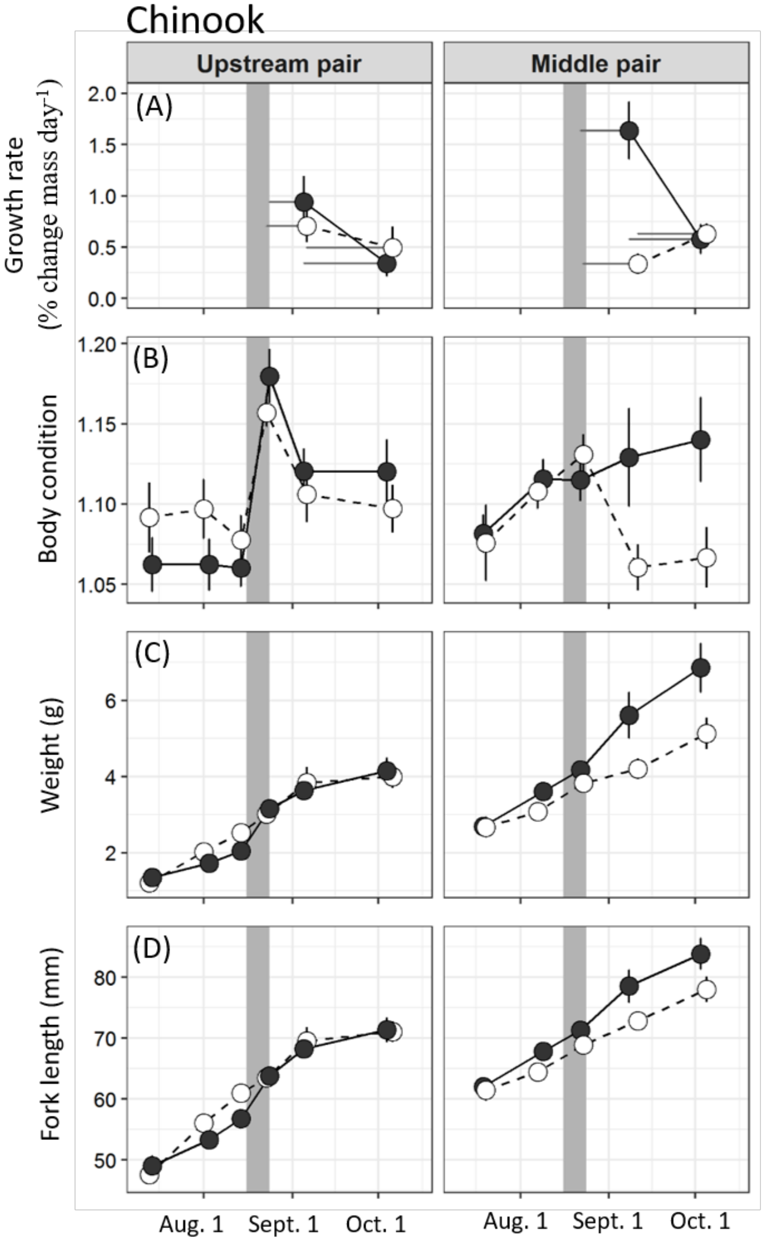


Figure 6.3: Juvenile Chinook mean instantaneous growth rate (A), condition (B), weight (C) and fork length (D) over time. See Figure 6.2 for details.

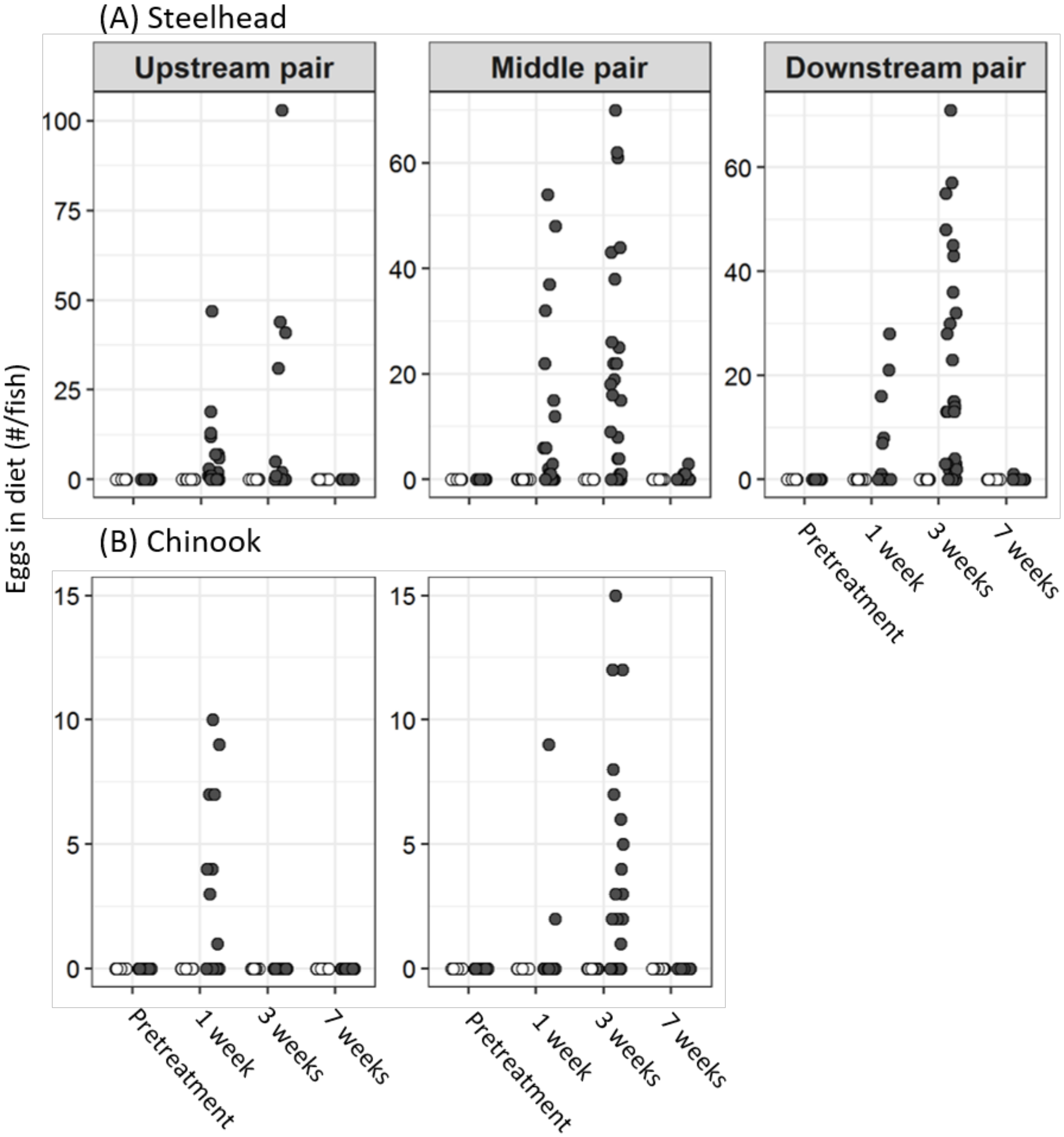


Figure 6.4: Number of eggs in O. mykiss (A) and Chinook (B) stomach contents in treatment reaches before the addition of carcasses (pretreatment), and 1 week, 3 weeks, and 7 weeks after the addition of carcasses in both control (open circles) and treatment (closed circles) reaches. Each point represents the number of eggs in one fish.

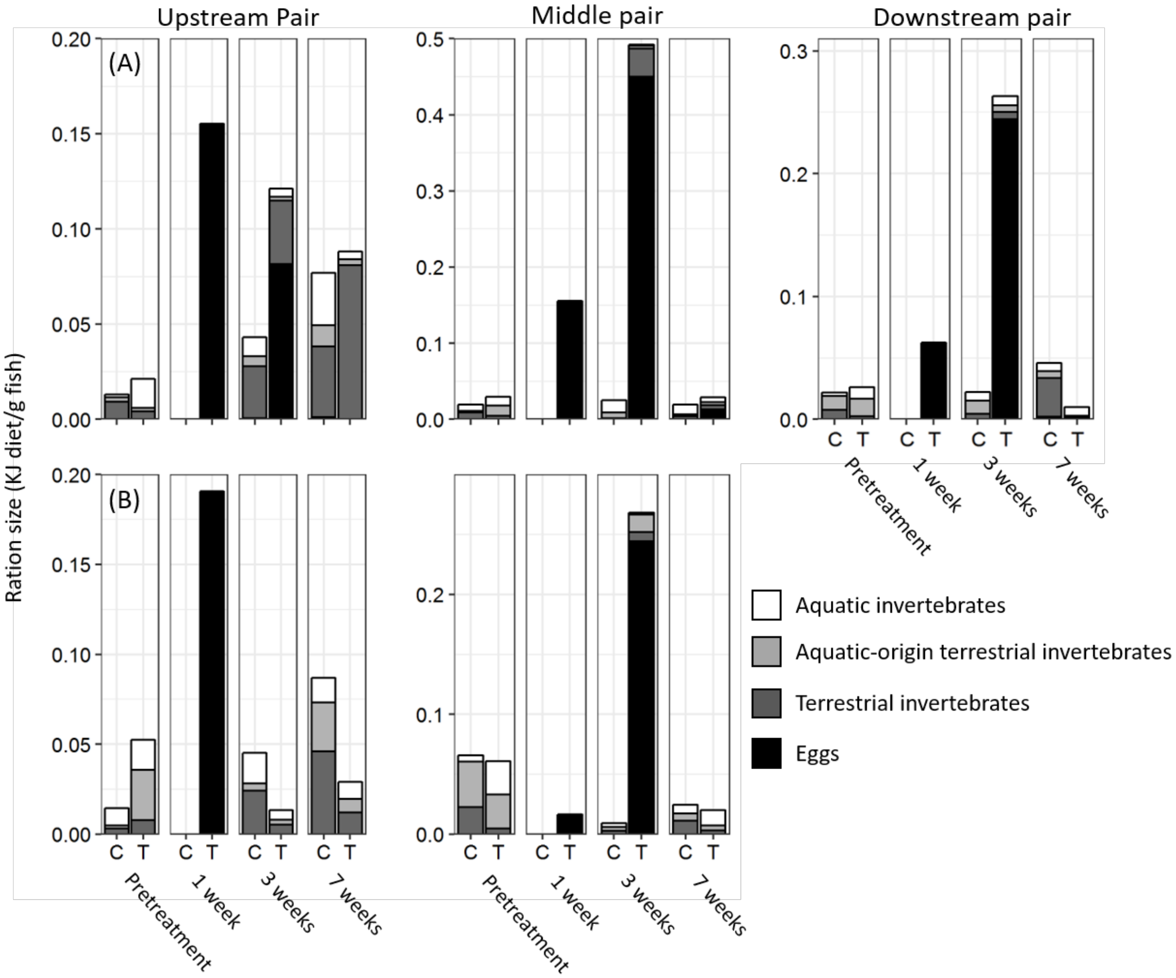


Figure 6.5: Standardized average instantaneous ration size and composition for steelhead (A) and Chinook (B) expressed as KJ of stomach contents per gram of fish. Samples were collected two weeks before carcass addition (pretreatment) and then one week, three weeks, and seven weeks after carcasses were added in both control (C) and treatment (T) reaches. *Week one samples were not collected in control reaches and only the ration size of the egg category is presented for treatment reaches.

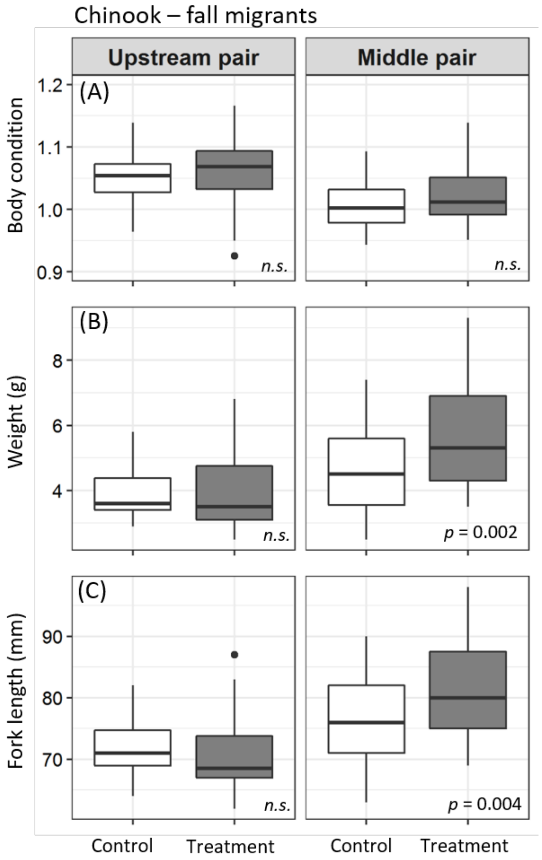


Figure 6.6: Juvenile Chinook mean condition (A), weight (B), and fork length (C) during fall emigration from study reaches. Juveniles were captured in a screw trap located between pairs 2 and 3 between 9/21/2017 and 11/29/17. The median capture date was 10/23/17.

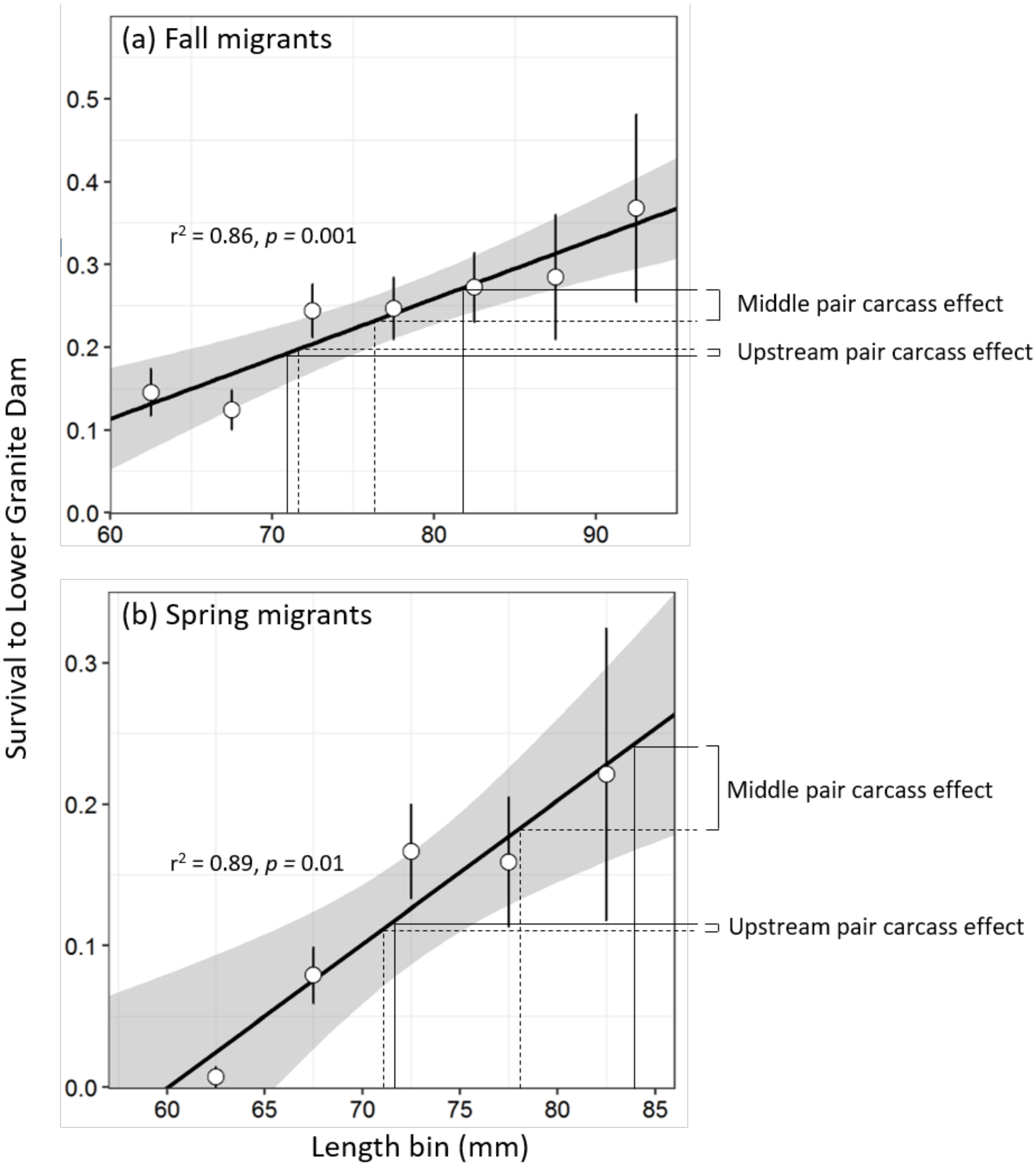


Figure 6.7: Relationship between fall migrant (a) and spring migrant (b) juvenile Chinook length and estimated mean annual survival (1997-2016) from the upper Grande Ronde to Lower Granite Dam on the Snake River. Error bars indicate standard error. The estimated survival of Chinook from our study reaches are indicated on the right side.

CHAPTER 7: CARCASS ADDITIONS INFLUENCE FOOD WEBS THROUGH BOTTOM-UP AND DIRECT CONSUMPTION PATHWAYS ALONG A NE OREGON STREAM WITH VARYING FISH SPECIES ASSEMBLAGES

Matthew J. Kaylor, Seth M. White, Edwin R. Sedell, Ashley M. Sanders, and Dana R. Warren

Abstract

The loss of subsidies delivered by anadromous fish to inland stream ecosystems may have profound influences on stream food webs. However, studies have focused on food web responses in ecosystems where the fish community is dominated by salmonids. We evaluate food web responses to steelhead carcass additions at three pairs of sites (each pair consisting of a treatment and an upstream control site) situated along a temperature and fish assemblage gradient in a stream within the interior Columbia River Basin. The upstream pair was dominated by juvenile salmonids while the farthest downstream pair was dominated by native non-salmonids. Increased periphyton biomass was observed 3 weeks after carcass additions in the treatment reaches of the middle and downstream pairs, but not the upstream pair where scavenging by bears removed the majority of carcasses. The initial responses observed in the middle and downstream pairs were not evident 8 weeks after carcass additions. Following carcass additions, stable isotope analysis revealed marine-derived nitrogen (MDN) enrichment of periphyton, invertebrate scrapers, and invertebrate predators was observed in the middle and downstream pairs (up to 12% of tissues were MDN derived), but not in the upstream pair. Crayfish assimilated MDN in all three pairs (between 10-12% MDN-derived), including in the upstream pair where bottom-up responses were not observed, suggesting direct consumption of carcass material. Across the three study pairs, Chinook (*Onchorhynchus tshawytscha*) and steelhead (*O. mykiss*) assimilated MDN rapidly (within 3 weeks) and obtained up to 25% and

57% of their nitrogen from carcasses, respectively. Diet analysis and nitrogen enrichment patterns indicate that assimilation occurred primarily through direct consumption of eggs and carcass tissue. Non-salmonids exhibited limited enrichment (~5 - 10% MDN-derived) relative to salmonids. The lack of eggs and carcass tissue in diets of non-salmonids suggests MDN assimilation occurred through bottom-up pathways. Our results indicate that the effects of carcass additions on these food webs was not ubiquitous. Bottom-up responses occurred in the middle and downstream pairs, but transfer of MDN to higher trophic levels was limited. Salmonids that were directly consuming eggs and carcass tissue exhibited far greater enrichment. These findings provide an increased understanding of stream food webs along a longitudinal gradient of fish assemblage composition, with implications for restoration practices involving carcass additions or nutrient enhancement.

Introduction

The flow of nutrients and energy between ecosystems can structure food webs and can influence primary and secondary productivity of recipient environments (Polis et al. 1997). The addition or loss of material flowing between ecosystems, or changes in the quality of these nutrient and carbon subsidies, can impact the productivity of recipient systems as well as trophic interactions within that system. In streams, the migration, spawning, and death of anadromous species is widely acknowledged as an important transfer of nutrient and carbon subsidies from marine environments to these oligotrophic tributaries (Naiman et al. 2002; Schindler et al. 2003; Wipfli and Baxter 2010). However, many regions have experienced drastic losses of this subsidy with large declines in returning anadromous fishes (Nehlsen et al. 1991; Humphries and Winemiller 2009). For example, in the Pacific Northwest of North America, marine-derived nutrients (MDN) contributed by Pacific salmon (*Onchorhychus spp.*) to streams is estimated to be less than 10% of historical levels (Gresh et al. 2000) and many populations have been lost entirely (Nehlsen et al. 1991; Gustafson et al. 2007). Declines of this magnitude have the potential to profoundly impact stream ecosystems that developed with this resource subsidy in place, which has prompted empirical research quantifying the effects of salmon subsidies on stream biota (see reviews by Janetski et al. 2009; Collins et al. 2015). Food webs are considered in this research, but most of this work has been conducted in stream ecosystems with low fish diversity dominated by salmonid species or in systems where responses have focus only on the juvenile salmon. This has left a gap in knowledge about how salmon subsidies influence larger streams fish communities that encompass salmonids and non-salmonids. Evaluating impacts to the broader fish community is necessary to fully understand how the loss of returning salmon and management efforts to compensate for these loses (e.g. carcass additions) may impact more diverse food webs.

Marine-derived nutrients and carbon (hereafter collectively referred to as MDN) enter stream food webs through two main pathways – bottom-up transfer and direct consumption. Bottom-up transfer occurs as dissolved nutrients released from eggs, carcasses, and live salmon metabolic waste are assimilated by organisms at the base of the food web, and then transferred up to higher trophic levels (Kohler et al. 2012; Benjamin et al. 2016; Morley et al. 2016; Samways et al. 2018). Alternatively, invertebrates, fish, and other consumers can consume eggs and carcass tissue during spawning or during carcass decomposition, providing a direct link between returning salmon and consumers (Bilby et al. 1998; Kiernan et al. 2010; Collins et al. 2016). Nutrients delivered through these two pathways may impact food webs and species differently. For example, in streams where MDN promote enhanced primary production, MDN may be broadly transferred to higher trophic levels due to connectivity to the base of the food web (Morley et al. 2016). Energy is lost with each trophic level transfer, resulting in greater enrichment and MDN energy contributions in lower trophic levels compared to higher trophic level consumers such as predatory fish. However, for consumers that feed directly on eggs and carcass tissue, more MDN associated energy is retained and passed directly to the consumer. Eggs and tissue are energy-rich food resources (Cummins and Wuycheck 1971) and combined with greater energy efficiency transfer, direct consumption may result in greater assimilation of these nutrients, and potentially higher growth rates (Kiernan et al. 2010). These pathways are not mutually exclusive, as consumers may assimilate MDN through both (Bilby et al. 1996). The relative magnitude these pathways influence food webs and specific organisms remains unclear, especially in streams with diverse fish communities.

Along a stream network, gradients in abiotic habitat conditions and biotic interactions can lead to shifts in fish communities (Rahel and Hubert 1991). This is particularly evident within the interior Columbia River Basin, where habitat and temperature shifts can occur over relatively short distances (Justice et al. 2017). Within the spawning distribution of salmonids in a given stream network, assemblages may shift from salmonid-dominated headwaters to a mix of salmonids and non-salmonids in warmer downstream sections (Torgersen et al. 2006). Fish along this assemblage gradient may receive MDN through different pathways due to differences in gape limitation, feeding niche, carcass availability, and interspecific competition (Armstrong et al. 2010; Bentley et al. 2012). Incorporating entire communities within a heterogeneous basin offers more robust evaluation of the flow of MDN to consumers, with potential for species interactions to mediate trophic pathways of MDN delivery.

There are two common approaches to assessing the delivery of MDN to food webs: stable isotope analysis and evaluation of diets. Adult salmon and steelhead feed at a high trophic position in the ocean and therefore have tissue enriched in $\delta^{15}N$ (indicative of trophic position) typically greater than consumers in stream ecosystems. Assimilation of this nitrogen by stream biota results in $\delta^{15}N$ enrichment of those consumers, and changes in $\delta^{15}N$ enrichment can be used to estimate the degree to which they assimilate carcass MDN (Bilby et al. 1996; Morley et al. 2016; Kiffney et al. 2018; Samways et al. 2018). Comparing $\delta^{15}N$ responses among taxa and evaluating the timing and magnitude of changes in consumer $\delta^{15}N$ provides insight into the pathways by which MDN are delivered to various taxa. In addition to isotopic analyses, an evaluation of diet may be used to assess whether fish are directly consuming eggs and carcass tissue (Bilby et al. 1998; Collins et al. 2016; Jones and Mackereth 2016). Coupling stable isotopes and diets allows for a robust evaluation of the degree of MDN assimilation and the pathways through which MDN enrichment occurred.

The objective of this study was to determine how, the addition of steelhead carcasses to a stream with depleted salmon runs influenced stream food webs along a temperature and fish assemblage gradient. In particular, we were interested in evaluating the bottom-up versus direct consumption pathways by which organisms assimilated MDN, and whether these pathways led to in differences in the magnitude of enrichment among taxa. Juvenile salmonids were present at all three of the stream sites we evaluated, but the total and relative abundance of salmonid species as well as non-salmonid species differed with stream position. The upstream site was dominated by juvenile salmonids, whereas the downstream site was dominated by native, non-salmonid species. We evaluated food web responses to the addition of carcasses by quantifying stream periphyton biomass (a common proxy for primary production responses), stable isotopes of the food web (periphyton, invertebrate functional feeding groups, and dominant fish species), and fish diets (salmonids and non-salmonids).

Carcass additions are used as a management tool in many areas throughout the interior Columbia River Basin with the goal of enhancing juvenile salmonid production (Collins et al. 2015). While a few studies have quantified the influence of carcasses or carcass analogs on salmon abundance and growth in this region (see Kohler et al. 2012 and Collins et al. 2016), responses of non-salmonid fish remain unclear. Evaluating effects of carcasses on the broader food web is necessary to fully understand the impacts of salmon losses and effects of carcass addition management actions on stream food webs.

Methods

Study Area

This study was conducted in the Grande Ronde River upstream of the town of La Grande, Oregon, referred to as the Upper Grande Ronde. The Upper Grande Ronde sub-basin originates in the Blue Mountains and drains approximately 1896 km². Flows are driven primarily by snowmelt, contributing to peak flows during the spring followed by low flows during hot, dry summers. Historically, this system supported multiple anadromous salmonid species and evolutionary life histories but due to a range of factors leading to suppressed salmonid stocks, only spring Chinook and summer steelhead currently have viable populations in the UGR (ODFW 1990; Nehlsen et al. 1991).

We established three reach pairs along the Upper Grande Ronde, with each pair consisting of an upstream control reach and a downstream treatment reach (Figure 7.1). After selecting three major river sections representing differences in stream temperature and fish community composition suitable for addressing our study questions, we chose specific reaches in those river sections for our study where the Columbia River Habitat Monitoring Program

(CHaMP 2016) had existing data and where we could leverage ongoing biological and physical habitat surveys. CHaMP sites within each pair were chosen based on proximity and similarity in habitat and fish species assemblages. Location within the watershed, stream temperature regimes, and physical habitat were comparable between reaches in a pair but differed between the sets of experimental pairs (Table 7.1), resulting in varying native fish assemblages across the three sets of reach pairs. The upstream pair contained primarily juvenile Chinook and juvenile steelhead*,* but also sculpin (*Cottus* spp.), bull trout (*Salvelinus confluentus*), and non-native brook trout (*Salvelinus fontinalis*) in lower abundances. The fish community of the middle pair was also dominated by juvenile Chinook but contained more steelhead*,* sculpin (mostly *Cottus confusus* with few *Cottus rhotheus*), longnose dace (*Rhinichthys cataractae*), and speckled dace (*Rhinichthys osculus*). The downstream pair was dominated by non-salmonids including northern pikeminnow (*Ptychocheilus oregonensis*), bridgelip sucker (*Catostomus columbianus*), and redside shiner (*Richardsonius balteatus*). Steelhead in the downstream pair were abundant but there were few Chinook at these sites (< 20 individuals) which prohibited analysis of juvenile Chinook in this pair. Both juvenile steelhead and resident *O. mykiss* occupy these stream pairs and we refer to the population collectively as steelhead due to the dominance of this life history in this basin (Ruzycki et al. 2003).

Adult steelhead carcasses were collected in the spring of 2017 and frozen until deployment in August of 2017. Adult Spring Chinook typically spawn in the Upper Grande Ronde between early August and early September, so although steelhead carcasses were used, the timing of the carcass additions reflects Spring Chinook spawning phenology. Steelhead were collected from hatcheries in the Grande Ronde River Basin (Wallowa and Big Canyon hatcheries) to prevent potential transmission of pathogens from other watersheds. We aimed to add carcasses at approximately the same abundance per surface water area in each treatment reach. The upstream, middle, and downstream treatment reaches increased in stream size, and therefore received 86, 123, and 163 steelhead carcasses, respectively. These additions translated to carcass stocking densities of 0.27 kg m^{-2}, 0.18 kg m^{-2}, and 0.19 kg m^{-2}, respectively. Approximately 55% of carcasses were female and the majority of females contained eggs (eggs were removed by the hatchery from approximately 30 of the nearly 200 females). To limit transport of carcasses out of the study reaches, carcasses were secured to a short section of rope attached to rebar pounded into the stream substrate. At each piece of rebar, four steelhead were secured to a 2 m section of rope with a ziptie inserted through a slit in the jaw.

Periphyton sampling

We quantified periphyton chlorophyll *a* (Chl *a*) concentration and ash-free dry mass (AFDM) on natural substrates at five time periods: twice before carcass addition and three times after the addition of carcasses (approximately 3 weeks, 5 weeks, and 8 weeks after additions). We sampled 6-7 riffle sections of each reach per sampling event. At each riffle, we randomly selected three rocks then scraped a 15 cm^2 circular section from each rock to form one composite sample per riffle, as outlined in Kaylor et al. (2018). We filtered a subsample for Chl *a* (Whatman GF/F) and a subsample for AFDM (Whatman GF/C) and froze samples for later laboratory analysis. We froze an additional, unfiltered subsample for stable isotope analysis (see below). We quantified Chl *a* using acetone extraction and fluorometric analysis (Arar and Collins 1997). AFDM samples were dried at 60 ºC for 24 hrs and weighed to the nearest mg. Samples were then combusted at 500 ºC for 2 h and reweighed. The difference between dried mass and ashed mass was divided by the proportional area sampled to obtain AFDM (g m^{-2}).

Overview of isotope sampling

We sampled periphyton, coarse particulate organic matter (CPOM - leaf litter), invertebrates, salmonids, and non-salmonid fish for stable isotope analysis at control and treatment reaches during three events: 1) two weeks before carcass addition, 2) three weeks after carcass addition, and 3) eight weeks after carcass addition. We additionally processed steelhead carcass eggs (n = 12) and tissue (n = 12) once prior to adding carcasses to streams. All samples were immediately frozen at -20 °C until laboratory preparation.

Periphyton was sampled as outlined above. To trace CPOM isotope signatures from a consistent standing stock, we constructed litter bags of white alder (*Alnus rhombifolia*) leaves which was the dominant riparian species. Fresh leaves were removed from streamside trees and placed into plastic mesh bags (n = 5 bags per reach) with holes wide enough to permit invertebrate and microbial colonization. Bags were placed in streams during carcass additions and sampled again three and eight weeks later.

We selected aquatic invertebrate taxa at control and treatment reaches that were abundant and represented different functional feeding groups (FFG). Functional feeding groups important to our analysis of food web responses included scrapers, shredders, and predators (Merritt et al. 2008). Scrapers were represented by larval mayflies (Ephemeroptera: Heptageniidae) in the middle and downstream pairs, and by larval riffle beetles (Coleoptera: Elmidae) in the upstream pair where larval mayflies were not abundant. Mixing model analysis of δ^{13}C reveals that larval riffle beetles are mostly reliant on periphyton and the classification of scraper FFG is reasonable (Fig. 3). Pteronarcid stoneflies (Plecoptera: Pteronarcyidae) represented shredders while perlid stoneflies (Plecoptera: Perlidae) represented macroinvertebrate predators, and these taxa were abundant in all three pairs. Invertebrates were collected using targeted kick net sampling in riffles. After collection, they were maintained alive for 24 hrs to clear samples of gut contents that could affect isotope signature. Lastly, Signal crayfish (*Pacifastacus leniusculus*), which were present in all reaches, were collected opportunistically while snorkel-herding for fish (see below) and kick-netting for invertebrates.

We used a snorkel-herding technique to capture fish as outlined in Tattam et al. (2017). Each individual (n = 8-12 per site visit) was measured, weighed, and a small caudal clip was taken for stable isotope analysis (Sanderson et al. 2009). Salmonids were PIT-tagged to evaluate growth rates (Chapter 6) and we targeted recaptured PIT-tagged salmonids to ensure these fish had remained within the reach during treatments.

All material for stable isotope analysis was dried at 50 °C for 24 hrs, ground with a mortar and pestle when necessary, then placed in tin (Sn) capsules. Prepared samples were analyzed at the UC Davis Stable Isotope Facility using a Thermo GC-C-IRMS system composed of a Trace GC Ultra gas chromatograph (Thermo Electron Corp., Milan, Italy) coupled to a Delta V Advantage isotope ratio mass spectrometer. $\delta^{13}C$ and $\delta^{15}N$ values are expressed as relative to the international standards for carbon (Vienna PeeDee Belemnite) and nitrogen (air).

Fish diet sampling

We sampled stomach contents of salmonids using non-lethal gastric lavage (Meehan and Miller 1978) to assess direct consumption of carcass tissue and eggs. Stomach contents were sampled one, three, and seven weeks following carcass additions. We sampled stomach contents of 10-12 individuals per visit of each species in control reaches, and 10-25 individuals in treatment reaches where egg and carcass tissue consumption was more likely (Table 7.2). Fish in control reaches were sampled to quantify consumption of eggs and carcass material from naturally spawning salmon. Samples were stored in 95% ethanol until laboratory analysis. Because gastric lavage is not an effective method on non-salmonids including pikeminnow, small dace, suckers, small sculpin and redside shiner, we obtained diet samples through lethal take (in accordance with permits). These individuals were quickly euthanized using an overdose of AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand), immediately placed on ice, and then frozen until laboratory analysis. In the upstream pair, diets of Chinook, steelhead*,* and sculpin were evaluated; in the middle pair, diets of Chinook, steelhead*,* speckled dace and sculpin were evaluated; and in the downstream pair, diets of steelhead*,* northern pikeminnow, redside shiner, and bridgelip sucker were evaluated. Chinook abundance was too low in the downstream pair to evaluate diet.

Data analysis

We used temporal changes in isotopic signatures to evaluate food web incorporation of MDN in response to carcass additions (comparing isotopic signatures in treatment reaches relative to controls). Studies have considered the use of both $\delta^{13}C$ and $\delta^{15}N$ to infer direct consumption versus bottom-up incorporation of MDN (Kiffney et al. 2018) or have estimated the both the percent carbon and nitrogen that taxa assimilated (Bilby et al. 1996; Chaloner et al. 2002). However, periphyton $\delta^{13}C$ signatures in our study changed seasonally in both the control and treatment reaches and the food web tracked these changes (Figure 7.3), which complicates interpretation of temporal changes in $\delta^{13}C$ to assess carcass addition effects. We therefore restrict analysis of food web MDN incorporation to $\delta^{15}N$ and use other metrics including periphyton biomass and fish diet to evaluate pathways of MDN to the food web.

A Bayesian mixing model framework (SIMMR) was used to assess taxa assimilation of MDN (Parnell et al. 2013). Bayesian mixing models estimate the likelihood of the proportion of sources contributing to a consumer group and allow for incorporation of uncertainty including the standard deviation of mean isotopic values for each source and the standard deviation of trophic enrichment factors (TEFs) (Parnell et al. 2013; Phillips et al. 2014). Our approach to estimating taxa proportional reliance on MDN is similar to mass balance equations that use isotopic signatures of taxa in the treatment reach relative to the same taxa in the control reach and the isotope signature of carcasses; however, utilization of a Bayesian modeling framework allows for incorporating uncertainty of source means and TEFs and thus provides better approximations of error (Phillips et al. 2014). The approach was similar to the following formula from Johnston et al. 1997.

$$\% \text{ MDN enrichment} = (Xst-Xc)/((Xs + (TL \times Xe)) - Xc) * 100$$

Where Xst is the δ^{15}N value of a taxa in the treatment reach of a pair, Xc is the δ^{15}N value of the same taxa in the control reach, Xs is the δ^{15}N value of carcass material (the mean of eggs and carcass tissue;), TL is the trophic level of the taxa , and Xe is the trophic enrichment factor. For invertebrates, we applied a TEF of 2.6 (SD = 2.0) based on a recent meta-analysis of invertebrate TEFs (Brauns et al. 2018), whereas A TEF of 3.4 (SD = 1.0) was applied to all fish species (Post 2002). The trophic level of each taxa (0 for periphtyon and CPOM; 1 for scrapers and shredders; 2 for invertebrate predators, crayfish, and bridgelip sucker; 2.5 for sculpin, speckled dace, northern pikeminnow, and redside shiner; and 3 for Chinook and steelhead) was derived from the literature (Bilby et al. 1996; Chaloner et al. 2002; Post 2002) and by examining δ^{15}N signatures of each taxa in control reaches (Post 2002).

We also used diet analysis and field observations to estimate the degree to which organisms assimilated MDN through direct consumption versus the bottom-up pathway for this model to better estimate the percent of consumer nitrogen that was derived from carcasses. This is critical because for an organism feeding directly on carcass tissue and eggs, trophic enrichment of carcass material would only reflect enrichment through one trophic level (δ^{15}N enrichment of 3.4). In contrast, for an organism with a trophic position of 3 that only assimilates MDN through bottom-up pathways, trophic enrichment of MDN would occur through each trophic level (total δ^{15}N enrichment of 10.2), resulting in a lower estimate of the proportion of that consumer's N derived from MDN. We assumed that invertebrate scrapers, shredders, and predators were obtaining all MDN through bottom-up pathways, as we never observed any of these invertebrate groups feeding on carcasses. We assumed crayfish obtained 50% of MDN through bottom-up pathways and 50% through direct consumption pathways. Crayfish were occasionally observed feeding on carcasses and they demonstrated enriched δ^{15}N in the upstream pair where no δ^{15}N enrichment was observed for periphyton or CPOM, indicating direct consumption. Eggs and carcass material were very rarely or never observed in the diets of non-salmonids so we assumed 10% direct consumption, allowing for some error in missed eggs and carcass material in diet samples. Eggs and carcass material were very common in the diets of salmonids, and they were highly enriched in the upstream pair despite no enrichment of lower trophic levels. This suggests that salmonids were obtaining the majority of MDN through direct consumption pathways, so we assumed 90% direct consumption. Given the potential for these assumptions to influence results, we evaluated how varying degrees of direct consumption would impact the estimated proportion derived from MDN for crayfish and steelhead. These two species were present in all three pairs, have different trophic positions, and exhibited different degrees of δ^{15}N enrichment.

Stomach contents were assessed to determine whether species were directly consuming carcass material and eggs. For each sample, we quantified the number of eggs present and we determined the presence or absence of carcass flesh. For each species and sampling event, we report the percentage of fish with stomach contents containing eggs and carcass material. We also report the median number of eggs present for each species during each sampling event.

Results

In the middle and downstream pairs, field observations confirmed that most carcasses decomposed rapidly within the stream, and little carcass material remained after 8 weeks. The outside of carcasses developed a thick biofilm within 1-2 weeks, but aquatic invertebrates (except crayfish) were not observed on carcasses. Trail camera footage revealed that bald eagles (*Haliaeetus leucocephalus*) were the dominant terrestrial scavenger, but most consumption occurred in the stream, likely releasing carcass material to the water. In the upstream pair, scavenging by black bears (*Ursus americanus*) resulted in a rapid loss of carcasses from the reach. After two weeks, only 44 of the original 86 carcasses remained, and after three weeks, less than 10 carcasses remained. Carcasses in this reach decomposed very little before they were scavenged, likely owing to the colder water temperatures relative to the other two pairs (Table 7.1). However, during the three weeks carcasses were present, we observed eggs released into the stream. Bears were not observed on trail cameras at the middle or downstream pairs.

Periphyton responses

The response of periphyton Chl *a* and AFDM to carcass additions was mixed. Prior to carcass addition, Chl *a* and AFDM concentrations on benthic substrates were similar between control and treatment reaches of all three pairs, as evidenced by overlapping confidence intervals (Figure 7.2A). In the upstream pair, Chl *a* and AFDM remained similar ($p > 0.05$) between control and treatment reaches during all post-carcass addition sampling events. In contrast, short-term effects were observed in the middle and downstream pairs. In the middle pair, both Chl *a* and AFDM were significantly greater ($p < 0.05$) in the treatment reach approximately 2 weeks after the addition of carcasses. Five weeks after carcass additions, Chl *a* remained significantly greater ($p < 0.05$) in the treatment reach but AFDM was not significantly different ($p > 0.05$) between the control and treatment reach. Eight weeks after carcass addition Chl *a* concentrations were similar ($p > 0.05$) between the control and treatment reach, while AFDM was significantly greater ($p < 0.05$) in the treatment reach compared to the control reach. In the downstream pair, Chl *a* and AFDM were significantly greater ($p < 0.05$) in the treatment reach compared to the control reach 2 weeks after carcass additions. Five weeks after carcass additions, Chl *a* was similar ($p > 0.05$) between control and treatment reaches while AFDM remained significantly greater ($p < 0.05$) in the treatment reach. Surprisingly, both Chl *a* and AFDM were significantly lower ($p < 0.05$) in the treatment reach compared to the control reach 8 weeks after carcass addition. Overall these results suggest nutrients released from carcasses resulted in a short-term increases in biofilm Chl *a* and AFDM in the middle and downstream pairs, but these effects did not persist 8 weeks after carcass additions.

Assimilation of MDN

Carcass tissue ($\delta^{15}N = 11.8$) and eggs ($\delta^{15}N = 12.7$) were enriched in $\delta^{15}N$ relative to all consumers (Figure 7.3) which allowed for evaluation of consumer MDN assimilation following the addition of carcasses. The degree of assimilation of MDN was not consistent among the three pairs, nor was it consistent among taxa (Figure 7.4). In the upstream pair, there was little evidence for enrichment of periphyton and CPOM 3 and 8 weeks after carcass additions (Figure 7.4a). Assimilation of MDN was minimal (< 5%) 3 weeks after carcass additions for all consumer groups except crayfish (11%), Chinook (20%) and steelhead (48%). After 8 weeks MDN assimilation of crayfish (7%), Chinook (11%) and steelhead (30%) was still evident but had declined. In the middle pair, most taxa exhibited some degree of MDN assimilation including periphtyon (7-8%) and CPOM (3-4%) at the base of the food web. MDN assimilation by scrapers was similar between 3 and 8 weeks (~ 9%), whereas increased assimilation was observed from 3 to 8 weeks for shredders, invertebrate predators, crayfish, speckled dace, and sculpin; however, the estimated proportion of MDN was < 10% for each of these taxa. Chinook and steelhead exhibited greater MDN assimilation both 3 weeks (20% and 46%, respectively) and 8 weeks (24% and 27%) after additions. In the downstream pair, enrichment patterns were similar to those observed in the middle pair with most taxa exhibiting MDN assimilation of 5-12% whereas steelhead were far more enriched. Periphyton was enriched 3 (9%) and 8 (8%) weeks after carcass additions. CPOM was also enriched 3 (10%) and 8 weeks (7%) after additions, but analysis also indicated enrichment prior to carcass additions (5%), complicating these results. Scrapers (12%), shredders (7%), invertebrate predators (6%), crayfish (9%), bridgelip sucker (7%), redside shiner (5%), and northern pikeminnow (4%) were enriched 3 weeks after carcass additions. Enrichment after 8 weeks was similar to enrichment observed after 3 weeks for scrapers (11%), shredders (5%), predators (6%), crayfish (8%), redside shiner (4%), and northern pikeminnow (5%), but decreased for bridgelip suckers (3%). The magnitude of enrichment was far greater for steelhead compared to other taxa after 3 weeks (44%) and 8 weeks (57%).

Estimates of taxa MDN assimilation were sensitive to model assumptions of the degree to which MDN was assimilated through direct consumption versus bottom-up pathways (Figure 7.5). Effects of this assumption were greater for steelhead (assumed trophic position of 3) compared to crayfish (assumed trophic position of 2). For example, steelhead estimated % MDN in the downstream pair eight weeks after carcass addition was 35% if we assumed assimilation occurred through bottom-up pathways but it was 62% if we assumed assimilation occurred entirely through direct consumption (Figure 7.5c) for a difference of 27%. In contrast the largest difference in crayfish MDN assimilation between the two pathways was just 2.7%, owing to less $\delta^{15}N$ enrichment and a lower assumed trophic position.

Fish diet responses

No eggs or carcass tissue were observed in stomach contents of fish from control reaches for any event or species. We therefore only report sample sizes and findings from treatment reaches. Sample sizes for each species and sampling event from treatment reaches are provided in Table 7.2. In the upstream treatment reach, 60% of steelhead and 32% of Chinook had consumed eggs 1 week after carcass additions. Up to 47 and 10 individuals eggs were found in stomachs of steelhead and Chinook respectively. In addition, 30% of steelhead contained carcass tissue, but no Chinook stomachs contained tissue. After 3 weeks, 32% of steelhead contained eggs (up to 103 individual eggs), but no Chinook stomachs contained eggs, and neither species had consumed carcass tissue. After 8 weeks, no tissue or eggs were found in stomachs of Chinook or steelhead. Eggs and carcass tissue were not found in sculpin stomachs during any sampling event. In the treatment reach of the middle pair, 54% of steelhead (up to 54 eggs) and 8.3% of Chinook (up to 9 eggs) stomachs contained eggs after 1 week, but no carcass tissue was observed in stomach contents during this event. After 3 weeks, 83% of steelhead (up to 70 eggs) and 58% of Chinook (up to 15 eggs) stomachs contained eggs and 21% of steelhead and 4% of Chinook stomachs contained carcass tissue. After 8 weeks, 11% of steelhead stomachs (up to 3 eggs) contained eggs but 18% of steelhead stomachs contained carcass tissue; no eggs and carcass tissue were present in any Chinook stomachs. No eggs or carcass tissue were observed in speckled dace stomachs during any event. Only one sculpin had consumed eggs during any event (n = 2 eggs), which occurred 3 weeks after carcass additions. In the treatment reach of the downstream pair, 24% of steelhead stomachs contained eggs after one week (up to 28 eggs) but carcass tissue was not found in any stomachs. After 3 weeks, 89% of steelhead stomachs contained eggs (up to 71 eggs) and 26% contained carcass tissue. After 8 weeks, eggs were only present in 4% of steelhead stomachs (only 1 egg found in a single fish) but carcass tissue was present in 17% of stomachs. No eggs or carcass material were found in stomachs of redside shiner or bridgelip suckers during any sampling event. Eggs were found in the stomach of a single pikeminnow (*n* = 2 eggs) 3 weeks after carcass additions but no other eggs are carcass tissue was found during other sampling events.

Discussion

Across the Columbia River Basin, as well as many other regions, the decline in spawning salmon and steelhead has led to a drastic loss of marine-derived subsidies delivered to stream ecosystems (Gresh et al. 2000). These marine subsidies have the potential to broadly influence recipient stream food webs through the release of inorganic nutrients and through direct supply of eggs and carcass material to consumers (Naiman et al. 2002; Schindler et al. 2003). Therefore the reduction in subsidies supplied by naturally spawning salmon in these systems may have substantial impacts on stream food webs throughout historic spawning distributions in a basin. Our results indicated that carcass addition effects were variable across the three treatment sites and among taxa including invertebrates, salmonids, and other native fish species. MDN were incorporated broadly into the food web through bottom-up pathways in the middle and downstream pairs as evidenced by δ^{15}N enrichment of periphyton and invertebrate scrapers, shredders, and predators. In the upstream pair, scavenging and removal of carcasses by bears likely inhibited nutrient release, and consequently, bottom-up responses were not apparent. Across all three pairs, MDN assimilation was greatest in juvenile salmonids (up to 25% and 57% of Chinook and steelhead N was MDN-derived, respectively) and diet analysis indicates that this enrichment was primarily attributed to direct consumption of eggs and carcass material. In contrast, in the middle and downstream pairs, stable isotope enrichment patterns of non-salmonids (maximum MDN-derived N of 11%), as well as the absence of eggs and carcass material in diets, suggest these species likely accessed MDN through bottom-up pathways.

Biofilm responses

Biofilm communities in the three stream sections evaluated in this study are strongly nutrient limited (Chapter 5) and we expected the release of inorganic nutrients from carcasses to stimulate biofilm production. Consistent with this hypothesis, short-term (2-5 weeks) increases in biofilm Chl *a* and AFDM were observed in the middle and downstream pairs and the proportion of biofilm N derived from carcasses ranged from 8-12%. While these responses indicate effects on carcass subsidies on biofilm biomass and MDN assimilation, the magnitude of these responses is relatively low compared to other studies (Bilby et al. 1996; Wipfli et al. 1998, 1999). In the upstream pair, biofilm Chl *a* and AFDM showed no significant increases in response to carcass additions and stable isotope analysis revealed little MDN assimilation. Scavenging of the majority of carcasses by bears occurred within 3 weeks in this treatment reach, likely limiting the release of nutrients. Given low biofilm standing stocks and rates of primary production in the upstream pair (Chapter 5), we suggest that in the absence of scavenging, biofilm biomass accumulation and isotopic enrichment would have been stronger. With lower stream temperatures causing slower carcass decomposition rates, these effects likely would have manifested later and persisted longer than the middle and downstream pairs.

Invertebrate responses

Benthic invertebrates can provide a trophic linkage for MDN from biofilms to predatory fish; however, invertebrate responses to carcass additions in this study, excluding crayfish, were mixed with no MDN enrichment observed in the upstream pair and only slight enrichment in the middle and downstream pairs (< 10% of invertebrate taxa N was MDN-derived). While this level of enrichment has been observed in response to naturally spawning salmon or carcass additions (Claeson et al. 2006; Morley et al. 2016; Kiffney et al. 2018), it is far less than what has been observed in others (Bilby et al. 1996; Chaloner et al. 2002; Winder et al. 2005). Enrichment patterns of scrapers, shredders, and predators mirrored those of periphyton and suggest assimilation of MDN assimilation occurred through bottom-up pathways. Further, we did not observe these taxa directly consuming carcass material. Other studies have demonstrated that invertebrates feeding directly on carcasses can exhibit far greater enrichment than those that do not (Winder et al. 2005), and it is possible that the invertebrate taxa we chose were not consuming carcasses directly. However, reaches were snorkeled 5-6 times after carcass additions and we did not observe any invertebrates feeding on carcasses, with the exception of crayfish.

Crayfish consistently exhibited MDN assimilation in response to carcass additions at all three pairs. Crayfish are generalists, feeding on a combination of detritus, biofilm, and other organisms (Momot and Jones 1978), so the enriched crayfish signal could be attributed to a combination of these sources if also enriched. In the upstream pair, we suggest that enrichment was primarily attributed to direct consumption because periphyton, leaf litter (CPOM), and other invertebrate groups showed very little enrichment. Therefore there is a missing link between nutrients released from carcasses and lower trophic levels. Evidence of direct consumption at this site is further supported by observations of crayfish feeding on carcasses while snorkeling reaches (MJ Kaylor personal observation). In the middle and downstream pairs, periphyton and other invertebrates were enriched, and crayfish enrichment patterns mirrored those of other invertebrate groups, suggesting bottom-up transfer of MDN was more likely. But because crayfish were also occasionally observed feeding directly on carcasses, a combination of bottom-up transfer and direct consumption likely caused the enrichment. It is important to note that direct consumption of carcasses by crayfish was always observed on carcasses that were no longer tethered to rebar. Instead crayfish were observed on loose carcasses that were deposited on the benthos in low velocity habitats. Distributing the carcasses freely rather than tethering them to rebar may have resulted in greater direct consumption by crayfish and perhaps other invertebrate scavengers such as caddisflies, as found in the study by Winder et al. (2005).

Fish assemblage responses

Numerous studies have evaluated responses of resident salmonids to carcass additions or naturally spawning salmon (see reviews by Janetski et al. 2009; Collins et al. 2015), but responses of other members of the fish assemblage are rarely quantified, despite their often high total and relative abundance in stream habitats. Surprisingly, even with an abundant supply of eggs and carcass material, non-salmonids rarely consumed these subsidies directly. This occurred during sampling events when the majority of salmonid stomach contents contained numerous eggs. Non-salmonids including northern pikeminnow, speckled dace, redside shiner, and bridgelip sucker were larger on average than juvenile Chinook that were consuming eggs, suggesting gape limitation was not a driver. Sculpin were smaller on average than Chinook and gape limitation may have inhibited some sculpin from consuming eggs. However, this result is surprising given that sculpin in other systems have been shown to consume an abundance of eggs (Swain et al. 2014). We suggest that in the upstream and middle pairs, which were dominated by salmonids, competition with salmonids may have prevented non-salmonids (sculpin and dace) from consuming eggs; Chinook and steelhead were observed positioning directly behind carcasses and immediately consuming released eggs. This has been observed in other systems where rainbow trout excluded other species (arctic grayling, *Thymallus arcticus*, in this case) from consuming eggs when availability was low (Bentley et al. 2012). While competition may explain the lack of egg consumption by non-salmonids (sculpin and dace) in the upstream and middle pairs, it does not explain the lack of egg consumption in the downstream pair. Loose eggs were abundant and spread across the stream benthos after carcasses decomposed. Given the high densities of non-salmonids and low amounts of prey in stomach contents (MJ Kaylor personal observations), non-salmonids were likely food limited during this period and it is surprising that they did not consume these high energy food resources.

Despite a paucity of evidence for egg and carcass tissue consumption by non-salmonids, limited MDS enrichment of non-salmonids did occur in the middle and downstream pairs (up to 11% of N was MDN-derived). In the middle pair, enrichment patterns of speckled dace and sculpin were similar to those observed for invertebrate shredders and predators, with greater enrichment after 8 weeks compared to 3 weeks after carcass addition. In contrast, bridgelip sucker and redside shiner enrichment in the downstream pair was lower 8 weeks after carcass additions compared to 3 weeks after. We suggest that movement of fish in and out of the study reach may have resulted in reduced observed enrichment. We PIT-tagged a subset of redside shiner, bridgelip sucker, northern pikeminnow, and speckled dace, and while we were not able to recapture individuals to obtain growth rates, detection at a downstream PIT-tag array in September and October suggests considerable movement within this timeframe (Edwin Sedell, unpublished data). Restriction of stable isotope analysis to fish that remained within the study reach for the duration of the study (which was done for salmonids) may have resulted in greater enrichment and less variability in enrichment patterns.

Salmonid enrichment was far greater than observed for any other taxa (up to 25% and 57% of N was MDN-derived for Chinook and steelhead, respectively). This degree of MDN assimilation, coupled with the abundance of eggs and carcass material observed in diets, is clear evidence that direct consumption was the dominant pathway of MDN assimilation. Salmonids in these study reaches also exhibited greater energy intake, growth rates, and body condition (Chapter 6), indicating that consumption of eggs and carcass material led to population level responses beyond assimilating MDN. The level of MDN assimilated by steelhead, and to a lesser degree Chinook, exceeds salmonid enrichment observed in other studies where carcasses or carcass analogs were added (Claeson et al. 2006; Morley et al. 2016; Kiffney et al. 2018). It has been suggested that the amount of carcass material added to streams is a key factor influencing the magnitude of fish responses (Janetski et al. 2009); however, carcass stocking density in this study (~0.20 - 0.25 kg m^{-2}) was among the lowest of the carcass addition studies of which we were aware. We additionally suggest that when considering carcass addition effects on salmonids, the presence of eggs in carcasses — which are often removed prior to carcass additions — is a key determinant of the magnitude of salmonid responses. For instance, when some eggs were retained in carcasses added to Washington streams (loading density ~0.60 kg m^{-2}), juvenile salmonids consumed eggs and carcass material and exhibited enrichment patterns similar to those observed in our study (Bilby et al. 1998). When adding carcasses to streams to enhance salmonid production, retaining eggs is more likely to achieve the desired effects.

Differences in direct consumption

Mixing models used to estimate the percent MDN assimilated by an organism are sensitive to assumptions of the relative magnitude of the pathways MDN were assimilated through (i.e. Figure 7.5). Fractionation of MDN occurs through each trophic link. For direct consumption there is only one trophic link, whereas bottom-up transfer of MDN can have multiple trophic links depending on the trophic level of the consumer, resulting in greater total fractionation of MDN. We demonstrate that for steelhead, which had an assumed trophic position of 3, varying MDN assimilated from direct consumption from 0% to 100% resulted in nearly a doubling of the estimated proportion derived from MDN in some instances. For crayfish (trophic position 2), the effect of varying direct consumption was consistently less (up to a 33% increase from 0% to 100% direct consumption). These results indicate that for organisms feeding at higher trophic levels, assumptions of MDN assimilated through direct consumption versus bottom-up pathways can profoundly impact interpretation of consumer MDN assimilation. By coupling stable isotope analysis with diet data, we were able to determine that steelhead and chinook were consuming an abundance of eggs and carcass material, which informed our assumptions of direct consumption. We believe that the value of 90% direct consumption we used is credible given diet analysis and the limited enrichment observed in invertebrate prey. Studies that have inferred direct consumption based on stable isotope patterns, but did not incorporate estimates of direct consumption into mixing models have likely underestimated the degree of consumer MDN assimilation, especially for organisms with higher trophic positions (e.g. > 2).

Caveats of study

There are a number of caveats that may have influenced the results observed in this study. First, the number of returning adult spring Chinook salmon was low in the year of this study compared to long-term averages (ODFW unpublished data), and therefore the number of naturally spawning salmon available for scavengers was low. The greatest density of salmon redds occurs in the section associated with the upper pair and spawning typically coincides with the dates in which carcasses were added. Bears accustomed to feeding on naturally spawning salmon had few carcasses to scavenge and may have increased consumption of added carcasses relative to a year with greater returns. Second, carcasses in this study were tethered in place, which could influence the retention, distribution, and impact of carcasses within stream reaches. Eagles were observed trying to remove tethered carcasses but they were usually unsuccessful and fed on carcasses within the stream, which may have facilitated the release of eggs and tissue to fish. Additionally, invertebrates may have been able to more easily feed directly on carcasses deposited in low velocity habitats if carcasses were not tethered. Lastly, while the added carcasses in this study clearly impacted stream food webs, naturally spawning salmon in these systems may yield different effects. Spring Chinook arrive to spawning habitats several weeks to months before spawning and excrete urea through metabolic waste. Highly labile ammonium within urea can stimulate primary production (Benjamin et al. 2016) and potentially bottom-up responses. In contrast, redd construction can scour spawning substrates, reducing biofilm standing stocks, but also dislodging invertebrates which may be consumed by fish (Moore and Schindler 2008; Tiegs et al. 2009). In our study, eggs were left in carcasses and therefore a greater proportion of eggs had the potential to be consumed by fish, compared to natural spawning activities which bury eggs. Ultimately, it is unclear whether the magnitude of MDN effects on stream food webs would differ between carcass additions and natural spawning in this system, but the proportional contributions of pathways (bottom-up, dislodged invertebrates, vs direct consumption) would likely differ.

Conclusions

As demonstrated elsewhere, the loss of anadromous salmon and associated subsides may have profound impacts on stream ecosystems and food webs. Our results indicate that the addition of salmon carcasses resulted in detectable MDN enrichment of invertebrates and non-salmonids and that this enrichment primarily occurred through bottom-up pathways. In contrast to non-salmonids, juvenile Chinook and steelhead consumed an abundance of eggs and carcass tissue and exhibited far greater enrichment. Therefore, while our results suggest salmon subsidies have the potential to broadly impact stream food webs in this region, species able to directly consume eggs and carcass material clearly benefited more from these subsidies. These results have two important implications for the use of carcass additions as a management tool to promote juvenile salmonid productivity. First, it is clear that the presence of eggs within carcasses was a key factor driving juvenile salmonid responses, and when possible, eggs should be retained within carcasses to yield the greatest effects. Second, our results suggest that within these streams, eggs and carcass material were clearly being directed to fish taxa of primary management concern (salmonids), and competition from non-target species was not apparent. However, competition between salmonids and non-salmonids for salmon subsidies clearly needs to be investigated further in other systems and in the presence of naturally spawning salmon.

Acknowledgments

We thank C. Hayes, J. Dowdy, the ODFW Early Life History crew, and the Bureau of Reclamation summer interns for their assistance in field work. J. Dowdy, A. Dutterer, S. Favrot, W. Morton, A. Simpson and staff of the Grande Ronde Model Watershed provided logistical assistance. B. Bilby, A. Kohler, and S. Collins provided feedback on initial experimental design. S. Johnson, W. Gerth and I. Arismendi provided laboratory space and assistance. Ruth Bowman provided access to sites located on private property. This research was supported by the Bonneville Power Administration as part of the Columbia Basin Fish Accords Agreement (Project # 2009-004-00), an Oregon Watershed Enhancement Board (OWEB) Focused Investment Partnership (Project # 216-8205-15449), and a National Science Foundation Graduate Research Fellowship (Grant No. 1314109-DGE).

Literature cited

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. Page US Environmental Protection Agency Method 445.0 Revision 1.2. Cincinnati, Ohio.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445–1454.

Benjamin, J. R., J. R. Bellmore, and G. A. Watson. 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. Freshwater Science 35(3):810–825.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, and P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):113.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Bilby, R. E., B. R. Fransen, and P. a Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53(1):164–173.

Brauns, M., D. Graeber, I. G. Bo, A. P. C. De Carvalho, T. Mehner, and D. Von Schiller. 2018. Consumer-resource stoichiometry as a predictor of trophic discrimination (D13C, D15N) in aquatic invertebrates. Freshwater Biology 63(10):1–10.

Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1257–1265.

CHaMP, (Columbia Habitat Monitoring Program). 2016. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program.

Claeson, S. M., J. L. Li, J. E. Compton, and P. A. Bisson. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. Canadian Journal of Fisheries and Aquatic Sciences 63:1230–1241.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):1–18.

Collins, S. F., A. M. Marcarelli, C. V Baxter, and M. S. Wipfli. 2015. A Critical Assessment of the Ecological Assumptions Underpinning Compensatory Mitigation of Salmon-Derived Nutrients. Environmental Management 56:571–586. Springer US.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen der Internationale Vereinigung fur Theoretische und Angewandte

Limnologie 18:1–158.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem : Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. Fisheries Habitat 25(1):15–21.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. Conservation Biology 21(4):1009–1020.

Humphries, P., and K. O. Winemiller. 2009. Historical Impacts on River Fauna, Shifting Baselines, and Challenges for Restoration. BioScience 59(8):673–684.

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, D. E. Nagel, C. H. Luce, S. W. Hostetler, J. B. Dunham, B. B. Roper, S. P. Wollrab, G. L. Chandler, D. L. Horan, and S. Parkes-payne. 2017. The NorWeST summer stream temperature model and scenarios for the western U.S.: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Water Resources Research 53:1–25.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.

Jones, N. E., and R. W. Mackereth. 2016. Resource subsidies from adfluvial fishes increase stream productivity. Freshwater Biology 61:991–1005.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management 188:212–227.

Kaylor, M. J., A. Argerich, S. M. White, B. J. Verwey, and I. Arismendi. 2018. A cautionary tale for in situ fluorometric measurement of stream chlorophyll a: influences of light and periphyton biomass. Freshwater Science 37(2):287–295.

Kiernan, J. D., B. N. Harvey, and M. L. Johnson. 2010. Direct versus indirect pathways of salmon-derived nutrient incorporation in experimental lotic food webs. Canadian Journal of Fisheries and Aquatic Sciences 67(12):1909–1924.

Kiffney, P. M., S. M. Naman, J. M. Cram, M. Liermann, and D. G. Burrows. 2018. Multiple pathways of C and N incorporation by consumers across an experimental gradient of salmon carcasses. Ecosphere 9(4):e02197.

Kohler, A. E., T. N. Pearsons, J. S. Zendt, M. G. Mesa, C. L. Johnson, and P. J. Connolly. 2012. Nutrient Enrichment with Salmon Carcass Analogs in the Columbia River Basin, USA: A Stream Food Web Analysis. Transactions of the American Fisheries Society 141(September 2014):802–824.

Meehan, W. R., and R. A. Miller. 1978. Stomach Flushing: Effectiveness and Influence on Survival and Condition of Juvenile Salmonids. Journal of Fisheries Research of the Board of Canada 35:1359–1363.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An introduction to the aquatic insects of North America. Kendell Hunt Publishing Company.

Momot, W. T., and P. D. Jones. 1978. The Dynamics of Crayfish and Their Role in Ecosystems. The American Midland Naturalist 99(1):10–35.

Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. Journal of Animal Ecology 77:275–284.

Morley, S. A., H. J. Coe, J. J. Duda, L. S. Dunphy, M. L. Mchenry, B. R. Beckman, M. Elofson, E. M. Sampson, and L. Ward. 2016. Seasonal variation exceeds effects of salmon carcass additions on benthic food webs in the Elwha River. Ecosphere 7(8).

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

ODFW (Oregon Department of Fish and Wildlife). 1990. Grande Ronde River Subbasin Salmon and Steelhead Production Plan. Portland, OR.

Parnell, A. C., D. L. Phillips, S. Bearhop, X. Brice, E. J. Ward, J. W. Moore, A. L. Jackson, J. Grey, D. J. Kelly, and R. Inger. 2013. Bayesian stable isotope mixing models. Environmetrics 24:387–399.

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward the integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28(1):289–316.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83(3):703–718.

Rahel, F. J., and W. A. Hubert. 1991. Fish Assemblages and Habitat Gradients in a Rocky Mountain-Great Plains Stream: Biotic Zonation and Additive Patterns of Community Change. Transactions of the American Fisheries Society 120:319–332.

Ruzycki, J. R., M. W. Flesher, R. W. Carmichael, and D. L. Eddy. 2003. Lower Snake River Compensation Plan: Oregon Evaluation Studies-Steelhead Life History, Genetics, and Kelt Reconditioning. Oregon Department of Fish and Wildlife, La Grande, OR.

Samways, K. M., D. X. Soto, and R. A. Cunjak. 2018. Aquatic food-web dynamics following incorporation of nutrients derived from Atlantic anadromous fishes. Journal of Fish Biology 92:399–419.

Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. A. Steel, and W. L. Reichert. 2009. Nonlethal Sampling of Fish Caudal Fins Yields Valuable Stable Isotope Data for Threatened and Endangered Fishes. Transactions of the American Fisheries Society 138(5):1166–1177.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen.

2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1(1):31–37.

Swain, N. R., M. D. Hocking, J. N. Harding, and J. D. Reynolds. 2014. Effects of salmon on the diet and condition of stream-resident sculpins. Canadian Journal of Fisheries and Aquatic Sciences 71:521–532.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of Oncorhynchus mykiss growth require year-round monitoring. Ecology of Freshwater Fish 26:434–443.

Tiegs, S. D., E. Y. Campbell, P. S. Levi, J. Ruegg, M. E. Benbow, D. T. Chaloner, R. W. Merritt, J. L. Tank, and G. A. Lamberti. 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. Freshwater Biology 54:1864–1875.

Torgersen, C. E., C. V Baxter, H. W. Li, and B. A. McIntosh. 2006. Landscape Influences on Longitudinal Patterns of River Fishes: Spatially Continuous Analysis of Fish – Habitat Relationships. American Fisheries Society Symposium 48:473–492.

Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Canadian Journal of Fisheries and Aquatic Sciences 62:2285–2293.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373–387.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Table 7.1: Site characteristics during the summer of 2017.

Pair	Treatment	Mean Aug. Temp. (°C)	Max Aug. Temp. (°C)	NO_3-N Aug. (µg/L)	PO_4-P Aug. (µg/L)	Q Sept. (m^3/s)	Reach Length (m)	Wetted width (m)	Carcasses added	Carcass density (kg/m^2)
Upstream	Control	12.3	16.1	0.94	2.87	0.28	190	5.1	0	0
	Treatment	13.1	19.2	0.74	3.24	0.28	180	4.9	86	0.27
Middle	Control	17.4	24.0	1.78	4.25	0.49	233	8.8	0	0
	Treatment	17.4	24.2	1.25	1.92	0.55	180	11.1	123	0.18
Downstream	Control	17.7	24.5	2.71	2.35	0.50	357	9.9	0	0
	Treatment	18.14	26.5	1.36	2.57	0.55	286	8.3	163	0.19

Table 7.2*:* Number (n) of fish sampled and the percentage of these fish with eggs and carcass tissue in stomach contents in treatment reaches during each of three sampling events conducted after carcass additions. No fish of any species contained eggs or carcass tissue in control reaches.

Pair	**Species**	**1 week**			**3 weeks**			**7 weeks**		
		n	Eggs	Tissue	*n*	Eggs	Tissue	*n*	Eggs	Tissue
Upstream	Steelhead	20	60.0	30.0	25	32.0	0.0	16	0.0	0.0
	Chinook	25	32.0	0.0	27	0.0	0.0	25	0.0	0.0
	Sculpin	9	0.0	0.0	10	0.0	0.0	12	0.0	0.0
Middle	Steelhead	24	54.2	0.0	24	83.3	20.8	28	10.7	17.9
	Chinook	24	8.3	0.0	26	57.7	3.8	23	0.0	0.0
	Sculpin	10	0.0	0.0	14	7.1	0.0	11	0.0	0.0
	Speckled dace	0	na	na	11	0.0	0.0	11	0.0	0.0
Downstream	Steelhead	25	24.0	0.0	27	88.9	25.9	23	4.3	17.4
	Pikeminnow	16	0.0	0.0	23	4.3	0.0	10	0.0	0.0
	Redside shiner	15	0.0	0.0	15	0.0	0.0	13	0.0	0.0
	Bridgelip sucker	15	0.0	0.0	14	0.0	0.0	13	0.0	0.0

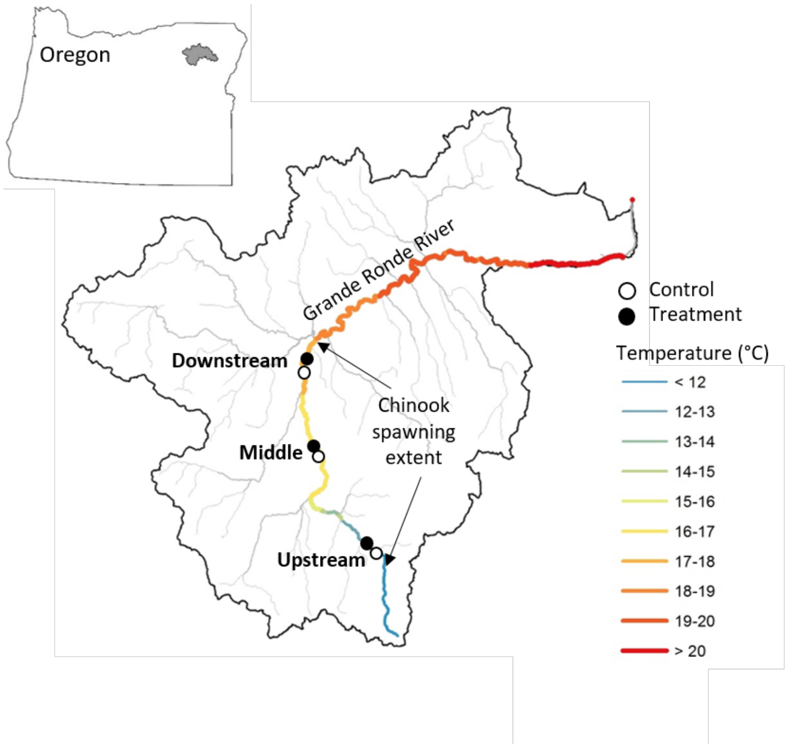


Figure 7.1: Three pairs of sites each with a control reach (open circles) and treatment reach (closed circles) in which carcasses were added in August. Temperature indicates the mean August temperature (1993-2011) derived from the NorWeST Stream Temperature Model (Isaak et al. 2017).

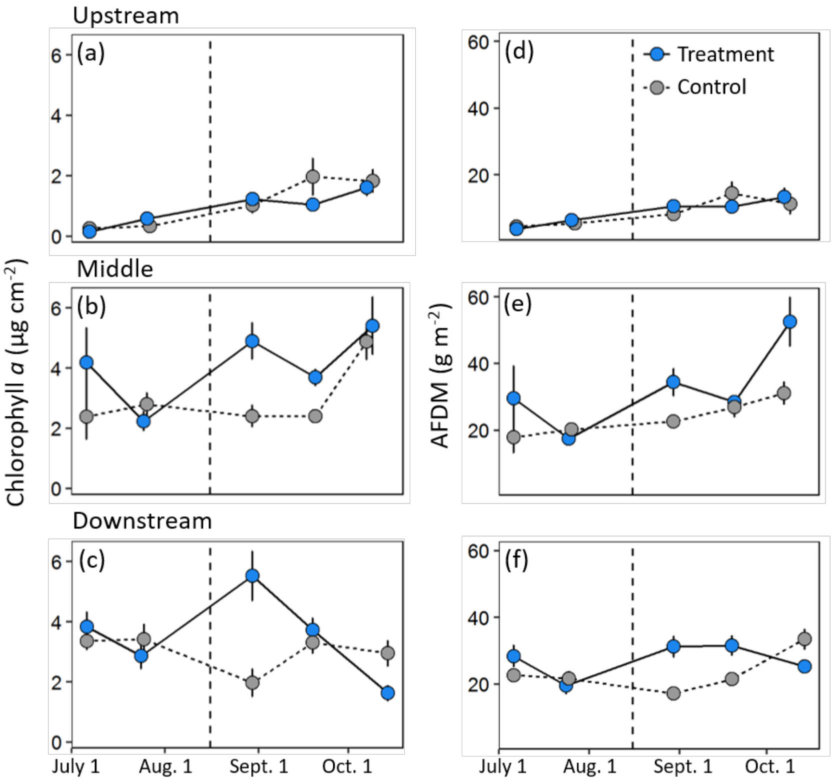


Figure 7.2: Chlorophyll a (a-c) and AFDM (d-f) in control (grey circles) and treatment (blue circles) before and after the addition of carcasses (dashed vertical line). Error bars indicate 95% confidence intervals.

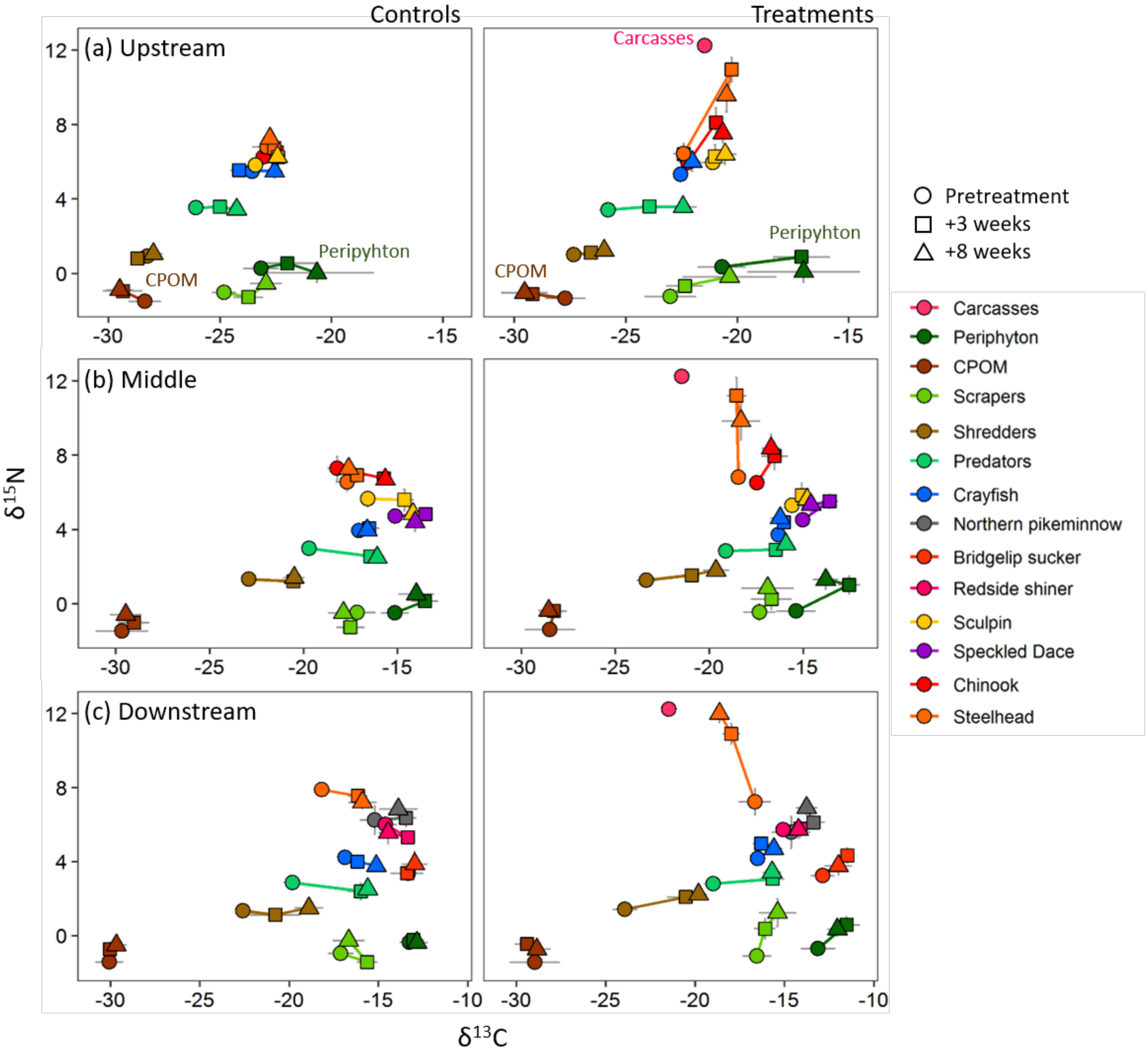


Figure 7.3: Isotopic signatures of taxa before the addition of carcasses (pretreatment; circles), three weeks after carcass additions (squares), and eight weeks after carcass additions (triangles) in the control (left panels) and treatment (right panels) reaches of the upstream (a), middle (b), and downstream (c) pairs.

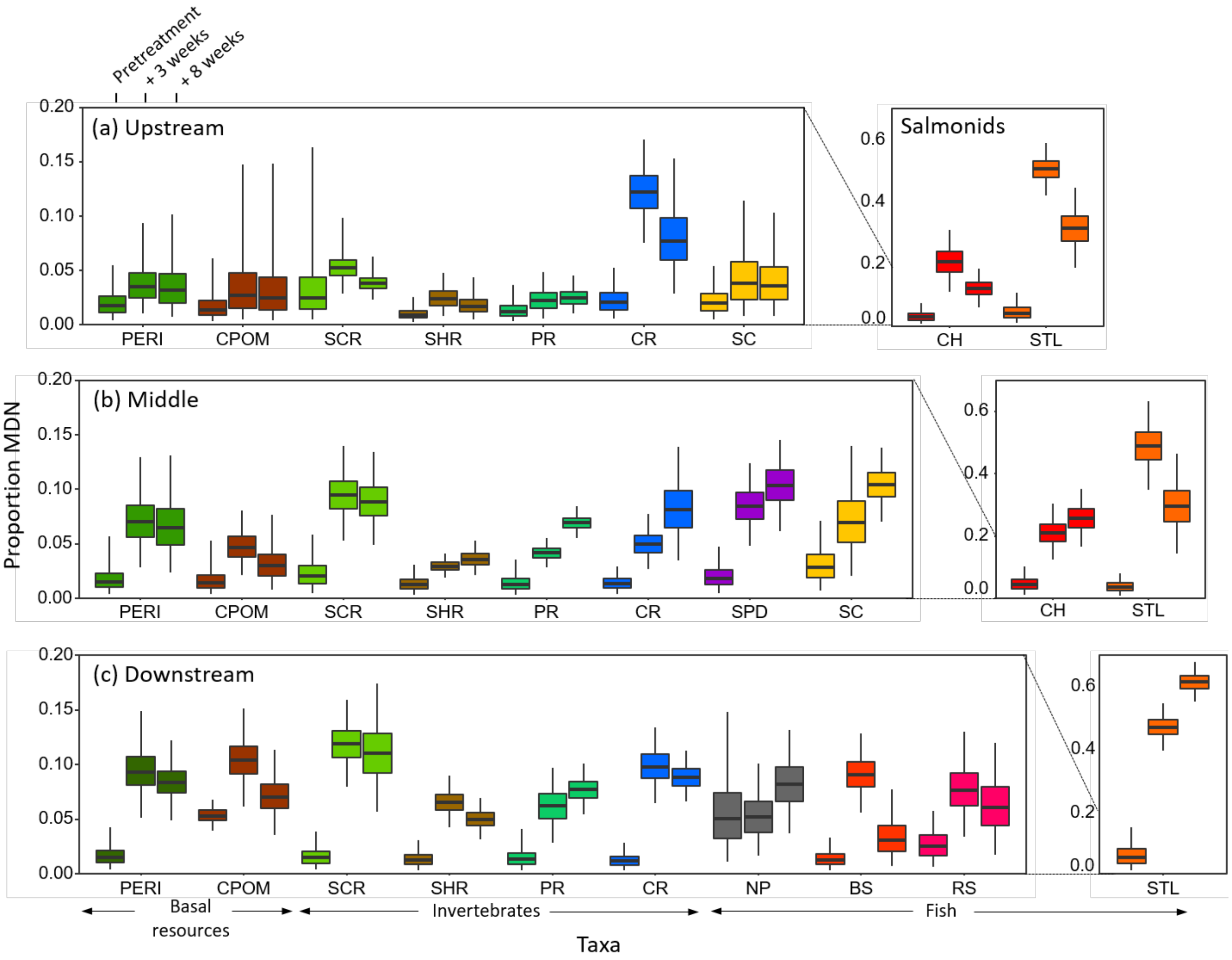


Figure 7.4: The estimated proportion of consumer nitrogen assimilated from carcasses (MDN) during three sampling periods (pretreatment; + 3 weeks after carcass addition; + 8 weeks after carcass addition). PERI = periphyton; CPOM = leaf litter (alder); SCR = invertebrate scrapers; SHR = invertebrate shredders; PR = invertebrate predators; CR = crayfish; SC = sculpin; SPD = speckled dace; NP = northern pikeminnow; BS = bridgelip sucker; RS = redside shiner; CH = juvenile Chinook salmon; and STL = juvenile steelhead.

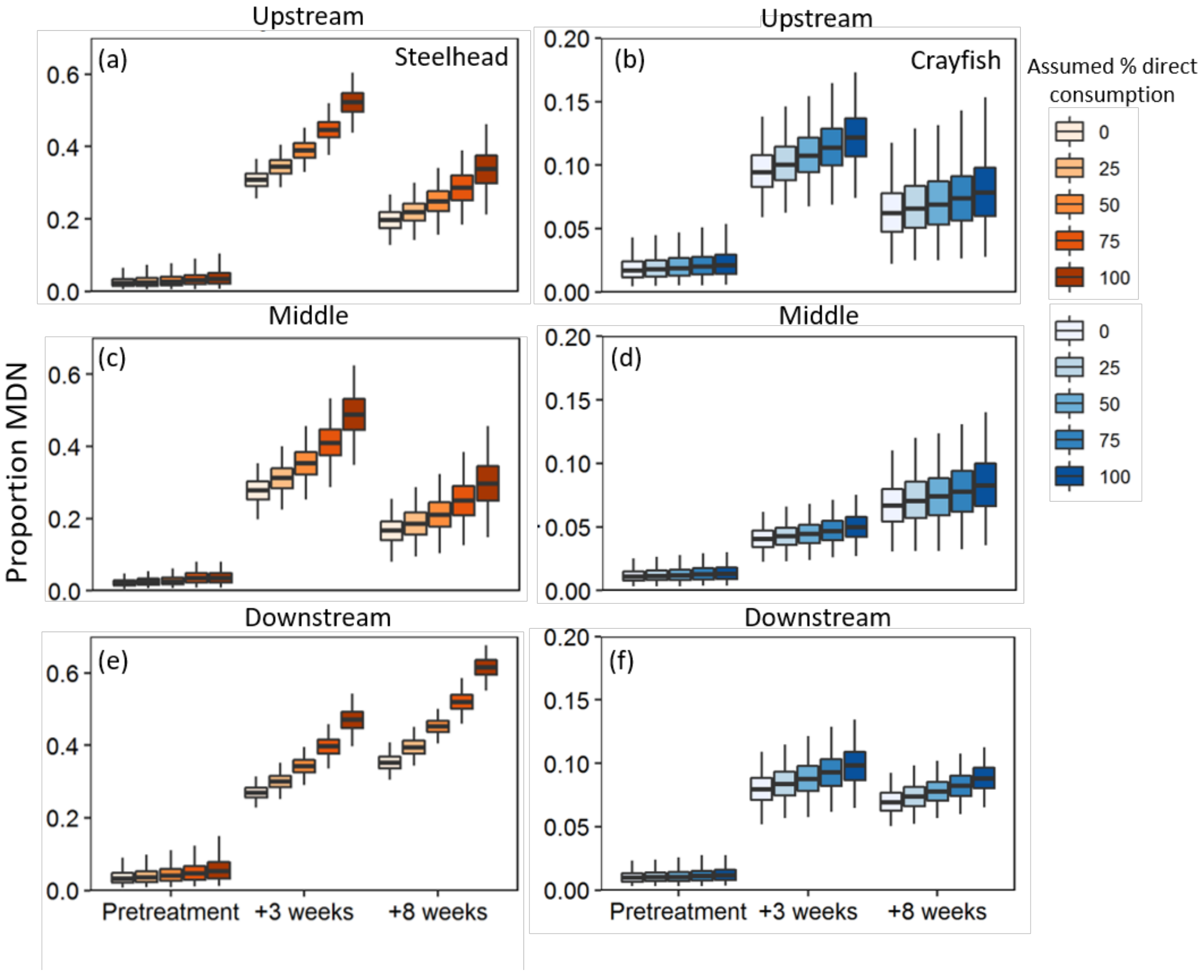


Figure 7.5: The estimated proportion derived from carcasses (MDN) for juvenile steelhead (a-c) and crayfish (d-f) during three sampling events (pretreatment, 3 weeks after carcass additions, and 8 weeks after carcass additions) for each of the three stream pairs. We altered the assumed percentage of MDN that was assimilated through direct consumption pathways (increased shading indicates a greater percentage assimilated through direct consumption), as less total enrichment occurs through this pathway compared to bottom-up assimilation.

CHAPTER 8: GENERAL CONCLUSIONS

Through my dissertation, I explored how factors affecting stream productivity could influence stream consumer populations with a focus on stream salmonids. The first three chapters focused on how riparian forest stand development processes can impact stream light availability and ultimately cutthroat trout and salamander populations through bottom-up controls. I first evaluated spatial and temporal patterns in stream light availability in western Pacific Northwest streams using high-frequency light measurements throughout a stream network and a meta-analysis of studies reporting stand age and stream light (Chapter 2). I then evaluate how spatial differences in light availability among forested streams of the western Cascades of Oregon related to algae, invertebrate, trout, and salamander biomass (Chapter 3). I then used a dataset from the 1970s to quantify how long-term changes in light as forests regenerated following riparian harvest (~40 years) influenced algae, invertebrate, and trout biomass (Chapter 4). In the second half of my dissertation, I shifted to NE Oregon where light was less likely to limit primary production due to differences in vegetation, land-use history, and climate. I first described the spatial dynamics of nutrients, light, temperature, and stream primary production throughout the upper Grande Ronde River and the adjacent Catherine Creek watershed, and related the spatial patterns of primary production to the spatial distribution of juvenile salmonids (Chapter 5). This allowed us to select areas of the network where primary production was low but salmonid abundance was high. In three of these areas I added steelhead carcasses to the stream and evaluated impacts of this potential management action on juvenile salmonid growth rates, body condition, diet, size, and survival (Chapter 6). I additionally quantified impacts to the broader food web including biofilm, invertebrates, and non-salmonid fish that were common in these reaches (Chapter 7). Below I highlight some the key findings and implications of these chapters.

Influences of riparian forest age, structure, and stand development on stream food webs

Historically, clear-cutting riparian forests was common practice and most riparian forests in the Pacific Northwest were harvested at least once in the 20th century (Richardson et al. 2012). However, stringent regulations, especially on federally owned land, have been implemented to protect riparian forests and their associated impacts on stream ecosystems (e.g. shade, large wood recruitment, bank stabilization). Consequently, many riparian forests in the Pacific Northwest are in various stages of stand development as they recover from riparian harvest. Results from Chapter 2 demonstrate that light availability in streams bordered by mid-seral, second growth forests is at a minimum in regard to stages of stand development. Yet modest spatial differences in light availability exist within streams and among streams, and light availability is likely to become more variable owing to local disturbance processes and natural stand development as stands progress to structurally complex late-successional stages. Numerous studies have evaluated how large differences in light availability, such as those between forested streams and those bordered by clear-cuts (e.g. ~0% vs ~100% canopy openness), influence stream biota (Murphy and Hall 1981; Bilby and Bisson 1992; Wootton 2012). However, smaller spatial differences or temporal changes in light availability have received less attention. Results from the work presented here highlight the potential for smaller differences in canopy openness (~0 – 50% canopy openness) to influence aquatic biota via increased stream primary production in light-limited headwater streams. Continued regeneration of riparian forests following 20th century harvesting, coupled with fine-scale disturbance will manifest in spatially variable stream light regimes at local and watershed scales. Our results suggest that these changes in riparian structure have the ability to influence food webs through bottom-up controls.

In chapters 3 and 4, I find evidence that bottom-up controls, as regulated by stream light availability, appeared to be greater drivers of consumer populations than factors associated with physical habitat (e.g. pool area, large wood). These results do not invalidate the large body of work highlighting the importance of stream wood and pool habitat for fish, particularly salmonids, in western U.S. headwater streams (Fausch and Northcote 1992; Connolly and Hall 1999; Roni and Quinn 2001; Roni 2019). Rather, these results demonstrate the importance of considering bottom-up forces (e.g., light and nutrients, sources of energy at the base of the food web) in addition to habitat as factors that can limit invertebrate, fish, and other vertebrates in a stream ecosystem. The physical condition of the streams I evaluated may have set the template for bottom-up forces emerging as important constraints on consumer populations relative to physical habitat; pools were abundant and habitat had not been substantially degraded, potentially due to the large substrates (cobble-boulder) and steep, step-pool or cascade geomorphology associated with headwater streams in this region (Montgomery and Buffington 1997). In addition, timber harvest was limited to small harvest units (4–20 ha) within predominantly unharvested basins, which may have limited negative effects of timber harvest on stream habitat. In Chapter 4, I discuss how short- and long-term biotic responses to timber harvest observed in this study may differ from those in other stream systems. The associated figure conceptualizes how differences in (1) stream habitat, (2) limiting factors for primary producers and trout populations, and (3) impacts of riparian harvest can result in alternative trajectories of resident trout populations over time. Our results support the trajectory that riparian harvesting may in some cases alleviate light limitation and promote enhanced primary and secondary production. This trajectory has been proposed earlier (Sedell and Swanson 1984; Gregory et al. 1987) and has prompted some researchers to advocate for increased riparian harvesting to enhance the productivity of salmonid populations (Newton and Ice 2015). However, this is only one of many different trajectories and we portray how riparian harvest induced changes in temperature and physical habitat may result in negative short- and long-term responses (e.g. decreases in abundance and biomass of salmonids). I demonstrate the importance of considering both short- and long-term (>30 years) responses even when short-term increases in primary and secondary production appear beneficial to biota of management concern (e.g. salmonids). Canopies typically close over streams within 30 y of riparian harvest resulting in decades or even centuries of low-light availability (Chapter 2) which may limit primary and secondary projection to minimal levels for long periods of time. However, changes in canopy cover over 40 years from one of our sites (LO703) demonstrate that canopy closure rates are variable and may occur over longer timescales owing to differences in local disturbance, climate, and vegetation. The trajectory we portrayed represents a common trend in canopy cover and fish biomass over time but we recognize that at the local scale, stand development and canopy closure will be variable and may not always follow this trend. Considering these multiple trajectories and both short- and long-term responses is important to consider potential effects of historic, current, or future harvesting on stream biota.

Nutrient limitation and influences of carcass additions on stream food webs

Recovery of salmonid populations within the Columbia Basin may require an integrated approach involving management actions that consider food webs in addition to physical habitat availability (Naiman et al. 2012). Chapters 2-4 demonstrate that light can be key factor controlling basal resource availability and consumer populations in forested western Oregon streams. In more arid eastern Oregon streams, differences in climate, vegetation, and land-use practices may limit canopy cover over streams, potentially shifting factors limiting primary production at to the base of the food web. I used spatial statistical network models to explore drivers of biofilms and metabolism across two sub-basins of NE Oregon. These models, which incorporate spatial autocorrelation functions, can account for non-independence of samples and improve understanding of how explanatory variables are related to response variables. We were able to explain 72% of the variation in primary production using temperature, solar exposure, and spatial autocorrelation. Fixed-effects explained the majority of the variation in GPP while autocorrelation explained a relatively small proportion. In contrast, autocorrelation explained the majority of the spatial variation in chl *a,* AFDM, and ER across these sub-basins demonstrating the potential value of including autocorrelation functions to predict response variables across a stream network. Without applying an SSN framework, we would not have known that fixed-effects would explain the majority of variation in GPP and we may lost prediction power or overinflated the importance of fixed-effects due to non-independent sites. Nutrients did not emerge as an important predictor of primary production in these spatial models, but analysis of spatial patterns in nutrient concentrations and a nutrient diffusing substrate experiment revealed high biotic demand for nutrients and nutrient limitation of primary producers in these sub-basins. Combining multiple statistical and spatial analysis approaches at the network-scale resulted in a more complete understanding of the processes regulating primary production throughout these sub-basins.

Quantifying spatial patterns in primary production in these NE Oregon sub-basins is important because autochthonous carbon is the dominant energy source fueling stream food webs including juvenile salmonids in systems with limited canopy cover (Finlay et al. 2002). We demonstrated that juvenile Chinook and steelhead were concentrated within areas of the stream network characterized by low rates of primary production and very low nutrient concentrations. These results differed from a similar study conducted in close proximity (<100 km), in which juvenile salmonid density at the network-scale was positively correlated with gross primary production (Saunders et al. 2018). The opposing relationships between these studies potentially reflect different landscape filters that regulate the distribution of salmonids between these basins (Poff 1997). In the sub-basins evaluated in our study, temperature has been shown to influence spawning locations and limit the distribution of juvenile salmonids (Justice et al. 2017; White et al. 2017). Therefore temperature may restrict juvenile salmonids to cool, oligotrophic areas where low rates of primary production may be limiting energy flow to the food web and ultimately juvenile salmonid productivity. Linking spatial patterns in primary production to biota is an important step to connect how the metabolic regimes and energy produced at the food web can shape the distribution and productivity of biota within a "riverscape" (Bernhardt et al. 2017).

Our results led us to believe that low rates of productivity at the base of the food web may be limiting the productivity of the food web, including juvenile Chinook and steelhead. In an effort to increase the productivity of these stream sections, we added steelhead carcasses to the stream, which has been shown to enhance algal, invertebrate, and fish production (Bilby et al. 1998; Minakawa et al. 2002; Verspoor et al. 2011; Collins et al. 2016). Carcass additions are a common management approach to increase the productivity of streams and ultimately juvenile salmonids (Collins et al. 2015), but the efficacy of these actions is uncertain with a number of studies finding no impacts on juvenile salmonid growth rates (Janetski et al. 2009; Harvey and Wilzbach 2010). Further, few studies have been conducted in the interior Columbia River Basin where species composition, seasonal hydrology, climate, disturbance, and notably the timing of spawning salmon may differ from coastal streams where the majority of carcass addition studies have been conducted (Janetski et al. 2009). Lastly, no studies have evaluated the impact of carcass additions on juvenile Chinook, a species of particular management focus in the interior Columbia Basin due to population declines that have prompted the listing of this species under the Endangered Species Act (Jonasson et al. 2015).

In response to carcass additions, we found that 1) juvenile Chinook and steelhead growth rates and condition increased, 2) growth responses were attributed to the direct consumption of eggs and carcass material, 3) energy rations of diets increased significantly, and 4) juvenile Chinook size, which increased due to enhanced growth rates, was positively related to rearing and emigration survival. The effect of carcass additions on growth rates and assimilation of carcass-derived nitrogen (Chapter 7) are among the highest reported of any study. It has been suggested that the biomass of carcasses added to streams (kg m^{-2}) is a key factor determining the magnitude of juvenile salmonid growth responses and stable isotope enrichment (Janetski et al. 2009). However, we added carcasses at among the lowest biomass of any reported study, suggesting other factors may be important determinants of the magnitude of juvenile salmonid effect sizes. We suggest that the presence or absence of eggs within carcasses may be a more important factor than the density of carcasses added. Juvenile Chinook and steelhead consumed an abundance of eggs and carcass material and this increased the energy rations of diets up to 30 times in some cases. These results make it clear that when adding carcasses to streams to promote juvenile salmonid production, eggs should be retained to achieve the greatest effects. Another management implication of this study is relating growth and size to survival. A key assumption of adding carcasses to streams is that increased growth rates will lead to greater rearing or emigration survival, but this has not been evaluated. We used an 18-year tagging and detection dataset to demonstrate the relationship between Chinook size and rearing and emigration survival, and we use this relationship to contextualize the effect of carcass additions on Chinook size and survival. Our results suggest that carcass additions or other management efforts to enhance juvenile Chinook size are likely to increase rearing and emigration survival.

Studies evaluating the effects of carcass additions or naturally spawning salmon have focused on streams where the fish community is dominated by resident salmonids or juvenile anadromous salmonids. In the interior Columbia Basin, numerous non-salmonid species are common throughout the spawning distribution of spring Chinook salmon (Torgersen et al. 2006). The reduction of spawning salmon in these regions may be having profound impacts on the entire fish community. Stable isotope analysis revealed that carcass nitrogen was assimilated by non-salmonids but enrichment was low (< 12% of non-salmonid N was from carcasses) relative to salmonids. The lack of eggs and carcass tissue in diets, as well as stable isotope enrichment patterns, revealed that non-salmonid enrichment of N occurred primary through bottom-up pathways. The lack of eggs in diets was a surprising result. In the downstream pair, eggs were readily available and scattered across the stream benthos. Juvenile steelhead stomachs were full of eggs, but this was not the case for non-salmonids including northern pikeminnow, redside shiner, and bridgelip sucker. Some of the pools in the farthest downstream pair contained hundreds of non-salmonids, and stream flow providing drifting invertebrates to supply these fish was very low in late summer. Examination of diets revealed that many non-salmonid stomachs were empty with no invertebrate prey. Given the high densities of non-salmonids and the low amounts of prey in stomach contents (MJ Kaylor personal observations), non-salmonids were likely food limited during this period and it is surprising that they did not consume these high energy food resources. Future research should evaluate non-salmonid responses to carcass additions in other systems and whether non-salmonids may be more attuned to subsidies provided by naturally spawning salmon rather than carcasses.

Overall, our results suggest salmon subsidies have the potential to broadly impact stream food webs in this region, but species able to directly consume eggs and carcass material clearly benefited most from these subsidies. These results have two important implications for the use of carcass additions as a management tool to promote juvenile salmonid productivity. First, it is clear that the presence of eggs within carcasses was a key factor driving juvenile salmonid responses, and when possible, eggs should be retained within carcasses to yield the greatest effects. Second, our results suggest that within these streams, eggs and carcass material were clearly being directed to fish taxa of primary management concern (salmonids), and competition from non-target species was not apparent. If carcass additions can be implemented at an appropriate scale to stimulate population level responses, this could be an effective way to increase juvenile salmonid productivity and likely survival. However, it is important to recognize that while carcass additions are an attempt to compensate for the loss of the subsidies naturally provided from spawning salmon, artificially placed carcasses, even with eggs, have different effects on stream ecosystems than spawning salmon. Spawning salmon can reduce periphtyon biomass and primary production during redd construction, they can dislodge invertebrates during redd construction that can be consumed by fish, and they can excrete nutrients through metabolism processes prior to and during spawning. Ultimately, it is unclear whether the magnitude of salmon subsidy effects on stream food webs would differ between carcass additions and natural spawning in this system, but the proportional contributions of pathways (bottom-up, dislodged invertebrates, vs direct consumption) would likely differ.

Concluding thoughts

Consumer populations are constrained by the availability of physical habitat needed to sustain biological functions (e.g. reproduction, predator avoidance) as well as by the amount of food available to support population densities and metabolic functions. This idea has early origins and has been a lasting fundamental concept in ecology (Lindeman 1942). However, the degree to which these concepts are reflected in management actions varies by the type of ecosystem and the individual species within these ecosystems that are being managed. For example, ask a sage grouse or large ungulate biologist “what is good habitat?”. They will likely stress habitat in terms of forage availability, predator avoidance, and reproductive success. Similarly, ask a large carnivore biologist and they will surely discuss the availability of their prey as a primary constraint on population carrying capacity and growth rates. Alternatively, ask a fish biologist what good habitat is for juvenile salmonids. Chances are that their emphasis will be on the physical environment — large wood, pool area, habitat complexity, cool temperatures — with less consideration of how prey availability may constrain population densities, individual growth rates, and survival. This is evidenced by management efforts to recovery suppressed trout and salmon populations which have focused on physical habitat improvement and supplementation efforts (e.g. hatcheries) in lieu of management aimed towards improving food webs and stream productivity (Wipfli and Baxter 2010; Naiman et al. 2012). Yet studies have demonstrated that stream consumers, particularly resident and juvenile salmonids, are often limited by food availability (Boss and Richardson 2002) and other studies have linked landscape factors and ecosystem processes to stream productivity and the availability of prey for stream consumers (Hawkins et al. 1983; Kiffney et al. 2007; Bellmore et al. 2015). Further evaluation and refinement of how food web structure and productivity can limit consumer populations, coupled with understanding of physical habitat constraints, provides a more holistic understanding of the abiotic and biotic factors that limit populations and influence their spatial variability within heterogeneous “riverscapes”. It is my hope that this dissertation encourages others to consider how stream productivity and the availability of food resources can influence fish and other consumers, in addition to physical habitat conditions.

Literature cited

Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, M. Arroita, A. P. Appling, M. J. Cohen, W. H. McDowell, R. O. J. Hall, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic. 2017. The metabolic regimes of flowing waters. Limnology and Oceanography (00).

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):1–18.

Collins, S. F., A. M. Marcarelli, C. V Baxter, and M. S. Wipfli. 2015. A Critical Assessment of the Ecological Assumptions Underpinning Compensatory Mitigation of Salmon-Derived Nutrients. Environmental Management 56:571–586. Springer US.

Connolly, P. J., and J. D. Hall. 1999. Biomass of Coastal Cutthroat Trout in unlogged and previously clear-cut basins in the central Coast Range of Oregon. Transactions of the American Fisheries Society 128:890–899.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influences of forest practices on aquatic production. Pages 233–255 *in* E. O. Salo and T. W. Cundy, editors. Streamside Management: Forestry and Fishery Interactions. University of Washington, Institute of Forest Resources, Seattle, Washington.

Harvey, B. C., and M. A. Wilzbach. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth, or retention in six northwestern California streams. North American Journal of Fisheries Management 30:1445–1451.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.

Jonasson, B. C., E. R. Sedell, S. K. Tattam, A. B. Garner, C. D. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, J. M. Hay, G. A. McMichael, B. C. Power, O. C. Davos, and J. R. Ruzycki. 2015. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. La Grande, Oregon.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management 188:212–227.

Lindeman, R. L. 1942. The trophic dynamics aspect of ecology. Ecology 23(4):399–418.

Minakawa, N., R. I. Gara, and J. M. Honea. 2002. Increased individual growth rate and community biomass of stream insects associated with salmon carcasses. Journal of the North American Benthological Society 21(4):651–659.

Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. GSA Bulletin 109(5):596–611.

Murphy, M. L., and J. D. Hall. 1981. Vaired effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109(52):21201–7.

Newton, M., and G. Ice. 2015. Regulating riparian forests for aquatic productivity in the Pacific Northwest, USA: addressing a paradox. Environmental Science and Pollution Research:1–9.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16(2):391–409.

Richardson, J. S., R. J. Naiman, and P. A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshwater Science 31(1):232–238.

Roni, P. 2019. Does River Restoration Increase Fish Abundance and Survival or Concentrate Fish ? The Effects of Project Scale , Location , and Fish Life History. Fisheries 44(1):7–19.

Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58(2):282–292.

Saunders, W. C., N. Bouwes, P. McHugh, and C. E. Jordan. 2018. A network model for primary production highlights linkages between salmonid populations and autochthonous resources. Ecosphere 9(3):e02131.

Sedell, J. R., and F. J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. Pages 9–16 *in* W. R. Meehan, T. R. Merrell, and T. A. Hanley, editors. Fish and Wwldlife relationships in old-growth forests. Juneau, Alaska.

Torgersen, C. E., C. V Baxter, H. W. Li, and B. A. McIntosh. 2006. Landscape Influences on Longitudinal Patterns of River Fishes: Spatially Continuous Analysis of Fish – Habitat Relationships. American Fisheries Society Symposium 48:473–492.

Verspoor, J. J., D. C. Braun, M. M. Stubbs, and J. D. Reynolds. 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. Ecosphere 2(February):1–17.

White, S. M., C. Justice, D. A. Kelsey, D. A. McCullough, and T. Smith. 2017. Legacies of stream channel modification revealed using General Land Office surveys, with implications for water temperature and aquatic life. Elem Sci Anth 5(0):3.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373–387.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7(12):1–9.

GENERAL BIBLIOGRAPHY

Acuna, V., A. Wolf, U. U., and K. Tockner. 2008. Temperature dependence of stream benthic respiration in an Alpine river network under global warming. Freshwater Biology 53:2076–2088.

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. MS thesis. Oregon State University, Corvallis, Oregon.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Ambrose, H. E., M. A. Wilzbach, and K. W. Cummins. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. The North American Benthological Society 23(4):701–712.

Appling, A. P., R. O. J. Hall, C. B. Yackulic, and M. Arroita. 2018. Overcoming equifinality: leveraging long time series for stream metabolism estimation. Journal of Geophysical Research: Biogeosciences 123:624–645.

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. Page US Environmental Protection Agency Method 445.0 Revision 1.2. Cincinnati, Ohio.

Arismendi, I., and D. Soto. 2012. Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from southern Chile. Knowledge and Management of Aquatic Ecosystems (405):01.

Armstrong, J. B., and M. H. Bond. 2013. Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. Journal of Animal Ecology 82(5):966–975.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445–1454.

Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. T. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams : Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94(9):2066–2075.

Baldigo, B.P., Murdoch, P.S., and Burns, D.A. 2005. Stream acidification and mortality of brook trout (Salvelinus fontinalis) in response to timber harvest in Catskill Mountain watersheds, New York, USA. Can. J. Fish. Aquat. Sci. **62**: 1168–1183. doi:10.1139/F05-022.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50(2):201–220.

Bechtold, H. A., E. J. Rosi-Marshall, D. R. Warren, and J. J. Cole. 2012. A practical method for measuring integrated solar radiation reaching streambeds using photodegrading dyes. Freshwater Science 31:1070–1077.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126:217–229.

Benda, L. E., P. Bigelow, and T. M. Worsley. 2002. Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A. Canadian Journal of Forest Research 32:1460–1477.

Benda, L., Miller, D., Sias, J., Martin, D., Bilby, R., Veldhuisen, C., and Dunne, T. 2003. Wood recruitment processes and wood budgeting. Am. Fish. Soc. Symp. **37**: 49–73.

Benjamin, J. R., J. R. Bellmore, and G. A. Watson. 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. Freshwater Science 35(3):810–825.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, and P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):113.

Berg, N., A. Carlson, and D. Azuma. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Canadian Journal of Fisheries and Aquatic Sciences 55:1807–1820.

Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, M. Arroita, A. P. Appling, M. J. Cohen, W. H. McDowell, R. O. J. Hall, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic. 2017. The metabolic regimes of flowing waters. Limnology and Oceanography (00).

Bernhardt, E. S., and G. E. Likens. 2004. Controls on periphyton biomass in heterotrophic streams. Freshwater Biology 49(1):14–27.

Bernot, M. J., D. J. Sobota, R. O. Hall, P. J. Mulholland, W. K. Dodds, J. R. Webster, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, W. H. Mcdowell, J. L. Meyer, B. Peterson, G. C. Poole, H. M. Valett, C. Arango, J. J. Beaulieu, A. J. Burgin, C. Crenshaw, A. M. Helton, L. Johnson, J. Merriam, B. R. Niederlehner, J. M. O'Brien, J. D. Potter, R. W. Sheibley, S. M. Thomas, and K. Wilson. 2010. Inter-regional comparison of land-use effects on stream metabolism. Freshwater Biology 55(9):1874–1890.

Beschta, R.L., Bilby, R.E., Brown, G.W., Holtby, L.B., and Hofstra, T.D. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. *In* Streamside management: Forestry and fishery interactions, vol. 57. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Institute of Forest Resources, Seattle, Washington. pp. 191–232.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53(1):164–173.

Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48:2499–2508.

Bisson, P.A., Gregory, S. V., Nickelson, T.E., and Hall, J.D. 2008. The Alsea Watershed Study: A comparison with other multi-year investigations in the Pacific Northwest. *In* Hydrological and Biological Responses to Forest Practices. *Edited by* J.D. Stednick. Springer. pp. 259–289.

Brauns, M., D. Graeber, I. G. Bo, A. P. C. De Carvalho, T. Mehner, and D. Von Schiller. 2018. Consumer-resource stoichiometry as a predictor of trophic discrimination (D13C, D15N) in aquatic invertebrates. Freshwater Biology 63(10):1–10.

British Columbia Ministry of Forests. 1995. Riparian management area guidebook. British Columbia, Ministry of Forests, Victoria, British Columbia. (Available from: https://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/riparian/rip-toc.htm)

Burgess, J. A. 2001. Response of trout, sculpins, and salamanders to experimental manipulation of large wood in Cascade Mountain streams. Oregon State University.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33(2):261–304.

Brito, E. F., T. P. Moulton, M. L. De Souza, and S. E. Bunn. 2006. Stable isotope analysis indicates microalgae as the predominant food source of fauna in a coastal forest stream, south-east Brazil. Austral Ecology 31(5):623–633.

Cairns, M. A., and K. Lajtha. 2005. Effects of succession on nitrogen export in the west-central Cascades, Oregon. Ecosystems 8:583–601.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Carroll, A. L., S. W. Taylor, J. Regniere, and L. Safranyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223–232 *in* T.L. Shore, J.E Brooks and J.E. Stone (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. Natural Resources Canada, Canadian Forest Service, and Pacific Forestry Centre. Victoria, BC.

Cattaneo, A., and M. C. Amireault. 1992. How artificial are artificial substrata for periphyton?

Journal of the North American Benthological Society 11(2):244–256.

Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1257–1265.

CHaMP, (Columbia Habitat Monitoring Program). 2016. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution, with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.

Claeson, S. M., J. L. Li, J. E. Compton, and P. A. Bisson. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. Canadian Journal of Fisheries and Aquatic Sciences 63:1230–1241.

Clapcott, J. E., and L. A. Barmuta. 2010. Forest clearance increases metabolism and organic matter processes in small headwater streams. Journal of the North American Benthological Society 29:546–561.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):1–18.

Collins, S. F., A. M. Marcarelli, C. V Baxter, and M. S. Wipfli. 2015. A Critical Assessment of the Ecological Assumptions Underpinning Compensatory Mitigation of Salmon-Derived Nutrients. Environmental Management 56:571–586. Springer US.

Collins, S. F., A. H. Moerke, D. T. Chaloner, D. J. Janetski, and G. A. Lamberti. 2011. Response of dissolved nutrients and periphyton to spawning Pacific salmon in three northern Michigan streams. Journal of the North American Benthological Society 30(3):831–839.

Connolly, P. J., and J. D. Hall. 1999. Biomass of Coastal Cutthroat Trout in unlogged and previously clear-cut basins in the central Coast Range of Oregon. Transactions of the American Fisheries Society 128:890–899.

Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography 24:675–695.

Cram, J. M., P. M. Kiffney, R. Klett, and R. L. Edmonds. 2011. Do fall additions of salmon carcasses benefit food webs in experimental streams? Hydrobiologia 675:197–209.

Croke, J.C., and Hairsine, P.B. 2006. Sediment delivery in managed forests: a review. Environ. Rev. **14**: 59–87. doi:10.1139/A05-016.

Cross, W. F., J. P. Benstead, P. C. Frost, and S. a. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshwater Biology 50(11):1895–1912.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detrital-based ecosystem. Ecology

87(6):1556–1565.

Cudmore, T. J., N. Björklund, A. L. Carroll, and B. Staffan Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. Journal of Applied Ecology 47:1036–1043.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen der Internationale Vereinigung fur Theoretische und Angewandte Limnologie 18:1–158.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. H. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and M. B. Wotton. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Danehy, R. J., S. S. Chan, G. T. Lester, R. B. Langshaw, and T. R. Turner. 2007. Periphyton and macroinvertebrate assemblage structure in headwaters bordered by mature, thinned, and clearcut Douglas-fir stands. Forest Science 53:294–307.

Davis, J. M., A. D. Rosemond, S. L. Eggert, W. F. Cross, and J. B. Wallace. 2010. Long-term nutrient enrichment decouples predator and prey production. PNAS 107(1):121–126.

Decamps, H., M. Fortune, F. Gazelle, and G. Pautou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology 1:163–173.

Deegan, L. a, and B. J. Peterson. 1992. Whole-river fertilization stimulates fish production in an arctic tundra river. Canadian Journal of Fisheries and Aquatic Sciences 49:1890–1901.

De Groot, J. D., S. G. Hinch, and J. S. Richardson. 2007. Effects of logging second-growth forests on headwater populations of coastal cutthroat trout: a 6-year, multistream, before-and-after field experiment. Transactions of the American Fisheries Society 136:211–226.

Demars, B. O. L., J. R. Manson, J. S. Ólafsson, and G. M. Gíslason. 2011. Stream hydraulics and temperature determine the metabolism of geothermal Icelandic streams. Knowledge and Management of Aquatic Ecosystems 402(05):1–17.

Denton, K. P., H. B. Rich, and T. P. Quinn. 2009. Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. Transactions of the American Fisheries Society 138(6):1207–1219.

Dodds, W. K. 2006. Eutrophication and trophic state in rivers and streams. Limnology and Oceanography 51(1):671–680.

Dong, X., A. Ruhí, and N. B. Grimm. 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proceedings of the National Academy of Sciences (6):201617571.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 60(10):1266–1280.

Ebersole, J. L., P. J. Wigington, J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansen, B. A. Miller, H. R. La Vigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats. Transactions of the American Fisheries Society 135:1681–1697.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–551.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Fausch, K. D., C. E. Torgersen, C V Baxter, and H. W. Ll. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6):483–498.

Feller, M.C. 2005. Forest harvesting and streamwater inorganic chemistry in western North America: A review. J. Am. Water Resour. Assoc. **41**(4): 785–811. doi:10.1111/j.1752-1688.2005.tb03771.x.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Forest Ecosystem Management Assessment Team, Portland, Oregon. (Available from: http://www.blm.gov/or/plans/nwfpnepa/FEMAT-1993/1993_%20FEMAT_Report.pdf)

Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology 13:133–144.

Fiala, A. C. S., S. L. Garman, and A. N. Gray. 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232:188–197.

Filipa, A., F. Lorenzo, Q. Ma, P. Beja, and M. F. Magalha. 2017. Geostatistical distribution modelling of two invasive crayfish across dendritic stream networks:2899–2912.

Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82(4):1052–1064.

Finlay, J. C. 2011. Stream size and human influences on ecosystem production in river networks. Ecosphere 2(8):1–21.

Finlay, J. C., J. M. Hood, M. P. Limm, M. E. Power, J. D. Schade, and J. R. Welter. 2011. Light-mediated thresholds in stream-water nutrient composition in a river network. Ecology 92(1):140–50.

Fish passage center 2016 annual report. 2017. Portland, Oregon.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

Frieden, J. C., E. E. Peterson, J. Angus Webb, and P. M. Negus. 2014. Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. Environmental Modelling and Software 60:320–330. Elsevier Ltd.

Frissell, C. a., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Garreta, V., P. Monestiez, and J. M. Ver Hoef. 2010. Spatial modelling and prediction on river networks: up model, down model or hybrid? Environmetrics 21:439–456.

Grace, M., and S. Imberger. 2006. Stream metabolism: performing & interpreting measurements. New South Wales Department of Environmental Conservation Stream metabolism workshop May 31(September):204.

Grace, M. R., D. P. Giling, S. Hladyz, V. Caron, R. M. Thompson, and R. Mac Nally. 2015. Fast processing of diel oxygen curves: Estimating stream metabolism with BASE (BAyesian Single-station Estimation). Limnology and Oceanography: Methods 13:103–114.

Gerwing, T. G., and E. Plate. 2019. Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. Restoration Ecology 27(2):279–288.

Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. PhD Dissertation, Oregon State University, Corvallis, Oregon.

Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influences of forest practices on aquatic production. Pages 233–255 *in* E. O. Salo and T. W. Cundy (editors). Streamside Management: Forestry and Fishery Interactions. University of Washington, Institute of Forest Resources, Seattle, Washington.

Gregory, S.V., Meleason, M., and Sobota, D. 2003. Modeling the dynamics of wood in streams and rivers. Am. Fish. Soc. Symp. **37**: 315–335.

Gregory, S.V, Schwartz, J.S., Hall, J.D., Wildman, R.C., and Bisson, P.A. 2008. Long-term trends in habitat and fish populations in the Alsea Basin. *In* Hydrological and Biological Responses to Forest Practices. *Edited by* J.D. Stednick. Springer. pp. 237–257. Available from http://www.springerlink.com/index/G011704122L53704.pdf.

Gregory, S. V, J. Swanson, W. A. Mckee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem : Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. Fisheries Habitat 25(1):15–21.

Groom, J. D., L. Dent, L. J. Madsen, and J. Fleuret. 2011. Response of western Oregon (USA) stream temperatures to contemporary forest management. Forest Ecology and Management 262:1618–1629.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and

J. J. Hard. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. Conservation Biology 21(4):1009–1020.

Hall, J.D., and Lantz, R.L. 1969. Effects of Logging on the habitat of coho salmon and cutthroat trout in coastal streams. *In* Symposium on Salmon and trout in streams. *Edited by* T.G. Northcote. H.R. MacMillan Lectures in Fisheries, University of British Columbia. pp. 355–375.

Hall, R. O. J., and J. J. Beaulieu. 2013. Estimating autotrophic respiration in streams using daily metabolism data. Freshwater Science 32(2):507–516.

Hall, R. O. J., and E. R. Hotchkiss. 2017. Stream metabolism. Page *in* G. A. Lamberti and F. R. Hauer, editors. Methods in Stream Ecology, 3rd edition. Academic Press.

Hall, R. O., G. E. Likens, and H. M. Malcom. 2001. Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. Journal of the North American Benthological Society 20(3):432–447.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

Harrington, C. 2006. Biology and ecology of red alder. Red alder—a state of knowledge. General Technical Report PNW-GTR-669. US Department of Agriculture, Forest Service, Portland, Oregon.

Harvey, B. C., and M. A. Wilzbach. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth, or retention in six northwestern California streams. North American Journal of Fisheries Management 30:1445–1451.

Hawkins, C. P., M. L. Murphy, N. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173–1185.

Hedman, C. W., D. H. Van Lear, and W. T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26:1218–1227.

Heifetz, J., M. L. Murphy, and K. V Koski. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaskan streams. North American Journal of Fisheries Management 6:52–58.

Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. Northwest Science 70:213–222.

Hicks, B. J. 1997. Food webs in forest and pasture streams in the Waikato region, New Zealand: A study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. New Zealand Journal of Marine and Freshwater Research 31(5):651–664.

Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125–132.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Hoellein, T. J., D. A. Bruesewitz, and D. C. Richardson. 2013. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. Limnology and Oceanography 58(6):2089–2100.

Hotchkiss, E. R., and R. O. J. Hall. 2015. Whole-stream 13C tracer addition reveals distinct fates of newly fixed carbon. Ecology 96(2):403–416.

Humphries, P., and K. O. Winemiller. 2009. Historical Impacts on River Fauna, Shifting Baselines, and Challenges for Restoration. BioScience 59(8):673–684.

Hurvich, C., and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Isaak, D. J., J. M. Ver Hoef, E. E. Peterson, D. L. Horan, and D. E. Nagel. 2017. Scalable population estimates using spatial-stream-network (SSN) models, fish density surveys, and national geospatial database frameworks for streams. Canadian Journal of Fisheries and Aquatic Sciences 74:147–156.

Isaak, D. J., E. E. Peterson, J. M. Ver Hoef, S. J. Wenger, J. A. Falke, C. E. Torgersen, C. Sowder, E. A. Steel, M.-J. Fortin, C. E. Jordan, A. S. Ruesch, N. Som, and P. Monestiez. 2014. Applications of spatial statistical network models to stream data. WIREs Water 1(June):277–294.

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, D. E. Nagel, C. H. Luce, S. W. Hostetler, J. B. Dunham, B. B. Roper, S. P. Wollrab, G. L. Chandler, D. L. Horan, and S. Parkes-payne. 2017. The NorWeST summer stream temperature model and scenarios for the western U.S.: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Water Resources Research 53:1–25.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465–485.

Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi. 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society 27(2):252–268.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.

Jeltsch, F., K. Moloney, and S. J. Milton. 1999. Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. Oikos 85(3):451–466.

Johnson, S. W., J. Heifetz, and K. V Koski. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. North American Journal of Fisheries Management 6:532–537.

Johnson, S. L. 2004. Factors influencing stream temperatures in small streams : substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61:913–923.

Johnson, S. L., and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences

57:30–39.

Johnson, L. T., J. L. Tank, and W. K. Dodds. 2009. The influence of land use on stream biofilm nutrient limitation across eight North American ecoregions. Canadian Journal of Fisheries and Aquatic Sciences 66(7):1081–1094.

Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. Canadian Journal of Fisheries and Aquatic Sciences 47:862–872.

Jonasson, B. C., E. R. Sedell, S. K. Tattam, A. B. Garner, C. D. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, J. M. Hay, G. A. McMichael, B. C. Power, O. C. Davos, and J. R. Ruzycki. 2015. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. La Grande, Oregon.

Jones, N. E., and R. W. Mackereth. 2016. Resource subsidies from adfluvial fishes increase stream productivity. Freshwater Biology 61:991–1005.

Julian, J. P., M. W. Doyle, and E. H. Stanley. 2008a. Empirical modeling of light availability in rivers. Journal of Geophysical Research 113.

Julian, J. P., S. Z. Seegert, S. M. Powers, E. H. Stanley, and M. W. Doyle. 2011. Light as a first-order control on ecosystem structure in a temperate stream. Ecohydrology 4:422–432.

Julian, J. P., E. H. Stanley, and M. W. Doyle. 2008b. basin-scale consequences of agricultural land use on benthic light availability and primary production along a sixth-order temperate river. Ecosystems 11:1091–1105.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management 188:212–227.

Kaenel, B. R., H. Buehrer, and U. Uehlinger. 2000. Effects of aquatic plant management on stream. Freshwater Biology 45:85–95.

Kamler, J. F., and K. L. Pope. 2001. Nonlethal Methods of Examining Fish Stomach Contents Nonlethal Methods of Examining Fish Stomach Contents. Nebraska Cooperative Fish and Wildlife Research Unit-Staff Publications 55.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46:303–316.

Kaylor, M. J., A. Argerich, S. M. White, B. J. Verwey, and I. Arismendi. 2018. A cautionary tale for in situ fluorometric measurement of stream chlorophyll a: influences of light and periphyton biomass. Freshwater Science 37(2):287–295.

Kaylor, M. J., D. R. Warren, and P. M. Kiffney. 2017. Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams. Freshwater Science 36.

Kaylor, M.J., and Warren, D.R. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere, 8(6): e01845.

doi:10.1002/ecs2.1845.

Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecological Applications 17:852–868.

Kelly, V. J., and S. White. 2016. A method for characterizing late-season low-flow regime in the upper Grand Ronde River Basin, Oregon. Page Scientific Investigations Report 2016-5041.

Kiernan, J. D., B. N. Harvey, and M. L. Johnson. 2010. Direct versus indirect pathways of salmon-derived nutrient incorporation in experimental lotic food webs. Canadian Journal of Fisheries and Aquatic Sciences 67(12):1909–1924.

Kiffney, P. M., E. R. Buhle, S. M. Naman, G. R. Pess, and R. S. Klett. 2014. Linking resource availability and habitat structure to stream organisms: an experimental and observational assessment. Ecosphere 5:1–27.

Kiffney, P. M., S. M. Naman, J. M. Cram, M. Liermann, and D. G. Burrows. 2018. Multiple pathways of C and N incorporation by consumers across an experimental gradient of salmon carcasses. Ecosphere 9(4):e02197.

Kiffney, P. M., and P. Roni. 2007. Relationships between productivity, physical habitat, and aquatic invertebrate and vertebrate populations of forest streams: an information-theoretic approach. Transactions of the American Fisheries Society 136:1088–1103.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40:1060–1076.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23:542–555.

Kohler, A. E., T. N. Pearsons, J. S. Zendt, M. G. Mesa, C. L. Johnson, and P. J. Connolly. 2012. Nutrient Enrichment with Salmon Carcass Analogs in the Columbia River Basin, USA: A Stream Food Web Analysis. Transactions of the American Fisheries Society 141(September 2014):802–824.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53(3):446–460.

Kreutzweiser, D.P., Hazlett, P.W., and Gunn, J.M. 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. Environ. Rev. **16**(NA): 157–179. doi:10.1139/A08-006.

Lamberti, G.A., and A.D. Steinman. 1997. Primary production in stream ecosystems. Journal of the North American Benthological Society. 16:95-104.

Larned, S. T. 2010. A prospectus for periphyton: recent and future ecological research. Journal of the North American Benthological Society 29(1):182–206.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28:426–439.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165–180.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123(4):627–640.

Liang, L., and S. Fei. 2013. Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change. Climatic Change:1–12.

Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall, Jr. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92(6):1215–1225.

Matthews, K. R., N. H. Berg, D. L. Azuma, and T. R. Lambert. 1994. Cool water formation and trout habitat use in a deep pool in the Sierra Nevada, California. Transactions of the American Fisheries Society 123:549–564.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. a. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

McCullough, D. A., S. White, C. Justice, M. Blanchard, R. Lessard, D. Kelsey, and J. Nowinski. 2016. Assessing the status and trends of spring Chinook habitat in the upper Grande Ronde River and Catherine Creek.

McCutchan, J. H., and W. M. Lewis, Jr. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742–752.

McGuire, K. J., C. E. Torgersen, G. E. Likens, D. C. Buso, W. H. Lowe, and S. W. Bailey. 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proceedings of the National Academy of Sciences of the United States of America 111(19):7030–5.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90(1):46–56.

McTammany, M.E., E.F. Benfield, and J.R. Webster. 2007. Recovery of stream ecosystem metabolism from historical agriculture. Journal of the North American Benthological Society. 26:532-545.

Meehan, W. R., and R. A. Miller. 1978. Stomach Flushing: Eftectiveness and Influence on Survival and Condition of Juvenile Salmonids. Journal of Fisheries Research of the Board of Canada 35:1359–1363.

Mellina, E., and S. G. Hinch. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Canadian Journal of Forest Research 39:1280–1301.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An introduction to the aquatic insects of North America. Kendell Hunt Publishing Company.

Meyer, J. L., and R. T. Edwards. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology 71(2):668–677.

Minakawa, N., R. I. Gara, and J. M. Honea. 2002. Increased individual growth rate and community biomass of stream insects associated with salmon carcasses. Journal of the North American Benthological Society 21(4):651–659.

Minore, D., and H. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. New Forests 8:249–263.

Minshall, G. W., W. Kenneth, R. C. Petersen, and D. A. Bruns. 1985. Developments in Stream Ecosystem Theory. Canadian Journal of Fisheries and Aquatic Sciences 42:1045–1055.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, R. L. Vannote, R. C. Petersen, T. L. Bott, and C. E. Cushing. 1983. Interbiome Comparison of Stream Ecosystem Dynamics. Ecological Monographs 53(1):1–25.

Momot, W. T., and P. D. Jones. 1978. The Dynamics of Crayfish and Their Role in Ecosystems. The American Midland Naturalist 99(1):10–35.

Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. GSA Bulletin 109:596–611.

Monzyk, F. R., B. C. Jonasson, T. L. Hoffnagle, P. J. Keniry, R. W. Carmichael, and P. J. Cleary. 2009. Migration Characteristics of Hatchery and Natural Spring Chinook Salmon Smolts from the Grande Ronde River Basin, Oregon, to Lower Granite Dam on the Snake River. Transactions of the American Fisheries Society 138:1093–1108.

Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. Journal of Animal Ecology 77:275–284.

Moore, R. D., D. L. Spittlehouse, and A. Story. 2006. Riparian microclimate and stream temperature response to forest harvesting : a review. Journal of the American Water Resources Association 41:813–834.

Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. Journal of the North American Benthological Society 18(3):299–307.

Morley, S. A., H. J. Coe, J. J. Duda, L. S. Dunphy, M. L. Mchenry, B. R. Beckman, M. Elofson, E. M. Sampson, and L. Ward. 2016. Seasonal variation exceeds effects of salmon carcass additions on benthic food webs in the Elwha River. Ecosphere 7(8).

Mulholland, P. J., C. S. Fellows, J. L. Tank, N. B. Grimm, J. R. Webster, S. K. Hamilton, E. Marti, L. R. Ashkenas, W. B. Bowden, W. K. Dodds, W. H. McDowell, M. J. Paul, and B. J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46:1503–1517.

Murphy, M. L. 1979. Predator assemblages in old-growth and logged sections of small cascade streams. Oregon State University.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. **110**(4): 469–478. doi:10.1577/1548-8659(1981)110<469.

Murphy, M. L., J. Heifetz, S. W. Johnson, K. V Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43:1521–1533.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109(52):21201–7.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nakano, S., H. Miyasaka, and K. Naotoshi. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80(7):2435–2441.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nelson, M. C., and J. D. Reynolds. 2014. Time-delayed subsidies: Interspecies population effects in salmon. PLoS ONE 9(6):1–9.

Newton, M., and Ice, G. 2015. Regulating riparian forests for aquatic productivity in the Pacific Northwest, USA: addressing a paradox. Environ. Sci. Pollut. Res.: 1–9. doi:10.1007/s11356-015-5814-7.

Noel, Di. S., C. W. Martin, and C. A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. Environmental Management 10:661–670.

Obedzinski, R. A., and C. G. Shaw. 2001. Declining woody vegetation in riparian ecosystems of the western United States. Western Journal of Applied Forestry 16:169–181.

ODFW (Oregon Department of Fish and Wildlife). 1990. Grande Ronde River Subbasin Salmon and Steelhead Production Plan. Portland, OR.

Ortiz-Zayas, J. R., W. M. J. Lewis, J. F. I. Saunders, J. H. J. McCutchan, and F. N. Scatena. 2005. Metabolism of a tropical rainforest stream. Journal of the North American Benthological Society 24(4):769–783.

Overpeck, J., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbances and vegetation. Nature 343:51–53.

Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–732.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Parker, M. S. 1994. Feeding ecology of stream-dwelling Pacific Giant Salamander larvae (Dicamptodon tenebrosus). American Society of Ichthyologists and Herpetologists 1994:705–718.

Parnell, A. C., D. L. Phillips, S. Bearhop, X. Brice, E. J. Ward, J. W. Moore, A. L. Jackson, J. Grey, D. J. Kelly, and R. Inger. 2013. Bayesian stable isotope mixing models. Environmetrics 24:387–399.

Pastor, J., and W. Post. 1988. Response of northern forests to CO_2-induced climate change. Nature 334:55–58.

Pellett, K. 2011. A review of twenty years of nutrient enrichment in the salmon river watershed, Vancouver Island (1989-2010). Nanaimo, BC.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The Influences of Body Size, Habitat Quality, and Competition on the Movement and Survival of Juvenile Coho Salmon during the Early Stages of Stream Recolonization. Transactions of the American Fisheries Society 140(4):883–897.

Peterson, E. E., and J. M. Ver Hoef. 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks 91(3):644–651.

Peterson, E. E., and J. M. Ver Hoef. 2014. STARS: An ArcGIS toolset used to calculate the statistical models to stream network data. Journal of Statistical Software 56(2):1:17.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. Mckinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74(3):653–672.

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835.

Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (Salmo salar) streams. Canadian Journal of Fisheries and Aquatic Sciences 55:201–217.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward the integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28(1):289–316.

Pollock, M. M., T. J. Beechie, M. Liermann, and R. E. Bigley. 2009. Stream temperature relationships to forest harvest in Western Washington. Journal of the American Water Resources Association 45:141–156.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Jones and J. H. Lawton (editors). Linking species and ecosystems, Springer Science and Business Media, Dordrecht, The Netherlands.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83(3):703–718.

Power, M. E., J. R. Holomuzki, and R. L. Lowe. 2013. Food webs in Mediterranean rivers. Hydrobiologia 719:119–136.

Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. New Zealand Journal of Marine and Freshwater Research 31:665–683.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (Oncorhynchus kisutch) in Big Beef Creek , Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Rahel, F. J., and W. A. Hubert. 1991. Fish Assemblages and Habitat Gradients in a Rocky Mountain-Great Plains Stream: Biotic Zonation and Additive Patterns of Community Change. Transactions of the American Fisheries Society 120:319–332.

Ralph, S.C., Poole, G.C., Conquest, L.L., and Naiman, R.J. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. Can. J. Fish. Aquat. Sci. **51**: 37–51. doi:10.1139/f94-006.

Ramirez, B. S. 2011. Experimental analysis of intra- and interspecific competitive interactions between cutthroat trout and sculpins in small streams. Oregon State University.

Reeves, G. H., J. E. Williams, K. M. Burnett, and K. Gallo. 2006. The aquatic conservation strategy of the Northwest Forest Plan. Conservation Biology 20:319–329.

Reid, D. J., G. P. Quinn, P. S. Lake, and P. Reich. 2008. Terrestrial detritus supports the food webs in lowland intermittent streams of south-eastern Australia: a stable isotope study. Freshwater Biology 53(10):2036–2050.

Reilly, M. J., and T. A. Spies. 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland northern California. Ecosphere 6:1-27.

Richardson, J. S., R. J. Naiman, and P. A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshwater Science 31:232–238.

Richmond, A. D., and K. D. Fausch. 1995. Characteristics and function of large woody debris in suba pine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences 52:1789–1802.

Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10(4):588–606.

Rodriguez-Castillo, T., E. Estevez, A. M. Gonzalez-Ferreras, and J. Barquin. 2018. Estimating Ecosystem Metabolism to Entire River Networks. Ecosystems.

Romero, N., R. E. Gresswell, and J. L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797–1807.

Roni, P. 2002. Habitat use by fishes and Pacific Giant Salamanders in small western Oregon and Washington streams. Transactions of the American Fisheries Society 131:743–761.

Roni, P. 2003. Responses of benthic fishes and giant salamanders to placement of large woody debris in small Pacific Northwest streams. North American Journal of Fisheries Management 23:1087–1097.

Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management 28:856–890.

Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:282–292.

Roni, P. 2019. Does River Restoration Increase Fish Abundance and Survival or Concentrate Fish ? The Effects of Project Scale , Location , and Fish Life History. Fisheries 44(1):7–19.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. Michael, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22(1):1–20.

Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for Rainbow Trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395–1410.

Rosenfeld, J. S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953–968.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585–593.

Rounick, J. S., M. J. Winterbourn, and G. L. Lyon. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. Oikos 39:191–198.

Ruff, C. P., D. E. Schindle, J. B. Armstrong, K. T. Bentle, G. T. Brooks, G. W. Holtgrieve, M. T.

McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92(11):2073–2084.

Ruzycki, J. R., M. W. Flesher, R. W. Carmichael, and D. L. Eddy. 2003. Lower Snake River Compensation Plan: Oregon Evaluation Studies-Steelhead Life History, Genetics, and Kelt Reconditioning. Oregon Department of Fish and Wildlife, La Grande, OR.

Sabater, F., A. Butturini, E. Martí, and I. Muñoz. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. Journal of the North American Benthological Society 19:609–620.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. North American Bentholocial Society 21:336–343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Samways, K. M., T. J. Blair, M. A. Charest, and R. A. Cunjak. 2017. Effects of spawning Atlantic salmon (Salmo salar) on total lipid content and fatty acid composition of river food webs. Ecosphere 8(6).

Samways, K. M., D. X. Soto, and R. A. Cunjak. 2018. Aquatic food-web dynamics following incorporation of nutrients derived from Atlantic anadromous fishes. Journal of Fish Biology 92:399–419.

Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. A. Steel, and W. L. Reichert. 2009. Nonlethal Sampling of Fish Caudal Fins Yields Valuable Stable Isotope Data for Threatened and Endangered Fishes. Transactions of the American Fisheries Society 138(5):1166–1177.

Saunders, W. C., N. Bouwes, P. McHugh, and C. E. Jordan. 2018. A network model for primary production highlights linkages between salmonid populations and autochthonous resources. Ecosphere 9(3):e02131.

Saunders, W. C., and K. D. Fausch. 2007. Improved Grazing Management Increases Terrestrial Invertebrate Inputs that Feed Trout in Wyoming Rangeland Streams. Transactions of the American Fisheries Society 136(5):1216–1230.

Saunders, W. C., and K. D. Fausch. 2012. Grazing management influences the subsidy of terrestrial prey to trout in central Rocky Mountain streams (USA). Freshwater Biology 57:1512–1529.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52(10):1944–1956.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Fronteirs in Ecology and the Environment 1(1):31–37.

Scown, M. W., M. G. Mcmanus, J. H. Carson, and C. T. Nietch. 2017. Improving predictive models of in-stream phosphorus concentration based on nationally-available spatial data coverages. Jounral of the American Water Resources Association 53(4):944–960.

Sedell, J. R., and F. J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. Pages 9–16 *in* W. R. Meehan, T. R. Merrell, and T. A. Hanley (editors). Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska. American Institute of Fisheries Research Biologists, Morehead City, North Carolina.

Sedell, E. R., S. K. Tattam, A. B. Garner, C. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, G. A. McMichael, E. N. Branigan, B. C. Power, O. C. Davis, and J. R. Ruzycki. 2018. Investigations into the Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin. 2017 Annual Report. BPA Project # 1992-026-04.

Siders, A. C., D. M. Larson, J. Ruegg, and W. K. Dodds. 2017. Probing whole-stream metabolism: influence of spatial heterogeneity on rate estimates. Freshwater Biology 62:711–723.

Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of Kuparuk River ecosystem to phosphorus fertilization. Ecology 85(4):939–954.

Stevens, D. L., and A. R. Olsen. 2004. Spatially Balanced Sampling of Natural Resources. Journal of the American Statistical Association 99(465):262–278.

Stewart-Oaten, A., Murdoch, W.W., and Parker, K.R. 1986. Environmental impact assessment: “pseudoreplication” in time? Ecology **67**(4): 929–940. doi:10.2307/1939815.

Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39:151–169.

Stoneman, C. L., and M. L. Jones. 2000. The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. Transactions of the American Fisheries Society 129:639–657.

Stovall, J. P., W. S. Keeton, and C. E. Kraft. 2009. Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams. Canadian Journal of Forest Research 39:2343–2354.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions American Geophysical Union 38:913–920.

Summers, R. P. 1982. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. MS Thesis, Oregon State University, Corvallis, Oregon.

Swain, N. R., M. D. Hocking, J. N. Harding, and J. D. Reynolds. 2014. Effects of salmon on the diet and condition of stream-resident sculpins. Canadian Journal of Fisheries and Aquatic Sciences 71:521–532.

Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, L.A., Newbold, J.D., Standley, L.J., Hession, W.C., and Horwitz, R.J. 2004. Riparian deforestation , stream narrowing , and loss of stream ecosystem services. Proc. Natl. Acad. Sci. **101**(39): 14132–14137. doi:10.1073/pnas.0405895101.

Tait, C. K., J. L. Li, G. A. Lamberti, T. N. Pearsons, and H. W. Li. 1994. Relationships between riparian cover and the Community structure of high desert streams. Journal of the North American Benthological Society 13(1):45–56.

Tank, J. L., and W. K. Dodds. 2003. Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. Freshwater Biology 48:1031–1049.

Tank, J. L., E. Marti, T. Riis, D. von Schiller, A. J. Reisinger, W. K. Dodds, M. R. Whiles, L. R. Ashkenas, W. B. Bowden, S. M. Collins, C. L. Crenshaw, T. A. Crowl, N. A. Griffiths, N. B. Grimm, S. K. Hamilton, S. L. Johnson, W. H. McDowell, B. M. Norman, E. J. Rosi, K. S. Simon, S. A. Thomas, and J. R. Webster. 2017a. Partitioning assimilatory nitrogen uptake in streams: an analysis of stable isotope tracer additions across continents. Ecological Monographs 0(0):1–19.

Tank, J. L., A. J. Reisinger, and E. J. Rosi. 2017b. Nutrient limitation and uptake. Pages 147–171 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology, 3rd edition. Academic Press.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118–146.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of Oncorhynchus mykiss growth require year-round monitoring. Ecology of Freshwater Fish 26:434–443.

Tiedemann, A.R., Quigley, T.M., and Anderson, T.D. 1988. Effects of timber harvest on stream chemistry and dissolved nutrient losses in northeast Oregon. For. Sci. **34**(2): 344–358.

Tiegs, S. D., E. Y. Campbell, P. S. Levi, J. Ruegg, M. E. Benbow, D. T. Chaloner, R. W. Merritt, J. L. Tank, and G. A. Lamberti. 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. Freshwater Biology 54:1864–1875.

Thedinga, F., M. L. Murphy, J. Heifetz, K. V Koski, and S. W. Johnson. 1989. Effects of logging on size and composition of juvenile Coho Salmon (Oncorhynchus kisutsch) and density of presmolts in southeast Alaska streams. Canadian Journal of Fisheries and Aquatic Sciences 46.

Thompson, S. K., and G. A. F. Seber. 1994. Detectability in conventional and adaptive sampling. Biometrics 50:712–724.

Torgersen, C. E., C. V Baxter, H. W. Li, and B. A. McIntosh. 2006. Landscape Influences on Longitudinal Patterns of River Fishes: Spatially Continuous Analysis of Fish – Habitat Relationships. American Fisheries Society Symposium 48:473–492.

Uehlinger, U. 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. Freshwater Biology 51:938–950.

Valett, H. M., C. L. Crenshaw, and P. F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. Ecology 83:2888–2901.

Van Dyke, E. S., D. L. Scarnecchia, B. C. Jonasson, and R. W. Carmichael. 2009. Ecology of Winter Concealment Behavior of Juvenile Spring Chinook Salmon in the Grande Ronde River Basin, Oregon. Northwest Science 84(1):9–19.

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Van Pelt, R., T. C. O'Keefe, J. J. Latterell, and R. J. Naiman. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecological Monographs 76:277–298.

Velasco, J., A. Millan, M. L. Suarez, C. Guerrero, and M. Ortega. 2003. Macrophytic, epipelic and epilithic primary production in a semiarid Mediterranean stream. Freshwater Biology 48:1408–1420.

Ver Hoef, J. M., E. E. Peterson, D. Clifford, and R. Shah. 2014. SSN: An R package for spatial statistical modeling on stream networks. Journal of Statistical Software 56(3):1–45.

Verspoor, J. J., D. C. Braun, M. M. Stubbs, and J. D. Reynolds. 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. Ecosphere 2(February):1–17.

Villarin, L. A., D. M. Chapin, and J. E. Jones. 2009. Riparian forest structure and succession in second-growth stands of the central Cascade Mountains, Washington, USA. Forest Ecology and Management 257:1375–1385.

Walter, J. K., R. E. Bilby, and B. R. Fransen. 2006. Effects of Pacific salmon spawning and carcass availability on the caddisfly Ecclisomyia conspersa (Trichoptera: Limnephilidae). Freshwater Biology 51:1211–1218.

Ward, J. V, and J. a Stanford. 1983. Serial Discontinuity Concept of Lotic Ecosystems.

Wallace, J. B. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277(5322):102–104.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of Resource Limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. The Journal of Wildlife Management 28(4):617–660.

Warren, D. R., E. S. Bernhardt, R. O. Hall, Jr., and G. E. Likens. 2007. Forest age, wood and nutrient dynamics in headwater streams of the Hubbard Brook Experimental Forest, NH. Earth Surface Processes and Landforms 32:1154–1163.

Warren, D. R., S. M. Collins, E. M. Purvis, M. J. Kaylor, and H. A. Bechtold. 2016. Spatial variability in light yields co-limitation of primary production by both light and nutrients in a forested stream ecosystem. Ecosystems.

Warren, D. R., W. S. Keeton, H. A. Bechtold, and E. J. Rosi-Marshall. 2013. Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. Aquatic Sciences 75:547–558.

Warren, D.R., Keeton, W.S., Kiffney, P.M., Kaylor, M.J., Bechtold, H.A., and Magee, J. 2016. Changing forests - changing streams: riparian forest stand development and ecosystem function in temperate headwaters. Ecosphere **7**(8): e01435. doi:10.1002/ecs2.1435.

Warren, D.R., and Kraft, C.E. 2003. Brook trout (Salvelinus fontinalis) response to wood removal from high-gradient streams of the Adirondack Mountains (N.Y., U.S.A.). Can. J. Fish. Aquat. Sci. **60**: 379–389. doi:10.1139/F03-031.

Warren, D. R., C. E. Kraft, W. S. Keeton, J. S. Nunery, and G. E. Likens. 2009. Dynamics of wood recruitment in streams of the northeastern US. Forest Ecology and Management 258:804–813.

Warren, D. R., W. S. Keeton, P. M. Kiffney, M. J. Kaylor, H. A. Bechtold, and J. Magee. 2016b. changing forests – changing streams: riparian forest stand development and ecosystem function in temperate headwaters. Ecosphere 7:1–19.

Warren, D. R., C. E. Kraft, W. S. Keeton, J. S. Nunery, and G. E. Likens. 2009. Dynamics of wood recruitment in streams of the northeastern US. Forest Ecology and Management 258:804–813.

Wetzel, R.G., and Westlake, D.F. 1969. Estimating quantity and quality of biomass - periphyton. *In* A manual on methods for measuring primary production in the aquatic environment. *Edited by* R.A. Voflenweider. Davis Co, Philadelphia. pp. 33–40.

White, S. M., C. Justice, D. A. Kelsey, D. A. McCullough, and T. Smith. 2017. Legacies of stream channel modification revealed using General Land Office surveys, with implications for water temperature and aquatic life. Elem Sci Anth 5(0):3.

Wilzbach, M. A., and J. D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. Verhandlungen International Verein Limnologie 22:2516–2522.

Wilzbach, M. A., B. C. Harvey, J. L. White, and R. J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:58–67.

Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Canadian Journal of Fisheries and Aquatic Sciences 62:2285–2293.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373–387.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 2004. Restoring productivity of salmon-based food webs : contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. Transactions of the American Fisheries Society 133:1440–1454.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, N. L. Mitchell, J. L. Lessard, R. A. Heintz, and D. T. Chaloner. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic levels in streamside experimental channels. Transactions of the American Fisheries Society 139:824–839.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Wollheim, W. M., S. Bernal, D. A. Burns, J. A. Czuba, C. T. Driscoll, A. T. Hansen, R. T. Hensley, J. D. Hosen, S. Inamdar, S. S. Kaushal, L. E. Koenig, Y. H. Lu, A. Marzahri, P. A. Raymond, D. Scott, R. J. Stewart, P. G. Vidon, and E. Wohl. 2018. River network saturation concept : factors influencing the balance of biogeochemical supply and demand of river networks. biogeochemistry.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7:e51839.

Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins, L. E. Stevens, S. Hueftle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. Ecological Modelling 183:157–172.

Young, K.A., Hinch, S.G., and Northcote, T.G. 1999. Status of resident Coastal Cutthroat Trout and their habitat twenty-five years after riparian logging. North Am. J. Fish. Manag. **19**: 901–911.

Young, M. K., E. A. Mace, E. T. Ziegler, and E. K. Sutherland. 2006. Characterizing and contrasting instream and riparian coarse wood in western Montana basins. Forest Ecology and Management 226:26–40.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85(3):795–806.

APPENDICES

Chapter 2

Table A2.1: Studies used in meta-analysis of riparian stand age versus canopy closure over the stream. Each study reported stand age and an estimate of canopy coverage. CO indicates streams from the Coast Range, U.S., while CA indicates studies from the Cascade Range, U.S.

Reference	Range	# of streams	Citation
Allen and Dent 2001	CO	6	Allen, M., and L. Dent. 2001. Shade Conditions Over Forested Streams in the Blue Mountain and Coast Range Georegions of Oregon. Oregon Department of Forestry technical report 13.
Banks et al. 2005	CO	13	Banks, J.L. 2005. Influences of clearcut logging on macroinvertebrates in perennial and intermittent headwaters of the central Oregon Coast Range. MS thesis. Oregon State University.
Frady et al. 2007	CA	6	Frady, C., S. Johnson, and J. Li. 2007. Stream macroinvertebrate community responses as legacies of forest harvest at the H.J. Andrews Experimental Forest, Oregon. Forest Science. 53: 281–293.
Murphy et al. 1981	CA	6	Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of Canopy Modification and Accumulated Sediment on Stream Communities. Transactions of the American Fisheries Society. 110: 469–478.
Hoover et al. 2011	CO	13	Hoover, T.M., Pinto, X., and Richardson, J.S. 2011. Riparian canopy type, management history, and successional stage control fluxes of plant litter to streams. Canadian Journal of Forest Research. 41: 1394–1404.
Kaylor, MJ (unpublished data)	CA	8	NA
Kibler 2007	CO	10	Kibler, K.M. 2007. The influence of contemporary forest harvesting on summer stream temperatures in headwater streams of Hinkle Creek, Oregon. MS thesis. Oregon State University.
Newton and Cole 2013	CO	4	Newton, M., and L. Cole. 2013. Stream Temperature and Streamside Cover 14 –17 Years after Clearcutting along Small Forested Streams, Western Oregon. Canadian Journal of Forest Research. 28: 107–115.
Summers 1982	CO & CA	17	Summers, R.P. 1982. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. MS thesis. Oregon State University.
Warren et al. 2013	CA	8	Warren, D.R., W.S. Keeton, H.A. Bechtold, and E.J. Rosi-Marshall. 2013. Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. Aquatic Sciences. 75: 547–558.

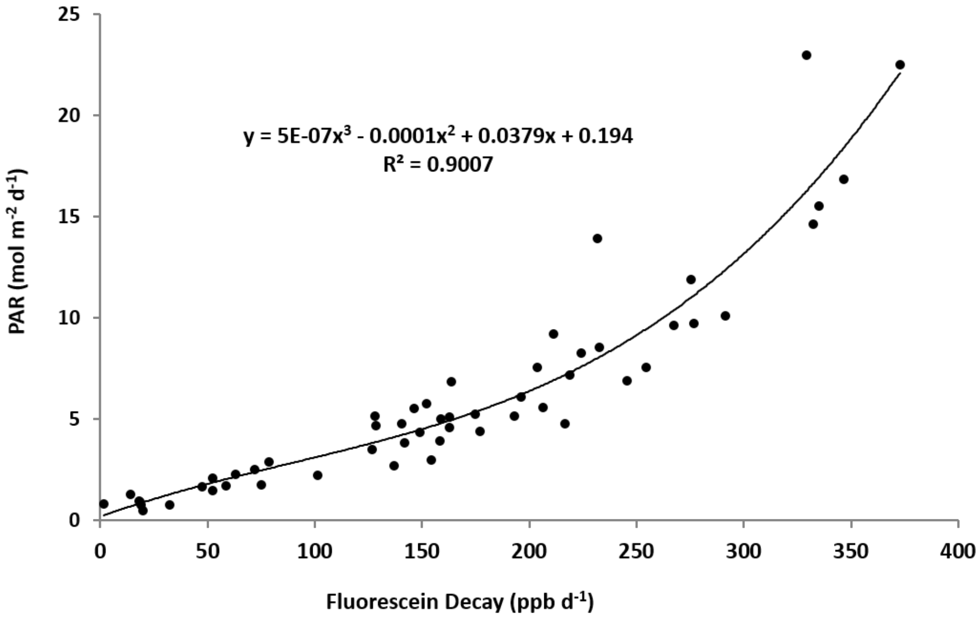


Figure 2A.1: Relationship between 24-h fluorescein decay and measured 24-h photosynthetically active radiation (PAR) (*n* = 58). The line is fitted with a 3-factor polynomial fit.

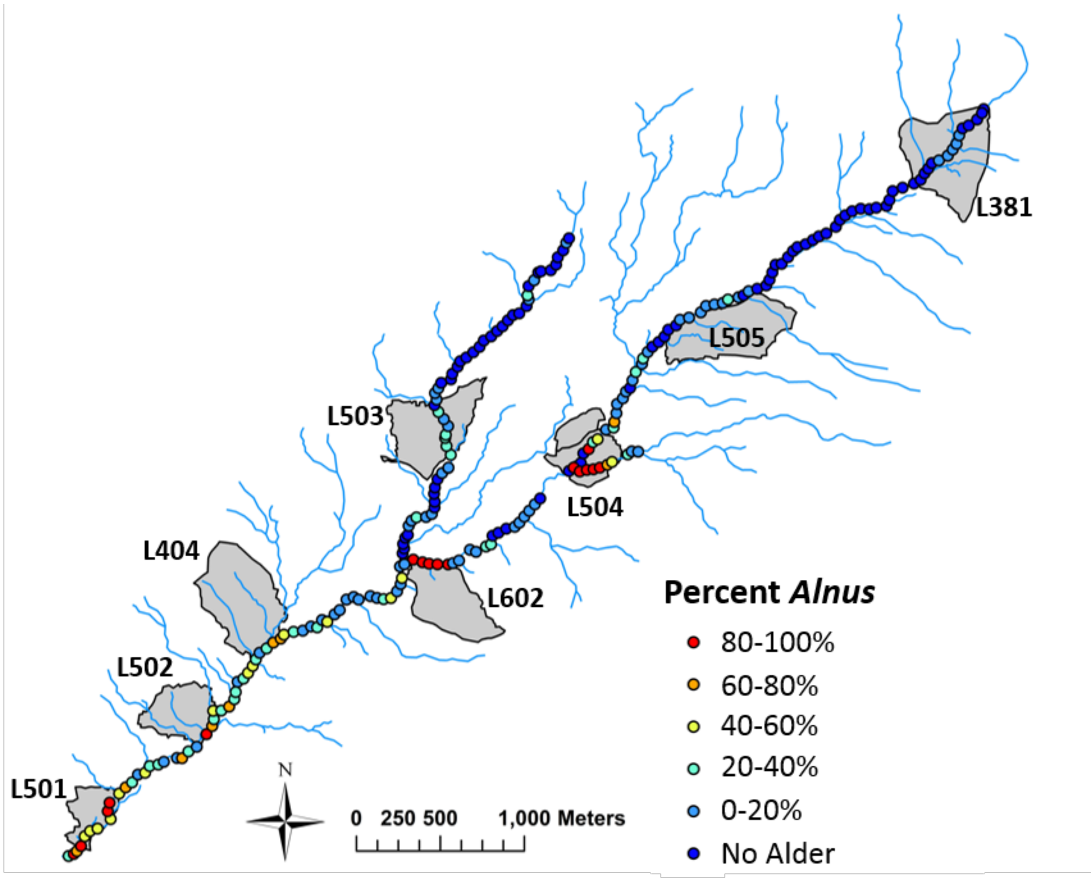


Figure 2A.2: Spatial distribution of red alder (*Alnus rubra*) in the McRae Creek network color-coded by % alder. Unit L381 was not surveyed for canopy cover or light because of logistical constraints.

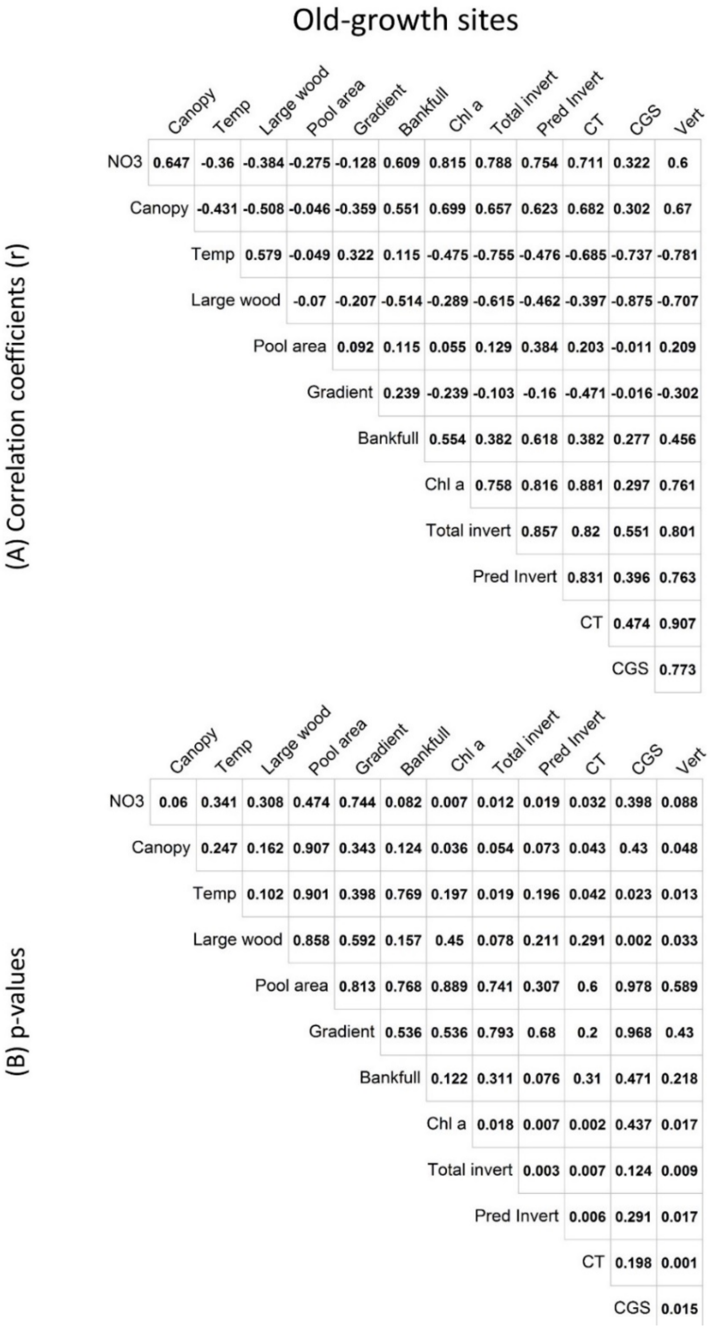
Chapter 3

Table A3.1: Rankings of a priori models relating covariates and the interaction with reach type to cutthroat trout biomass, salamander biomass, and total vertebrate biomass. Models in bold represent the plausible set of models within 7 AICc units of the highest ranked model.

Response variable	Rank	Model	DF	Loglik	AICc	ΔAICc	w_i
Cutthroat trout biomass	1	**Invert biomass*Reach type**	6	-21.975	63.6	0.0	0.956
	2	**Canopy*Reach type**	6	-25.248	70.1	6.5	0.036
	3	Temp*Reach type	6	-27.144	73.9	10.3	0.005
	4	NO_3*Reach type	6	-27.788	75.2	11.6	0.001
	5	Pool area*Reach type	6	-29.563	78.8	15.2	0.000
	6	Bankfull*Reach type	6	-30.920	81.5	17.9	0.000
	7	Gradient*Reach type	6	-30.923	81.5	17.9	0.000
	8	Large wood*Reach type	6	-31.788	83.2	19.6	0.000
Salamander biomass	1	**Temp*Reach type**	6	-27.559	74.8	0.0	0.999
	2	Invert biomass*Reach type	6	-35.251	90.1	15.4	0.000
	3	Canopy*Reach type	6	-36.189	92.0	17.3	0.000
	4	Large wood*Reach type	6	-38.937	97.5	22.8	0.000
	5	NO_3*Reach type	6	-39.471	98.6	23.8	0.000
	6	Bankfull*Reach type	6	-40.446	100.5	25.8	0.000
	7	Gradient*Reach type	6	-40.579	100.8	26.0	0.000
	8	Pool area*Reach type	6	-40.836	101.3	26.6	0.000
Total vertebrate biomass	1	**Canopy*Reach type**	6	-34.805	89.2	0.0	0.664
	2	**Invert biomass*Reach type**	6	-35.600	90.8	1.6	0.300
	3	**Temp*Reach type**	6	-37.717	95.1	5.8	0.036
	4	NO_3*Reach type	6	-44.424	108.5	19.2	0.000
	5	Large wood*Reach type	6	-45.445	110.5	21.3	0.000
	6	Bankfull*Reach type	6	-45.668	111.0	21.7	0.000
	7	Pool area*Reach type	6	-46.166	112.0	22.7	0.000
	8	Gradient*Reach type	6	-46.574	112.8	23.5	0.000

Table A3.2: Set of best approximating models (within 7 ΔAICc) for each response variable, and model coefficient estimates and associated p-values. β_1 is the coefficient for the habitat or productivity variable in the model (e.g. temp or canopy), β_2 is the coefficient for the reach type indicator variable (old-growth = 0, previously harvested = 1), and β_3 is the coefficient for the interaction between the habitat/productivity variable and reach type. The units for each response variable are g/m^2. The units for invertebrate biomass are g/m^2; the units for canopy openness are % open canopy; and the units for temperature are °C.

Response variable	Rank	Model	β_1 value	β_1 p-value	β_2 value	β_2 p-value	β_3 value	β_3 p-value
Cutthroat trout biomass	1	Invert biomass*Reach type	1.87	<0.001	0.86	0.395	-0.09	0.869
	2	Canopy*Reach type	0.13	0.002	1.45	0.096	-0.04	0.260
Salamander biomass	1	Temp*Reach type	-0.69	0.002	14.77	<0.001	-1.14	<0.001
Total vertebrate biomass	1	Canopy*Reach type	0.28	<0.001	2.44	0.029	-0.03	0.498
	2	Invert biomass*Reach type	1.32	0.074	-2.43	0.048	2.60	<0.001
	3	Temp*Reach type	-1.28	0.001	16.06	0.010	-1.19	0.017



Old-growth sites

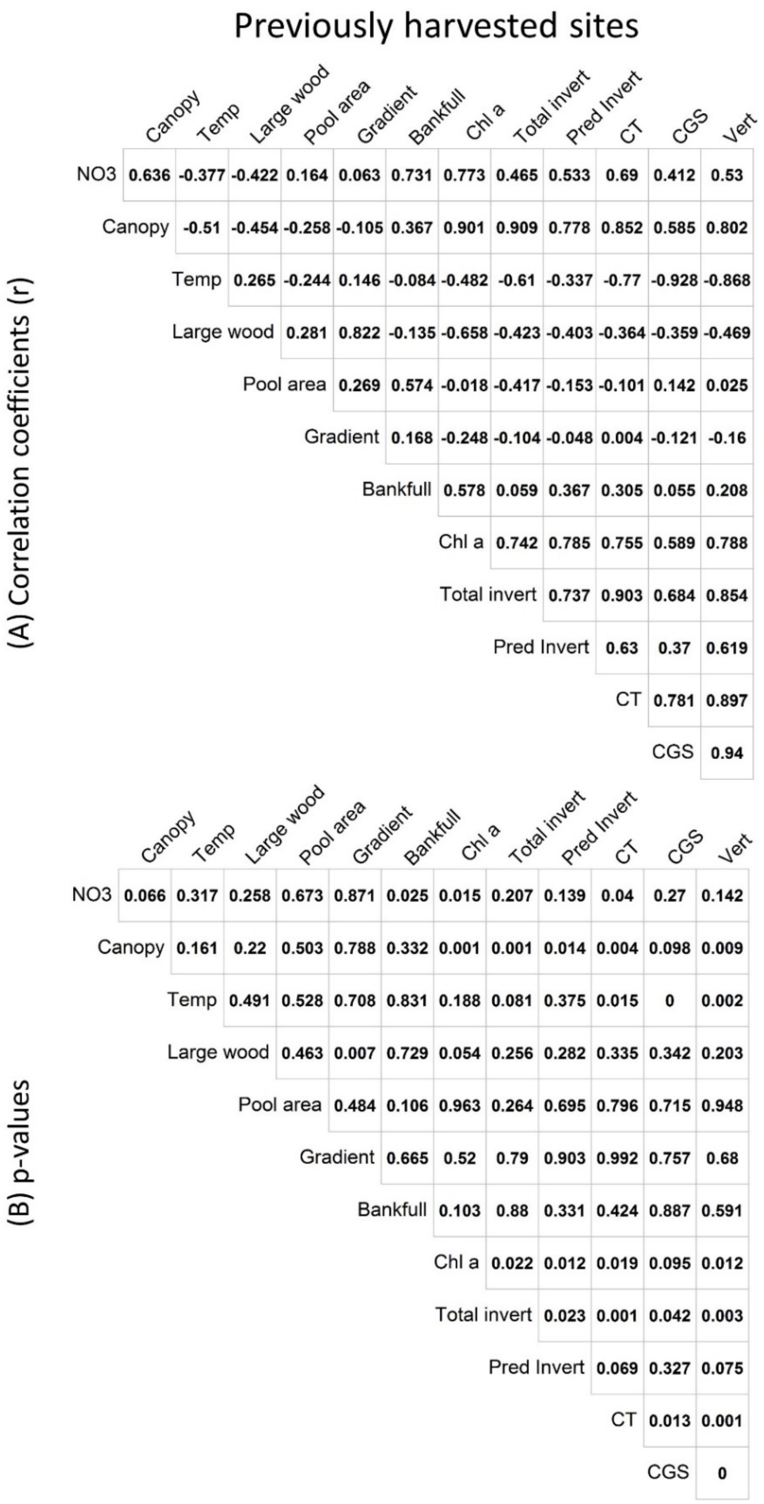
(A) Correlation coefficients (r)

	Canopy	Temp	Large wood	Pool area	Gradient	Bankfull	Chl a	Total invert	Pred Invert	CT	CGS	Vert
NO3	0.647	-0.36	-0.384	-0.275	-0.128	0.609	0.815	0.788	0.754	0.711	0.322	0.6
Canopy		-0.431	-0.508	-0.046	-0.359	0.551	0.699	0.657	0.623	0.682	0.302	0.67
Temp			0.579	-0.049	0.322	0.115	-0.475	-0.755	-0.476	-0.685	-0.737	-0.781
Large wood				-0.07	-0.207	-0.514	-0.289	-0.615	-0.462	-0.397	-0.875	-0.707
Pool area					0.092	0.115	0.055	0.129	0.384	0.203	-0.011	0.209
Gradient						0.239	-0.239	-0.103	-0.16	-0.471	-0.016	-0.302
Bankfull							0.554	0.382	0.618	0.382	0.277	0.456
Chl a								0.758	0.816	0.881	0.297	0.761
Total invert									0.857	0.82	0.551	0.801
Pred Invert										0.831	0.396	0.763
CT											0.474	0.907
CGS												0.773

(B) p-values

	Canopy	Temp	Large wood	Pool area	Gradient	Bankfull	Chl a	Total invert	Pred Invert	CT	CGS	Vert
NO3	0.06	0.341	0.308	0.474	0.744	0.082	0.007	0.012	0.019	0.032	0.398	0.088
Canopy		0.247	0.162	0.907	0.343	0.124	0.036	0.054	0.073	0.043	0.43	0.048
Temp			0.102	0.901	0.398	0.769	0.197	0.019	0.196	0.042	0.023	0.013
Large wood				0.858	0.592	0.157	0.45	0.078	0.211	0.291	0.002	0.033
Pool area					0.813	0.768	0.889	0.741	0.307	0.6	0.978	0.589
Gradient						0.536	0.536	0.793	0.68	0.2	0.968	0.43
Bankfull							0.122	0.311	0.076	0.31	0.471	0.218
Chl a								0.018	0.007	0.002	0.437	0.017
Total invert									0.003	0.007	0.124	0.009
Pred Invert										0.006	0.291	0.017
CT											0.198	0.001
CGS												0.015

Figure A3.1: Correlation matrix for old-growth sites portraying Pearson’s correlation coefficients (A) and associated p-values (B). For a description of each variable see Figure 3.3.



Previously harvested sites

(A) Correlation coefficients (r)

	Canopy	Temp	Large wood	Pool area	Gradient	Bankfull	Chl a	Total invert	Pred Invert	CT	CGS	Vert
NO3	0.636	-0.377	-0.422	0.164	0.063	0.731	0.773	0.465	0.533	0.69	0.412	0.53
Canopy		-0.51	-0.454	-0.258	-0.105	0.367	0.901	0.909	0.778	0.852	0.585	0.802
Temp			0.265	-0.244	0.146	-0.084	-0.482	-0.61	-0.337	-0.77	-0.928	-0.868
Large wood				0.281	0.822	-0.135	-0.658	-0.423	-0.403	-0.364	-0.359	-0.469
Pool area					0.269	0.574	-0.018	-0.417	-0.153	-0.101	0.142	0.025
Gradient						0.168	-0.248	-0.104	-0.048	0.004	-0.121	-0.16
Bankfull							0.578	0.059	0.367	0.305	0.055	0.208
Chl a								0.742	0.785	0.755	0.589	0.788
Total invert									0.737	0.903	0.684	0.854
Pred Invert										0.63	0.37	0.619
CT											0.781	0.897
CGS												0.94

(B) p-values

	Canopy	Temp	Large wood	Pool area	Gradient	Bankfull	Chl a	Total invert	Pred Invert	CT	CGS	Vert
NO3	0.066	0.317	0.258	0.673	0.871	0.025	0.015	0.207	0.139	0.04	0.27	0.142
Canopy		0.161	0.22	0.503	0.788	0.332	0.001	0.001	0.014	0.004	0.098	0.009
Temp			0.491	0.528	0.708	0.831	0.188	0.081	0.375	0.015	0	0.002
Large wood				0.463	0.007	0.729	0.054	0.256	0.282	0.335	0.342	0.203
Pool area					0.484	0.106	0.963	0.264	0.695	0.796	0.715	0.948
Gradient						0.665	0.52	0.79	0.903	0.992	0.757	0.68
Bankfull							0.103	0.88	0.331	0.424	0.887	0.591
Chl a								0.022	0.012	0.019	0.095	0.012
Total invert									0.023	0.001	0.042	0.003
Pred Invert										0.069	0.327	0.075
CT											0.013	0.001
CGS												0

Figure A3.2: Correlation matrix for previously harvested sites portraying Pearson's correlation coefficients (A) and associated p-values (B).

Reach pair differences (OG-PH)

(A) Correlation coefficients (r)

	Canopy	Temp	Large wood	Pool area	Gradient	Bankfull	Chl a	Total invert	Pred Invert	CT	CGS	Vert
NO3	-0.268	0.147	0.093	-0.575	-0.253	0.002	0.485	0.261	0.642	0.062	-0.196	-0.098
Canopy		-0.059	-0.047	-0.229	0.051	0.406	0.339	0.552	0.236	0.53	0.79	0.917
Temp			0.476	0.291	0.56	0.632	-0.275	-0.355	-0.183	0.099	0.226	0.113
Large wood				0.475	0.378	0.101	0.031	-0.282	-0.193	0.32	-0.106	-0.006
Pool area					0.283	-0.191	-0.584	-0.477	-0.591	0.108	-0.226	-0.247
Gradient						0.634	0.106	-0.138	-0.12	0.338	0.074	0.097
Bankfull							0.115	0.065	-0.031	0.226	0.663	0.573
Chl a								0.677	0.793	0.638	-0.03	0.305
Total invert									0.839	0.615	0.387	0.64
Pred Invert										0.542	0.023	0.306
CT											0.189	0.548
CGS												0.911

(B) p-values

	Canopy	Temp	Large woo	Pool area	Gradient	Bankfull	Chl a	Total inver	Pred Inver	CT	CGS	Vert
NO3	0.485	0.705	0.811	0.105	0.511	0.995	0.186	0.497	0.062	0.874	0.614	0.802
Canopy		0.88	0.904	0.554	0.897	0.278	0.372	0.123	0.542	0.142	0.011	0
Temp			0.196	0.448	0.117	0.068	0.473	0.349	0.637	0.8	0.558	0.773
Large wood				0.196	0.315	0.796	0.936	0.463	0.62	0.401	0.785	0.988
Pool area					0.461	0.623	0.099	0.194	0.094	0.782	0.559	0.522
Gradient						0.067	0.787	0.723	0.758	0.374	0.849	0.804
Bankfull							0.767	0.868	0.937	0.558	0.052	0.107
Chl a								0.045	0.011	0.064	0.939	0.425
Total invert									0.005	0.078	0.304	0.063
Pred Invert										0.132	0.952	0.423
CT											0.626	0.127
CGS												0.001

Figure A3.3: Correlation matrix for reach pair differences (OG-PH) portraying Pearson's correlation coefficients (A) and associated p-values (B).

Chapter 4

4A

Table A4.1: Salamander biomass and canopy openness in previously harvested and old-growth reaches in 2014. Salamander biomass includes 95% confidence intervals on population estimates in parentheses.

Site	Riparian type	Salamander biomass ($g\ m^{-2}$)	Canopy openness (%)
LO703	OG	9.82 (5.79-13.96)	34.0
	PH	14.95 (7.41-22.48)	53.8
Mack	OG	6.91 (6.22-7.59)	23.9
	PH	7.95 (7.06-8.84)	32.2
LO701	OG	10.58 (1.46-19.70)	20.2
	PH	12.86 (3.95-21.78)	10.5
Cook	OG	8.09 (5.14-11.05)	23.8
	PH	4.41 (2.81-6.02)	4.8
MR404	OG	5.87 (2.04-9.71)	29.0
	PH	6.69 (3.55-9.83)	32.7

Table A4.2: Description of reach locations.

Site	Riparian type	Site Location Description
LO703	OG	Upstream end 10 m downstream of cold creek and downstream end 70 m upstream of L703 cut break.
	PH	Upstream end 90 m downstream of L703 cut break. Downstream end located 5 m upstream of channel braid.
Mack	OG	Contact S.V. Gregory for reach information.
	PH	Contact S.V. Gregory for reach information.
LO701	OG	Downstream end of reach located 75 m upstream of L701 cut break.
	PH	Upstream end of reach located 175 m downstream of L701 cut break.
Cook	OG	Downstream end of reach approximately 200 m upstream of cut break.
	PH	Upstream end of reach located approximately 100 m downstream of cut break.
MR404	OG	Downstream end of reach located approximately 80 m upstream of L404 cut break.
	PH	Upstream end of reach located approximately 110 m downstream of L404 cut break.

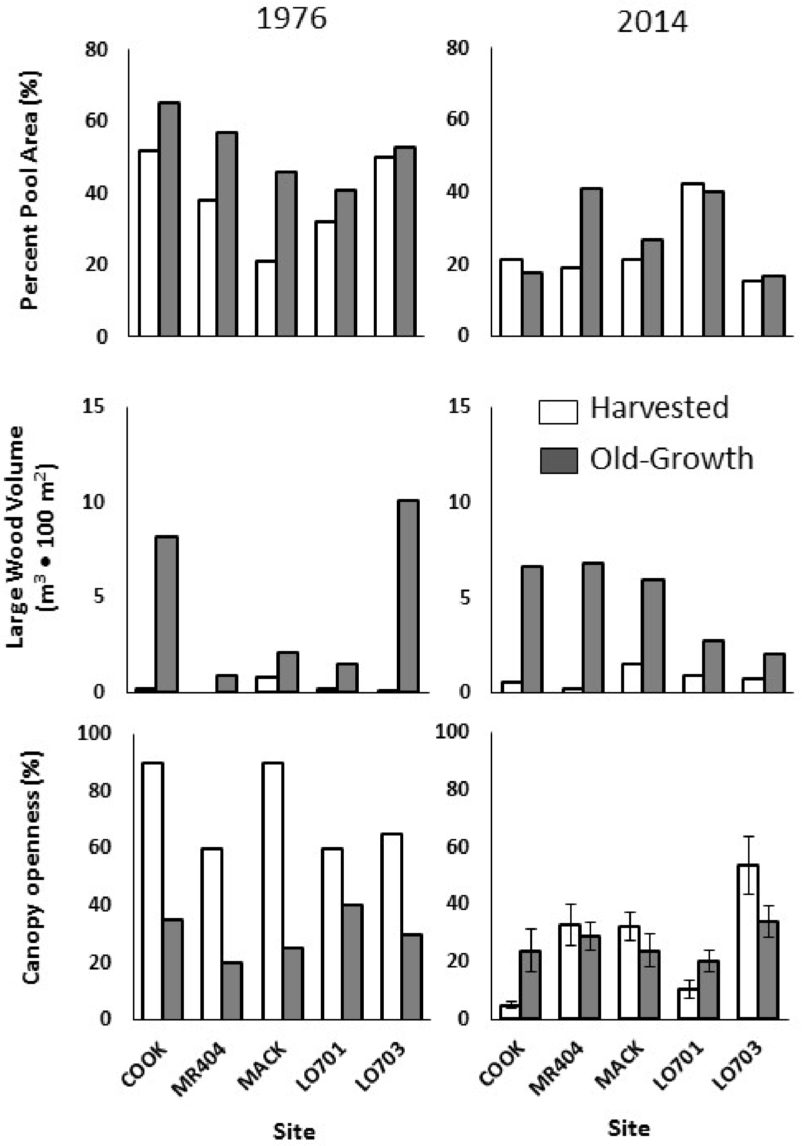


Figure A4.1: Percent pool area, large wood volume and canopy openness in 1976 (left) and 2014 (right). Unshaded bars represent reaches within harvested riparian forest and shaded bars are within the upstream old-growth reference. 2014 canopy openness is shown with 95% confidence intervals of the estimated mean.

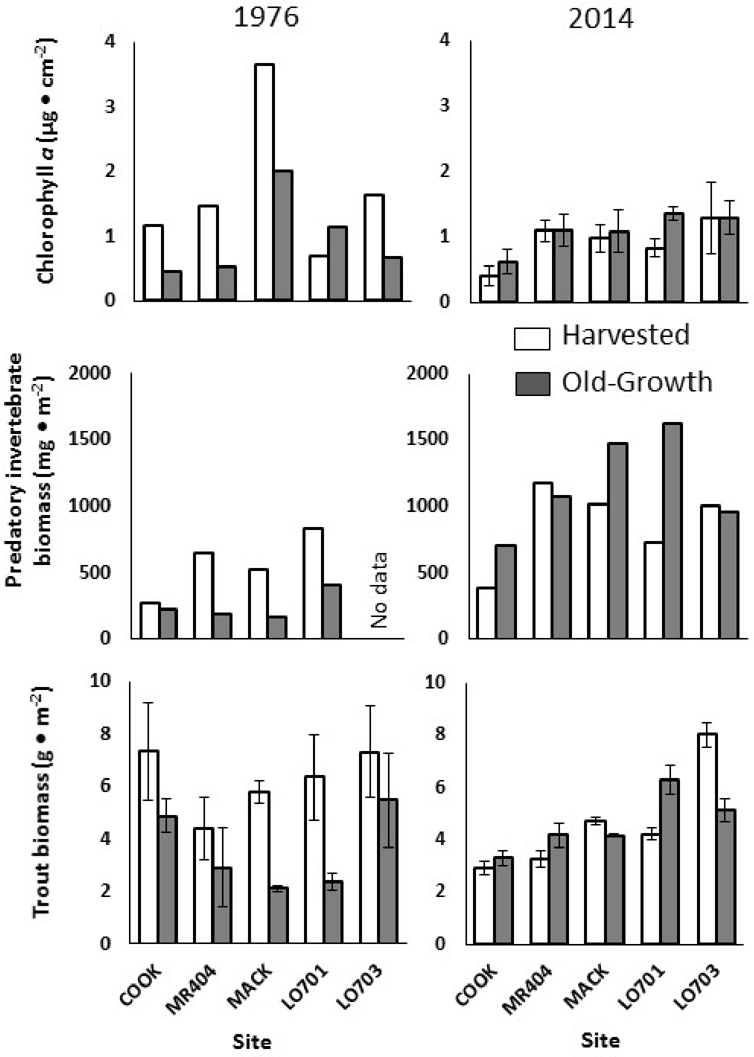


Figure A4.2: Chlorophyll a, predatory invertebrate biomass, and trout biomass in 1976 (left) and 2014 (right). Unshaded bars represent reaches within harvested riparian forest, and shaded bars are within the upstream old-growth reference. Error bars for chl a, and trout biomass are 95% confidence intervals.

4B

Explanations of alternative trajectories of resident salmonid populations following timber harvest

Scenario 1: a short-term positive response (increased biomass) to harvesting associated with greater light and primary production. In this scenario, habitat is minimally effected, temperature increases are minimal or temperature remains relatively low, primary producers are light-limited (at least for part of the year), and invertebrates and resident salmonids are food-limited. Biomass decreases as canopies close and biomass eventually reaches levels below reference conditions because canopy openness (and understory light) is at a minimum in regenerated, second-growth forests (Donato et al. 2012; Kaylor et al. 2017). As stands age and canopy gaps form, biomass slightly increases back to reference (old-growth) levels. This is based on results from this study (Figure 4.2), previous studies that document positive resident salmonid responses to harvest (Aho 1976; Murphy and Hall 1981; Hawkins et al. 1983; Bilby and Bisson 1992; Wootton 2012), and previous conceptual diagrams predicting this trend (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009).

Scenario 2: a short-term positive response that is smaller in magnitude and shorter in duration than that of Scenario 1. This could reflect the effect of increased light associated with harvesting outside of riparian buffers (Kiffney et al. 2003). Because changes in light are relatively small compared with historical clear-cutting, the potential effect size is smaller. Increased stream light may be shorter in duration due to regrowth outside the riparian buffer or to increased branch and understory shrub growth within riparian buffers due to increased light. The same conditions apply as in Scenario 1 — minimal habitat effects and light limitation of primary production.

Scenario 3: the resident salmonid response to harvest is minimal with no clear directionality or long-term population trend (inter-annual variation excluded). Relatively small, short-term responses were observed in Deer Creek in the Alsea Watershed in which only partial harvest occurred (Gregory et al. 2008) and in a section of East Creek (section B), British Columbia, where clear-cut harvesting occurred but large wood and logging debris were left in the stream (Young et al. 1999). Conditions leading to this scenario may include streams where primary production is limited by other factors (e.g., nutrients), increases in light and primary production are too small to result in an observable invertebrate response, or increased primary production is accumulated by inedible herbivores, which prevents energy flow to higher trophic levels (Power and Dietrich 2002; Power et al. 2013). There are numerous examples of light limitation within heavily forested streams (Gregory 1980; Bilby and Bisson 1992; Ambrose et al. 2004; Warren et al. 2017), but in nutrient-poor, oligotrophic streams, limitation of primary production may only occur at very low light levels. For example, Warren et al. (2017) found that in a stream with low summer nutrient concentrations (~5 μg L^{-1}), the light threshold at which limitation switched from light to nutrient limitation was estimated at just 8% of full-sun values.

Scenario 4: there is a short-term negative response (decreased biomass) but a relatively quick recovery. In this scenario, short-term negative responses could be attributed to temperatures exceeding thermal maximums but then recovering as shrubs and trees shade the stream, excess sedimentation that is reduced after vegetative regrowth, altered habitat conditions that are modified by habitat improvement projects, or a combination of these (potentially East Creek, section A; Young et al. 1999). In these streams, major changes to structural habitat (large wood, pools, pool complexity) remain minimally affected. When temperatures or sedimentation rates reduce to preharvest levels or substantially reduce, resident salmonid biomass may return to preharvest levels if light has minimal influence on stream production. Alternatively, but not shown, resident salmonids may increase to levels greater than preharvest if increased light promotes increased primary production after temperatures or sedimentation rates are restored.

Scenario 5: there is a negative response that is sustained over the long term with slow recovery in the absence of management actions. Negative responses are attributed to habitat degradation associated with loss of large wood and pool habitat. Wood inputs to streams, especially large diameter wood, are extremely low following riparian removal and recover slowly as riparian stands develop (Gregory et al. 2003). Full recovery in this scenario could take centuries and would be a high priority for habitat enhancement projects such as large wood addition. In these systems, resident salmonid populations are more strongly habitat-limited, and increased prey availability, if any, is outweighed by the effects of habitat degradation.

Scenario 6: harvesting operations, loss of wood, and intensified debris flows may result in the loss of stream substrates that would take centuries or millenniums to recover. In this “state change”, habitat may remain highly degraded and show little sign of recovery over the time frame portrayed in Figure 4.4. Scour and the loss of substrates associated with historical splash dams may result in this trajectory. As with Scenario 5, these streams would be high priorities for habitat enhancement projects.

Appendix 4B: Literature cited

Aho, R.S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. Oregon State University. Available from https://ir.library.oregonstate.edu/xmlui/handle/1957/21777.

Ambrose, H.E., Wilzbach, M.A., and Cummins, K.W. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. North Am. Benthol. Soc. **23**(4): 701–712. doi:doi/10.1899/0887-3593(2004)023<0701:PRTILA>2.0.CO;2.

Bilby, R.E., and Bisson, P.A. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. **49**: 540–551. doi:10.1139/f92-064.

Donato, D.C., Campbell, J.L., and Franklin, J.F. 2012. Multiple successional pathways and precocity in forest development: Can some forests be born complex? J. Veg. Sci. **23**(3): 576–584. doi:10.1111/j.1654-1103.2011.01362.x.

Gregory, S., Meleason, M., and Sobota, D. 2003. Modeling the dynamics of wood in streams and rivers. Am. Fish. Soc. Symp. **37**: 315–335.

Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. Oregon State University. Available from http://ir.library.oregonstate.edu/xmlui/handle/1957/17914.

Gregory, S. V., Lamberti, G.A., Erman, D.C., Koski, K. V., Murphy, M.L., and Sedell, J.R. 1987. Influences of forest practices on aquatic production. *In* Streamside Management: Forestry and Fishery Interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Institute of Forest Resources, Seattle, Washington. pp. 233–255.

Gregory, S. V, Schwartz, J.S., Hall, J.D., Wildman, R.C., and Bisson, P.A. 2008. Long-term trends in habitat and fish populations in the Alsea Basin. *In* Hydrological and Biological Responses to Forest Practices. *Edited by* J.D. Stednick. Springer. pp. 237–257. Available from http://www.springerlink.com/index/G011704122L53704.pdf.

Hawkins, C.P., Murphy, M.L., Anderson, N., and Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Can. J. Fish. Aquat. Sci. **40**(8): 1173–1185. doi:10.1139/f83-134.

Kaylor, M.J., Warren, D.R., and Kiffney, P.M. 2017. Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams. Freshw. Sci. **36**(1). doi:10.1086/690624.

Kiffney, P.M., Richardson, J.S., and Bull, J.P. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. J. Appl. Ecol. **40**(6): 1060–1076. doi:10.1111/j.1365-2664.2003.00855.x.

Mellina, E., and Hinch, S.G. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Can. J. For. Res. **39**(7): 1280–1301. doi:10.1139/X09-037.

Murphy, M.L., and Hall, J.D. 1981. Vaired effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. **38**: 137–145. doi:10.1139/f81-018.

Power, M.E., and Dietrich, W.E. 2002. Food webs in river networks. Ecol. Res. **17**: 451–471.

Power, M.E., Holomuzki, J.R., and Lowe, R.L. 2013. Food webs in Mediterranean rivers. Hydrobiologia **719**(1): 119–136. doi:10.1007/s10750-013-1510-0.

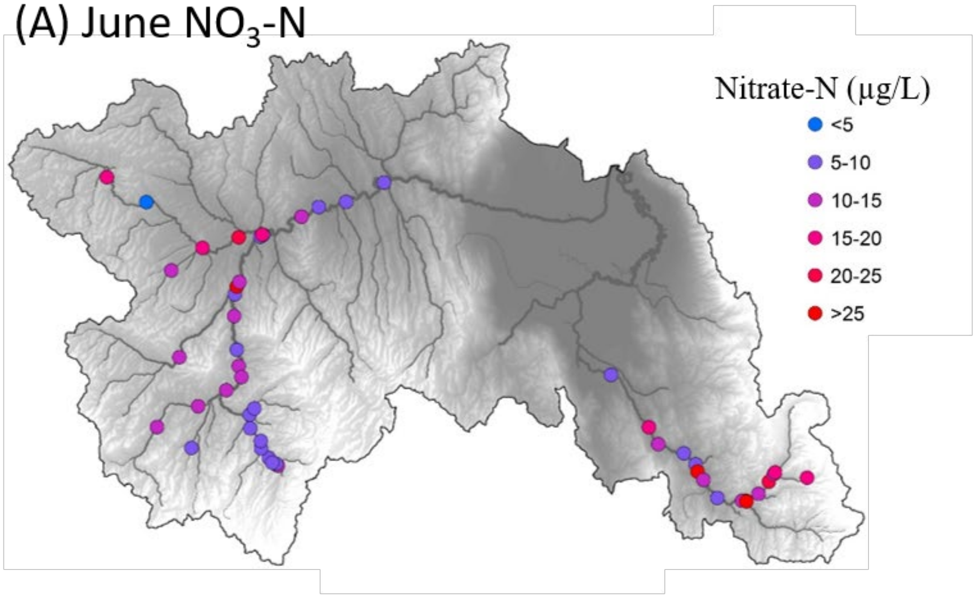
Sedell, J.R., and Swanson, F.J. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. *In* Fish and Wwldlife relationships in old-growth forests. *Edited by* W.R. Meehan, T.R. Merrell, and T.A. Hanley. Juneau, Alaska. pp. 9–16.

Warren, D.R., Collins, S.M., Purvis, E.M., Kaylor, M.J., and Bechtold, H.A. 2016. Spatial variability in light yields co-limitation of primary production by both light and nutrients in a forested stream ecosystem. Ecosystems. Springer US. doi:10.1007/s10021-016-0024-9.

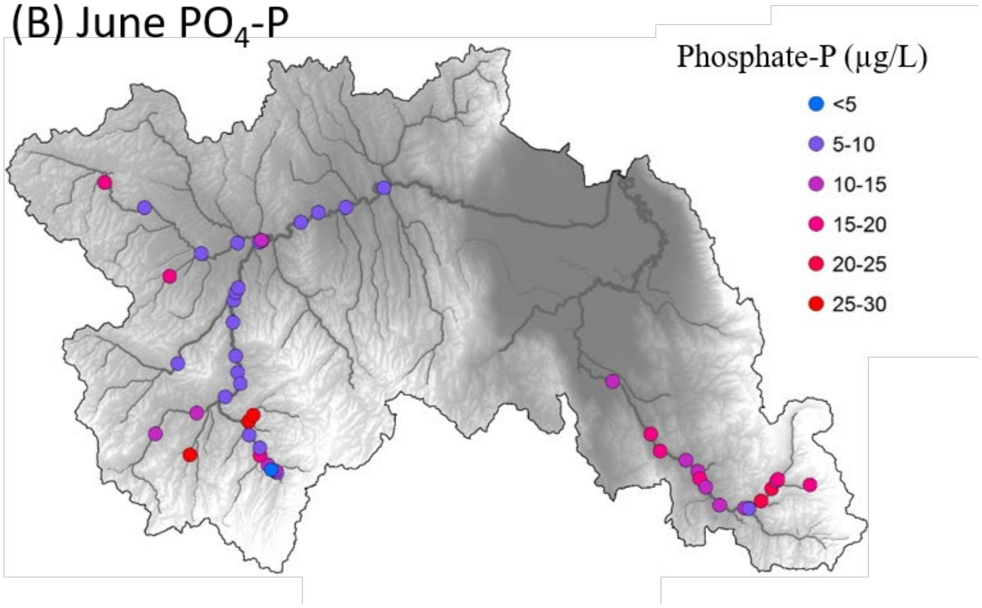
Wootton, J.T. 2012. River food web response to large-scale riparian zone manipulations. PLoS One **7**(12): 1–9. doi:10.1371/journal.pone.0051839.

Young, K.A., Hinch, S.G., and Northcote, T.G. 1999. Status of resident Coastal Cutthroat Trout and their habitat twenty-five years after riparian logging. North Am. J. Fish. Manag. **19**: 901–911. doi:10.1577/1548-8675(1999)019<0901:SORCCT>2.0.CO;2.

Chapter 5



(A) June NO_3-N



(B) June PO_4-P

Figure A5.1: Nitrate-N (A) and phosphate-P (B) concentrations sampled in June in the upper Grande Ronde River and Catherine Creek.

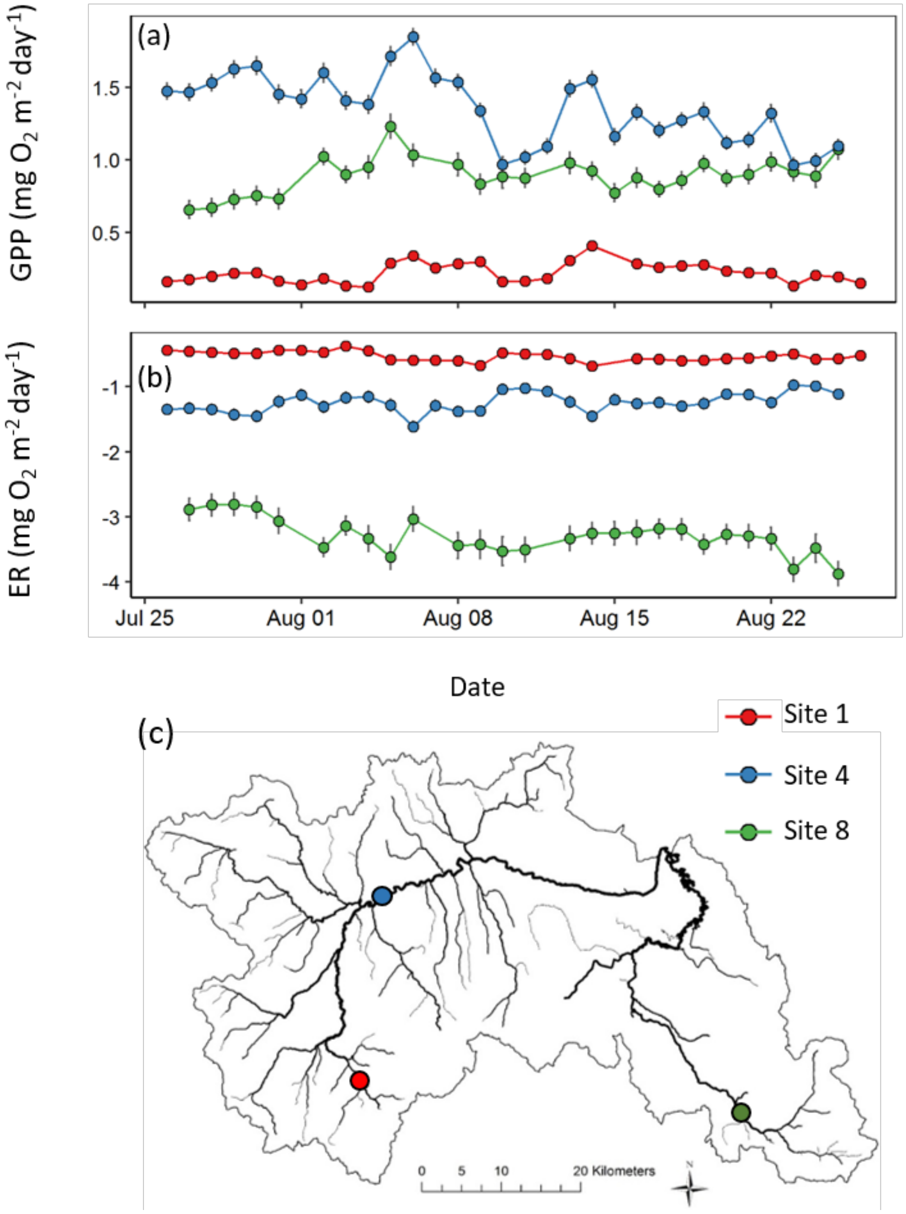
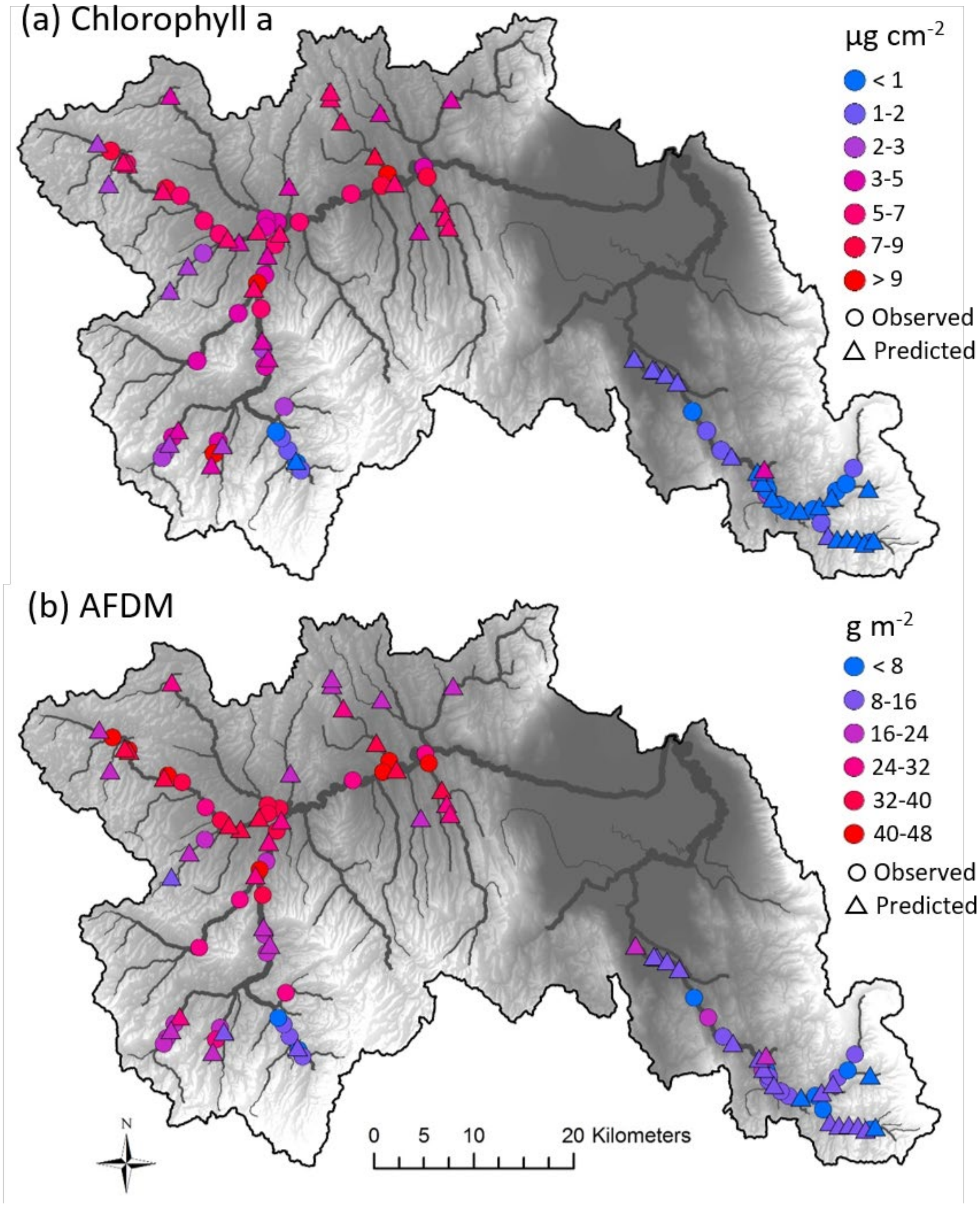


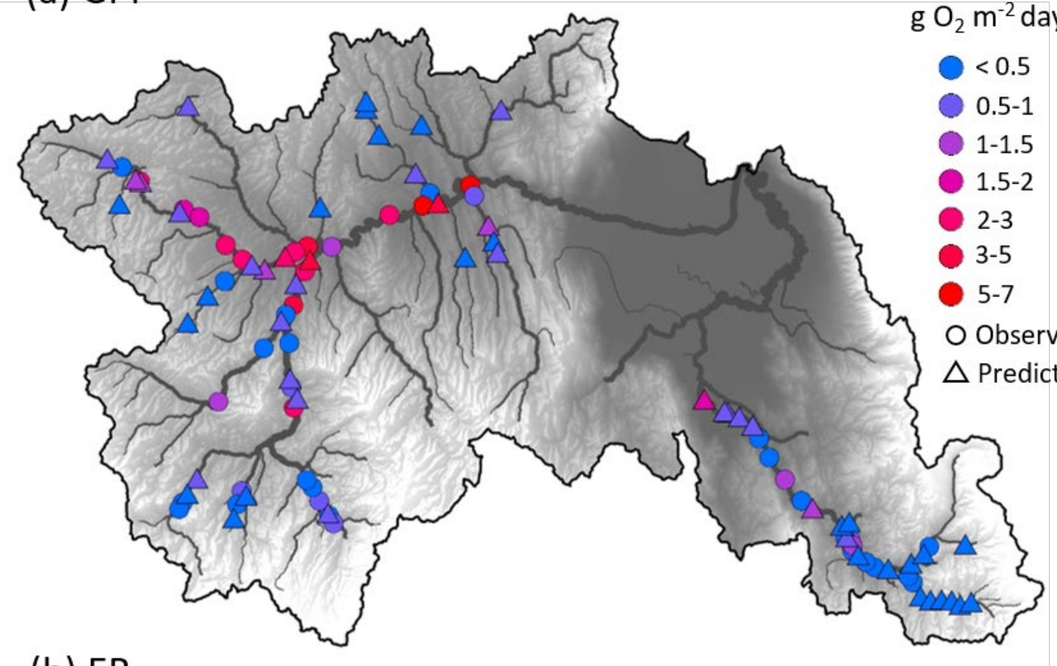
Figure A5.2: Gross primary production (a) and ecosystem respiration (b) at 3 sites — two in UGR and one in CC (c) — where metabolism was measured over longer intervals to evaluate any potential temporal changes during the deployment of sensors at other sites.


(a) Chlorophyll a

(b) AFDM

Figure A5.3: Chlorophyll *a* (A) and ash-free dry mass (B) at observed (circles) and predicted (triangles) locations. The model used to predict Chl *a* was model 1 in Table 5.1. The model used to predict AFDM was model 1 in Table 5.1.

(a) GPP



(b) ER

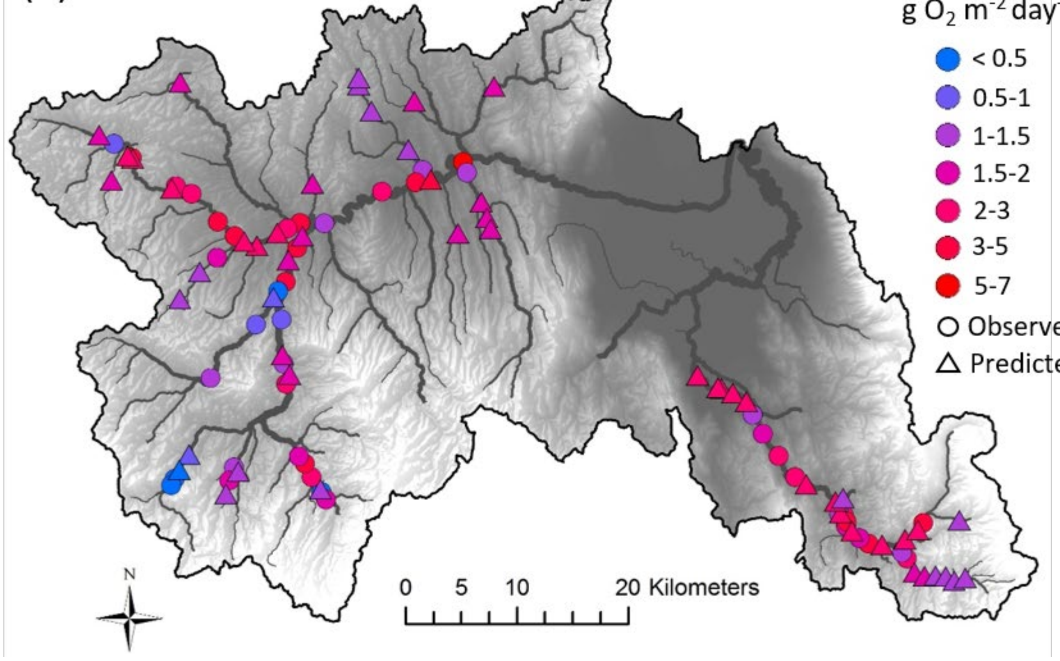


Figure A5.4: Gross primary production (A) and ecosystem respiration (B) sampled at observed locations (circles) and predicted at unsampled locations (triangles). The model used to predict GPP was model 1 in Table 5.1. The model used to predict AFDM was model 2 in Table 5.1. Model 1 was not used because phosphate-P concentrations were not available at all prediction sites.

Chapter 6

Table A6.1: Estimated densities (fish m^{-2}) of O. mykiss and Chinook approximately two weeks before carcass addition and approximately two weeks after carcass addition in each of the study reaches.

Pair	Treatment	O. mykiss		Chinook	
		Before	During	Before	During
Pair 1	Control	0.19	0.31	1.16	1.84
	Treatment	0.10	0.26	0.59	0.80
Pair 2	Control	0.07	0.08	0.11	0.22
	Treatment	0.36	0.27	0.22	0.34
Pair 3	Control	0.02	0.05	0.02	0.02
	Treatment	0.03	0.10	0.00	0.01

Table A6.2: Number of recaptured individuals of each salmonid species at each sampling event. An individual was only considered a recapture if it was measured during the most recent previous sampling event.

Pair	**Treatment**	**Species**	**Event 2**	**Event 3**	**Event 4**	**Event 5**	**Event 6**
Pair 1	Control	O. mykiss	4	8	4	7	6
	Treatment	O. mykiss	6	9	10	9	7
	Control	Chinook				36	7
	Treatment	Chinook				55	20
Pair 2	Control	O. mykiss	11	12	9	7	
	Treatment	O. mykiss	15	7	6	7	
	Control	Chinook			70	15	
	Treatment	Chinook			23	18	
Pair 3	Control	O. mykiss	3	3	5	12	1
	Treatment	O. mykiss	3	10	9	5	5