AN ABSTRACT OF THE THESIS OF

Emily Heaston for the degree of Master of Science in Forest Ecosystems and Society presented on August 9, 2017.

Title: Aquatic Food Web Responses to Patchy Shading Along Forested Headwater Streams

Abstract approved: ____

Dana Warren

In small forested streams, changes in age and structure of riparian vegetation covering the stream have been shown to directly influence the amount of light reaching the stream benthos. Light has the potential to impact in-stream resources that support secondary production through constraints on primary productivity. The influence of landscape changes in riparian vegetation cover and their effect on in-stream light has been evaluated; however smaller, patchy changes of in-stream light have yet to be thoroughly explored. We worked to clarify the role of light as a bottom-up driver of in-stream food webs in the western Cascade Mountain range streams, in Oregon, through exploring how decreased light availability, via patchy shading, affected in-stream biota. With patchy decreases in the amount of light reaching the stream benthos we expected to see a reduction in the growth of in-stream autotrophs through the summer and subsequently a decrease in macroinvertebrates, cutthroat trout (*Oncorhynchus clarkii clarkii*) and salamanders as a result of decreasing resource availability in the manipulated reaches. We established three sets of paired stream reaches and experimentally manipulated light in one reach from each pair by adding patches of shade. We then evaluated how periphyton, invertebrates, fish, and total vertebrate predators responded in the manipulated reach relative to the unmanipulated reference reach in a before-after control-impact (BACI) study design. Our patchy shading manipulation significantly decreased light, causing a decrease in algal biomass and subsequently invertebrate, fish, and salamander biomass. Local decreases in light fluxes to forested headwater streams along a larger reach decreased biota throughout the aquatic food-web. This trend was consistent in streams bordered by both second-growth and old-growth forests. This research indicates that smaller changes in riparian forest structure which impact in-stream light, such as those that occur in forests develop processes, can impact in-stream biota.

Aquatic Food Web Responses to Patchy Shading Along Forested Headwater Streams

by

Emily Heaston

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Master of Science

Presented August 9, 2017

Commencement June 2018

Master of Science thesis of Emily Heaston presented on August 9, 2017

APPROVED:

Major Professor, representing Forest Ecosystems and Society

Head of the Department Forest Ecosystems and Society

Dean of the Graduate School

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

Emily Heaston, Author

ACKNOWLEDGEMENTS

I would like to thank my committee, Dana Warren (Forest Ecosystems & Society), Lisa Ganio (Forest Ecosystems & Society), Jonathan Armstrong (Fisheries & Wildlife), and Dan Edge (College Agricultural Sciences) for their support, time, and guidance through the process of competing my thesis. I appreciate Lisa's support with my statistical analyses and her time to help me improve my methods. Further, many thanks to Dana Warren's role as my advisor. Dana was very generous with his time and I am very appreciative of his supportive nature, mentorship, and endless supply of well-timed dad jokes. Through culturing an enjoyable, open, and multi-disciplinary learning environment, he helped to expand my understanding of the meaning of my work and develop a greater appreciation for the power of laughter.

Many thanks to the HJ Andrews Experimental Forest for funding a portion of my time and research efforts for this thesis and my degree. We conducted this research at HJ Andrews Experimental Forest, which is funded by the US Forest Service, Pacific Northwest Research Station. Data and facilities were provided by the HJ 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.

A would also like to thank my lab mates, Matt Kaylor and Allison Swartz for their friendship and encouragement. They were both amazing sounding boards and I will miss discussing science, philosophy, and our research projects over beer with you two. Without the intrepid efforts of Brian Verway and Kate Pospisil, I would not have completed my fieldwork and data collection.

Lastly, I would like to give a special thank you my husband and family for their unyielding emotional and physical support throughout my thesis project. Whether it was an extra set of hands to help with fieldwork, encouraging me when I didn't think I could continue on, or giving me just the comical relief that I needed, they were always there for me when I needed them. My husband graciously listened to me talk about my research and engaged in conversations about the biotic, chemical, and physical properties of forests, streams, and fish with me. I am so very thankful to have your support through all the difficult and complicated instances life throws at us.

CONTRIBUTIONS OF AUTHORS

Emily Heaston and Dana Warren convened and designed the experiments. Emily Heaston collected data with much help 2016 field crew members. Data analysis and interpretation was conducted by Emily Heaston with input and help from Dana Warren and Lisa Ganio.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Table Page

Introduction

Forested stream ecosystems are directly and indirectly influenced by plant communities in the riparian zone. Riparian vegetation impacts basal resources of stream food webs through the direct input of externally derived carbon subsidies (allochthonous carbon), and indirectly through controls on light availability that can influence in-stream benthic primary productivity (autochthonous carbon). While forested streams are generally net heterotrophic, with most of the available carbon coming from outside the system (Battin et al. 2008, Hall et al. 2016, Hoellein et al. 2016), allochthonous carbon in forested headwaters is often lower in quality relative to stream diatoms and other benthic primary producers (Tranvik 1992, Cross et al. 2005, Jaffé et al. 2008). Therefore, when considering resources that support secondary production, autochthonous carbon can be a disproportionately important food source for consumers (Mayer and Likens 1987, McCutchan and Lewis 2002, Brett et al. 2009, Guo et al. 2016). Given the importance of in-stream primary production, factors that affect stream autotrophy provide potentially import controls on bottom-up drivers of the larger stream food web. In this study, we explored how decreased light availability via patchy shading affected benthic algal biomass, macroinvertebrate biomass, macroinvertebrate communities, and the biomass of trout and salamanders.

Light is a primary abiotic constraint on algal growth in small, forested streams (Boston and Hill 1991, Hill et al. 1995, Julian et al. 2008). Experimental studies removing all riparian vegetation have clearly demonstrated the importance of riparian shading and light availability on stream primary production, with implications for bottom-up drivers of fish abundance (Noel et al. 1986, Wilzbach et al. 2005, Wootton 2012). While riparian clearing and controlled stream channel studies have shown the importance of light, those experimental manipulations do not necessarily reflect natural light environments in forested stream systems, or further, the more moderate changes in stream light availability that are likely to occur with natural stand development processes of the riparian forest

(Warren et al. 2016). Indeed, the wholesale loss or removals of riparian forests along an entire stream is uncommon with today's forest management regulations, but more moderate changes in the canopy may become increasingly common. For example, invasive pests that kill riparian trees, and stand development dynamics in riparian forests are expected to change light availability reaching the stream by creating a more patchy, heterogeneous, light environment. (Kiffney et al. 2003) manipulated riparian buffer widths yielding a range of in-stream light responses. Reaches with larger buffers had less light reaching the stream, resulting in lower periphyton accumulation, and the reaches with smaller riparian buffers had more light reaching the stream, resulting in larger amounts of periphyton accumulation (Kiffney et al. 2003). In experimental channels that allow for the isolation of light as the only modified variable, altering levels of photosynthetically-active radiation (PAR) reaching the stream benthos had clear and dramatic influences on benthic primary productivity (Kiffney et al. 2004, Matheson et al. 2012).

Shading studies in experimental stream channels have demonstrated the importance of light for primary production (Quinn et al. 1997, Matheson et al. 2012), however, *in-situ* studies assessing stream shading impacts on stream primary production or biota are less common. Natural and anthropogenic events can directly impact the amount of light reaching the stream benthos in forested headwaters. These events can not only increase light, but they can also dramatically decrease light flux in a forested stream and thereby directly influence the primary productivity. In British Columbia, Canada, one study covered a 5 meter riffle section with shade cloth in two replicate streams and found that shading these small sections resulted in no difference in periphyton standing stock chlorophyll-*a* concentrations, but there was a significant decline in gross primary production (GPP) in manipulated sites relative to control sites (Gjerløv and Richardson 2010). That research demonstrated the possible link between modification of local light conditions and in-stream primary production, but it did not assess impacts of their effect on higher trophic levels in the food web, as effects of increased GPP can manifest in macroinvertebrate consumers even if no change is observed in standing stocks due to increased grazing pressure that compensates for increased production (Kiffney et al. 2003).

When whole food web responses are considered, changes in light may manifest through all trophic levels (Wootton 2012), or they may appear only in a consumer due to top-down controls masking initial effects on lower trophic levels (Kiffney et al. 2003). With increasing in-stream light due to riparian forest loss, top stream consumer biomass frequently increases along with in-stream GPP. A meta-analysis of the effects of riparian forest harvest and stream cleaning (removal of large wood) on salmonid juveniles, found a positive response in fish biomass and densities after logging, even with a decrease in abundance of large wood and pool area (Mellina and Hinch 2009). Average fry biomass was also found to increase more than average juvenile biomass, also the magnitudes of these responses were independent of stream size, gradient, and time since logging (Mellina and Hinch 2009). A recent review of the response of fish to a variety of riparian changes (including forest harvest, livestock grazing, and restoration efforts) found inconsistent responses of trout populations, with riparian afforestation, which increases canopy cover, having the strongest negative effect on fish populations (Sievers et al. 2017). Wootton (2012) found that logging only one side of a forested stream resulted in a 40% decrease in canopy cover. This decrease in canopy cover subsequently caused a 42-fold increase in light reaching the stream benthos. With this large increase of in-stream light availability, algal production and algal standing stocks increased along with aquatic invertebrate and juvenile salmonid densities. Increases in canopy cover have also been associated with biotic responses. In a correlative study, Kaylor and Warren (2017a), found associations of algal, macroinvertebrate, fish, and total vertebrate biomass with increased canopy cover. This supports the conceptual model that bottom-up processes, influenced by abiotic factors, are correlated with changes in primary and secondary productivity and prey availability. Furthermore, with 40 years of stand regeneration after clear cut forest management, consistent decreases in reach scale algal chlorophyll-*a* accrual and macroinvertebrate biomass were observed when compared to old-growth forested reference stream reaches (Kaylor and Warren 2017b). Trout biomass also decreased and was lower in 3 out of 5 previously harvested reaches compared to the old-growth reaches (Kaylor and Warren 2017b). This is consistent with other conceptual models of changes in fish biomass over time following canopy closure (Mellina and Hinch 2009, Warren et al. 2016), however these conceptual models generalize light patterns spatially and temporally. To date, no studies have implemented *in-situ* manipulations of stream light that explicitly investigate the occurrence of low and high irradiance patches of light and shade that occur in a natural stream system or specifically the effects of patchy changes in light on fish and other stream consumers.

In this study, we quantified changes in stream primary production and stream biota (macroinvertebrates, fish and salamanders) resulting from a patchy decrease in light availability in headwater streams. We established three sets of paired stream reaches and experimentally manipulated light in one reach from each pair by adding patches of shade. We then evaluated how periphyton, invertebrates and fish responded in the manipulated reach relative to the unmanipulated reference reach in a before-after control-impact (BACI) study design. The objective of this research was to clarify the role of light as a bottom-up driver of the food web in this system and to test hypothesized interactions between moderate, patchy decreases in light and responses of in-stream periphyton, invertebrates, and vertebrate predators. Our hypotheses were derived from earlier correlative studies in this system (Kaylor et al. 2017). With decrease in light reaching the stream benthos, the amount of light reaching the stream benthos we expected to see a reduction in the growth of in-stream autotrophs through the summer and thereby a decrease in macroinvertebrates, cutthroat trout (*Oncorhynchus clarkii clarkii*) and salamanders as a result of decreasing resource availability in the manipulated reaches.

Methods

Study location

This study was conducted in the HJ Andrew's Experimental Forest (HJA), a US Forest Service experimental forest and a National Science Foundation long-term ecological research site located within the Willamette National Forest in the Western Cascade Mountains of Oregon (Figure 1**)**. This region of the Pacific Northwest has a Mediterranean climate with wet winters and dry summers. The HJA ranges in elevation from 400 to 1,600 meters and encompasses the 6,400 hectares of the Lookout Creek watershed. Beginning in the 1950's, areas of the HJA were harvested as part of experimental forest management research. These historic cuts laid the foundation for applied research exploring vegetation succession, nutrient dynamics, forest-stream interactions and ecosystem function that remains an ongoing component of the site's long-term ecological research program. Currently, the HJA consists of a mixture of forests types, including late-successional forests (~500 years old), un-managed mature forests (~100-150 years old) and early succession second-growth forests (<70 years old). Primary forests are dominated by Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Tsuja plicata*). Second-growth forests are dominated by Douglas fir with red alder (*Alnus rubra*) and vine maple (*Acer circinatum*) occurring at higher densities in riparian zones. Resident cutthroat trout (*Oncorhynchus clarkii clarkii*) and Pacific giant salamanders (*Dicamptodon tenebrosus*) are the dominant vertebrate predators in these lower order streams. Sculpin (*Cottus sp.*) are also present at limited densities in one of the lower elevation streams.

Historic forest manipulations in the HJA have created a study area in which there are small forested streams bordered by late-successional, primary forests, and by younger, second-growth forests. This variation in riparian forest structure, and the consequent variability of available in-stream light, make this area an ideal location to conduct a study evaluating the influences of changes in light on in-stream productivity and stream ecosystem function. Our study used paired reaches at two locations on mainstem Lookout Creek and one location on mainstem of McCrae Creek (Figure 1).

We worked on six, 90-meter, reaches (three reach pairs) from two third order streams in HJA (Lookout and McRae Creek; Figure 1). All six reaches were on third order streams, two on the mainstem section of McRae Creek and four on separate sections of Lookout Creek. Reach pairs were separated by 150 to 200 linear meters of stream, but were still comparable in size and geomorphology. Bankfull widths for these reaches ranged from 7.4 to 10.4 meters (Table 1). In all reach pairs one of the reaches was bordered by old-growth riparian forests, and one by second-growth riparian forests. In McRae Creek both reaches were comparable in light availability with slightly greater canopy cover in the second-growth site (Table 1)**.** In the Lookout Creek 701 (hereafter Lookout 701) reach pair, the old-growth reach had more light (less canopy cover) on average, and in the Lookout Creek 703 (hereafter Lookout 703) reach pair, the second-growth reach had less canopy cover (or more light) than the old-growth reach (Table 1). For all three reach pairs, the old-growth reach was upstream from the second-growth reach.

Shading manipulation

We used a BACI study design where pre-treatment data were collected in all six reaches in 2014 (June-September). Shading manipulations were implemented in May 2016 and were left in place until October 2016. Post treatment data were collected in 2016 (June-September). In each reach pair, we applied the shading manipulation to the reach with higher light (lower canopy cover; Table 1). Using tarps that were oriented to shed all allochthouos litter into the stream, shading manipulations were applied to the reach in each reach pair with more canopy openness. This resulted in the shading manipulation placed within the reach bordered by second-growth forests in McRae 404 and Lookout 703 and in the reach bordered by old-growth forests in Lookout 701. Collectively, the shading manipulation covered a total of ~45% of each stream manipulation reach (Table 1, Figure 2). Specific tarp placement throughout stream reaches was determined during deployment based on logistical limitations and access. Tarps were supported by cord tethered to trees and rocks and were positioned with a peaked centerline perpendicular to the stream. The bottom of the tarp was weighted on both sides in the center to ensure that all litter was shed into the stream thereby changing light without impacting inputs from leaf litter and terrestrial invertebrates falling into the stream from the surrounding riparian forest canopy (Figure 2). Tarp peaks were generally between 3 and 5 meters above the stream and tarp edges ranged from 1 to 3 meters above the stream. The reference reach in each reach pair did not receive any shading manipulations. We walked through the reference reaches in May 2016 without deploying the tarps to mimic stream disturbance associated with setting up the shading manipulation. The reference reach and manipulation reaches received the same sampling regimes in both years, 2014 and 2016.

Quantifying abiotic variables

Light

To quantify stream light availability, we used arrays of photo-degrading fluorescein dye, deployed every five meters along each study reach in the summer of both 2014 and 2016 (Table 1). An array of fluorescein vials consisted of three, 3.5ml vials zip-tied to a metal flag and deployed in the stream thalweg for 24 hours. Following methods previously detailed in (Bechtold et al. 2012 and Warren et al. 2013), in addition to the exposed glass vials, three individual control vials were placed throughout each reach and were wrapped in aluminum foil to prevent exposure. These dark foil-covered vials allowed us to determine any background photo degradation not caused by solar radiation. Each 3.5 ml vial was filled with 400 ppb fluorescein standard (Turner Designs, Sunnyvale, CA), to have a consistent starting fluorescein concentration for all samples. Vials were laid in the thalweg of the stream in the afternoon and were picked up the following afternoon (24 hours later). All deployment occurred on cloudless days, reflecting maximum potential summer light. After in-stream deployment, vials were stored at room temperature in the dark for at least 12 hours to return the vials to the same temperature as the initial reading, as temperature can influence readings of fluorescein values (Bechtold et al. 2012). A Turner Designs AquaFluor, handheld fluorometer was then used to measure fluorescein concentration in each vial. The difference between the average fluorescein value for the controls and the average fluorescein value for each array served as a proxy for light accumulation on the stream benthos at each sample location for a 24-hour period. The resulting fluorescein value for every measurement was converted to photoactive radiation (PAR) in µmol m^{-2} s^{-1} (Warren et al. 2017). Fluorescein values from evert 5 meters throughout each 90-meter reach were averaged to produce one value for each reach. To assess the impact of patchy shading on reach-scale light availability, the ratio of average light in the manipulation reach over the reference reach was compared between the two study years (before and after shading), for each reach pair. We were also curious how light was impacted on a localized patch-scale. We compared the average light reaching the stream benthos directly under the tarps as shaded samples to light reaching the benthos in unshaded locations within the manipulation reaches in 2016. Light measurements taken directly under tarps were averaged to produce a single value for shaded locations throughout each manipulation reach and light measurements recorded between tarps along every 5 meters in the manipulation reach were averaged to produce a single value for unshaded locations. This process was repeated across all three manipulation reaches in 2016.

Stream habitat and temperature

Physical stream characteristics were sampled at transects set every 10 meters along each of the six study reaches, starting at meter 0 and ending at meter 90 for a total of 10 transects for each study reach. In summer of 2014, at each transect, we quantified bankfull width, wetted width, depth in the thalweg, canopy cover, abundance and volume of large wood (fallen wood >10 cm diameter and >1 m length), and dominant substrate type (based on Wentworth scale categorization; Table 1). We also quantified length, width, max depth, and outflow depth of each pool to determine total pool area within each study reach (Table 1). In summer 2016, we resampled for bankfull width, wetted width, and depth in the thalweg at each transect throughout all six study reaches (Table 1).

Increases in light often go hand-in-hand with increases in stream temperature, a fundamental biological control that can also affect fish and biota in streams (Brown and Krygier 1970, Johnson 2003, Cole and Newton 2015). Short-wave radiation from direct sunlight is considered a dominant factor influencing stream temperature (Johnson 2004), while air temperature has been shown to be a relatively weak determinant of stream temperature (Arismendi et al. 2014). Factors that regulate light exposure along extended sections of a stream, such as buffer widths, have been shown to influence stream temperature (Kiffney et al. 2004, Groom et al. 2011a, 2011b). However, the influence of a patchy light environment along the stream is not as well explored or understood. The question of whether light patches can be manipulated in a natural system without impacts on temperature is important in considering how development of a heterogenous light environment will affect multiple aspects of the stream and whether light can be considered in isolation in a natural system (Kiffney et al. 2003). In 2014 temperature loggers were deployed at the downstream end of each reach from early August to the end of September. In 2016 temperature loggers were deployed from early June through the end of September at the top and bottom of each reference reach, and from early May (when tarps were deployed) through the end of September at the top and bottom of each manipulation reach. We used HOBO temperature data loggers (encased in white PVC pipe to eliminate direct sunlight and potential damages) placed in the thalweg of each stream to measure temperature (°C) every 15 minutes. Loggers were taken out of the stream during electrofishing surveys.

Quantifying biotic variables

Periphyton

We estimated periphyton biomass accrual during the summer in 2014 and 2016 through quantification of benthic chlorophyll-*a* accrual on 15 x 15 cm unglazed ceramic tiles (225 cm^2). In 2014, one tile was deployed in the stream thalweg every 10 meters in each of the six study reaches (n=10 per reach) for six weeks in mid-summer. During this first year of the study, chlorophyll-*a* on tiles was quantified using laboratory methods of fluorometric methods and phaeophytin correction outlined in EPA method 445.0 (Arar and Collins 1997). Accrued chlorophyll-*a* on each tile was measured using a handheld flourometer as µg m^{-2}. Values for accrued chlorophyll-*a* were averaged across the 10 samples taken in each study reach to produce a single value for each reach in 2014.

In 2016, chlorophyll-*a* accrual was again quantified on the same set of 15 x 15 cm unglazed ceramic tiles. Given the potential for tiles to flip or become covered with sediment or litter, we deployed three tiles ever 10 meters (n=30 per reach for 3 weeks) in 2016. Accrued chlorophyll-*a* measurements were averaged across all 30 samples in each reach to produce a single value as µg m^{-2} in 2016. We also compared average accrued chlorophyll-*a* measurements directly under the tarps as shaded samples to measurements taken in unshaded locations within the manipulation reaches in 2016. Accrued chlorophyll-*a* measurements taken directly under tarps were averaged to produce a single value for shaded locations throughout each manipulation reach and Accrued chlorophyll-a measurements taken between tarps in the manipulation reach were averaged to produce a single value for unshaded locations. This process was repeated across all three manipulation reaches in 2016.

In 2016, *in situ* chlorophyll-*a* measurements were conducted using a BenthoTorch **(**BBE Moldaenke GmbH). The BenthoTorch is a portable field instrument used for the quantification of chlorophyll-*a* fluorescence on different substrates and provides a real-time measurement of benthic algae concentrations (Kahlert and McKie 2014). The BenthoTorch has been shown to accurately quantify periphyton biomass expressed as chlorophyll-*a* µg cm^{-2} (Kahlert and McKie 2014). In a preliminary assessment of BenthoTorch accuracy and precision relative to established methods, we compared lab sample results to values from the BenthoTorch that were taken from the same tiles (or natural substrates) at our sites. We found that unacidified relationships were much stronger. Therefore, unacidified values from chlorophyll-*a* measurements were used to represent multiple photosynthetic pigments which were a better fit with BenthoTorch data and provided an internally consistent measure of relative algal biomass on tiles. Ash free dry mass (AFDM) from periphyton accrued on tiles was not collected in 2014, therefore AFDM was not used in the 2016 portion of this BACI analysis, however, in earlier work at the HJA we found chlorophyll-*a* was reasonable proxy for periphyton accrual in HJA streams (Warren et al. 2017). In 2016, we verified our use of chlorophyll-*a* as a proxy for AFDM in 2016 and found relationships (r^2 = 0.57) between the two, with no influence of light on the chlorophyll-*a* : AFDM ratio in these sites (Appendix: pg. 42). Because sampling methods were not consistent between years for chlorophyll-*a*, we evaluated the effect of patchy shading on accrued in-stream algae using the ratio of average chlorophyll-a in the manipulation reach to the reference reach for each of our reach pairs (n=3). To allow for comparison across all response metrics, this reference to manipulation ratio change was applied for all metrics, including light, macroinvertebrate biomass, and in-stream vertebrate biomass.

Macroinvertebrates

In 2014 and 2016 macroinvertebrates were sampled in July and August using a surber sampler (500 µm, .25 m^2). In 2014, six surber samples were collected at regular intervals from riffle sections of each study reach. In 2016, three surber samples were collected at regular intervals from riffle sections of each of the three reference reaches. In order to compare the more localized changes in invertebrate biomass and community composition with the shaded reaches, we collected a total of 6 invertebrate samples in each manipulation reach; three surber samples were collected from riffle sections under tarps, and three from riffle sections outside of the shading of the tarps. Each sample was immediately preserved in 90% ethanol until laboratory analysis. For all 2014 reaches and for the 2016 reference reaches, all collected samples within a reach were combined for identification and biomass analyses. In 2014, data were also pooled samples for each reach; a single biomass estimate per unit area in each reach. Sorting and biomass analyses (mg m^{-2}) were conducted on macroinvertebrate samples the winter following each field season. Macroinvertebrate samples collected in 2014 were analyzed on Oregon State University campus. In the 2016, within each manipulation reach, samples from unshaded reach sections were pooled separately from shaded reach section samples. This resulted in three samples pooled for reference, shaded-manipulation, and unshaded-manipulation reaches. In 2016, total macroinvertebrate biomass estimates (mg m^{-2}) from shaded and unshaded manipulation samples were averaged to calculate the estimated manipulation biomass estimates, correcting for total number of samples between the reference and manipulation reaches, to produce one value for each reach. In 2016 macroinvertebrate samples were analyzed by Rithron Associates Inc., Montana. For analyses in both 2014 and 2016 macroinvertebrate communities were identified to genus and then categorized into functional feeding groups based on taxa according to Merritt and Cummins (1996).

We expected the shading manipulations to have the largest influence on macroinvertebrate herbivores, mainly scrapers. We also explored the response of other functional feeding groups (shredders, predators, collector-gatherers, and collector-filters) to the shading manipulation. To quantify how decreases in light influenced invertebrate biomass, as with light and periphyton chlorophyll-*a*, we compared the manipulation to reference ratio of total, reach-scale, invertebrate biomass between the two study years. Focusing on localized effect in the 2016 shading experiment, we also evaluated differences within each of the manipulation reaches between open and shaded sections of the stream.

Vertebrates

In 2014 and 2016 populations of fish and salamanders were surveyed using a backpack electrofisher (Smith-Root model LR20B). Vertebrate surveys occurred in late July to early August (no sampling prior to July 20th to minimize mortality of young of the year that emerge in late spring to early summer). Mark-recapture methods were used to obtain population size and biomass estimates of in-stream vertebrates in both years. Nets were used to close the system by blocking the upper and lower ends of the study reaches while mark-recapture surveys were in progress (over a 24-hour period). Reference-manipulation reach pairs were surveyed, over two consecutive days of fieldwork. Mark-recapture surveys include one pass of electrofishing the reach to collect vertebrates for marking (small clips on the caudal fins of fish and on tails of salamanders) and then a second pass to recapture vertebrates.

The Chapman mark-recapture estimation was used to estimate vertebrate predator population sizes (Chapman 1951).

$$\widehat{N} = \frac{(M+1)(C+1)}{m+1} - 1$$

Where,

N_{hat} = estimated number of animals in the population

C = number of animals marked on the 1st visit

M = number of animals captured on the 2nd visit

m = number of animals recaptured on the 2nd visit (that were marked on the 1st visit)

Standard error for the population estimates were calculated as the square root of the variance in the population estimate.

$$Variance\ of\ N = \frac{[(M+1)(C+1)(M-m)(C-m)]}{[(m+1)^2(m+2)]}$$

A 95% confidence interval was calculated for each population estimate N ± SE * $z_{a/2}$, where $z_{a/2} = 1.96$ as more than 60 fish are initially marked (Lockwood and Schneider 2000).

Length (mm) and weight (g) were recorded for all individual salamanders and fish caught while mark-recapture surveys. Biomass (g m^{-2}) estimates were calculated through multiplying the average weight (g) by the estimated number of individuals in the population (n), and then dividing by the area of the 90-meter reach (m^2). The young-of-the-year (age 0+) age class was clearly identifiable in each site and in each year via length-frequency histograms. Young-of-the-year trout (hereafter YOY) growth in each reach was estimated in September from a second, single pass, sampling of the YOY population in each stream. This second sampling of YOY growth was done under the assumption that their movement is limited due to their small size and that changes in size of individuals within a reach represent mean growth rates of YOY for that reach.

To quantify if patchy decreases in light influenced the biomass of in-stream vertebrate predators, we compared the ratio of vertebrate biomass in the manipulation reach to the reference reach in 2014 to the ratio in 2016. This analysis was performed on biomass ratios of adult cutthroat trout, YOY, salamanders, as well as total vertebrate biomass (all three groups summed). The ratio of YOY growth (g day^{-1}) in the manipulation reach to the reference reach was also compared with a paired t-test between 2014 and 2016 to discern if there was a difference between the median YOY growth of the two study years.

Forest age class comparison

Since forests surrounding our three stream reach pairs consisted of both old-growth and second-growth stands, we evaluated if forest successional development stage class was associated with our shading manipulation results. In this analysis, we used data from the two study reaches surrounded by second-growth forests at Lookout 701 and Lookout 703. The second-growth forested reach at Lookout 701 was a reference reach and the second-growth frosted reach at Lookout 703 was a manipulation reach. Using these two second-growth forested stream sections, we compared the manipulation to reference reach ratio between 2014 and 2016.

Statistical Analysis

We used a paired t-test to assess the null hypothesis that there was no difference in average ratio of manipulation to reference reach across the three reach pairs between the two study years (2014 and 2016) for all reach-scale metrics: average light (PAR), average chlorophyll-a, macroinvertebrate biomass, trout biomass, YOY biomass, salamander biomass, and total in-stream vertebrate biomass (data used in ratios for all metrics listed in Appendix; Table A1). We did not find any evidence that model assumptions were not met for any of our comparisons. For all analyses, statistical significance was identified when 95% confidence intervals did not include 0 and when p-values were less than 0.05. We also used a paired t-test to assess the local scale difference mean light, chlorophyll-*a*, and macroinvertebrate biomass between shaded and unshaded sites within the manipulation reaches in 2016. Because variation among responses from unshaded locations was substantially larger than those in shaded locations, the assumption of equal variance was not met. Due to the assumption violation and that this analysis is also based on raw data, unlike the other ratio comparisons between years, data were natural logarithm transformed. These within manipulation reach comparisons are therefore conducted on the estimated median difference between shaded and unshaded locations for the amount of light (PAR), algae biomass (chlorophyll-*a*), and invertebrate biomass using a paired t-test.

Results

Abiotic Response

Local PAR flux decreased with the shading manipulation in place (Figure 3). On average, across all three study reach pairs, experimental shading decreased light flux in the treatment reaches by 55.8% in 2016 relative to 2014 (Table 4; Figure 5a). The light ratio between the reference and manipulation reaches at McRae 404 declined by the largest amount (76.2% from 2014 to 2016). The ratio of mean PAR values between manipulation and reference reaches declined by 59.2% in Lookout 703 and by 32.1% in Lookout 701. Within the manipulation reaches, while the shading was in place in 2016, median light reaching the stream benthos was 14.7 (95% CI: (1.1,1.191.2)) times less in shaded locations than in unshaded locations (Table 5; Figure 6a).

During the shading treatment, there was no significant difference in the daily average in-stream temperature between the upstream and downstream ends of the manipulation reaches (Appendix: Figure

A1). In Lookout 703, there was no difference in mean summer temperatures between the manipulation and reference reaches sampled at the bottom of the study reaches in 2014. In 2016 mean summer temperature was 5.5% lower in the manipulation reach than the reference reach at Lookout 703. Maximum daily temperature at Lookout 703 was 2.2% lower in the manipulation reach than the reference reach in 2014 and there was no difference in average maximum temperature in 2016. Mean summer temperature sampled at the bottom of the study reaches at McRae 404 was 3.3% lower in the manipulation reach than the reference reach in 2014 and 8.3% lower in 2016. Maximum daily temperature at McRae 404 was 2.1% higher in the manipulation reach than the reference reach in 2014 and 1.2% higher in 2016. At Lookout 701, mean daily temperature sampled at the bottom of the study reaches was 2.7% lower in the manipulation reach than the reference reach in 2014 and 2.9% lower in 2016. And at the same site, maximum daily temperature was 4% higher in the manipulation reach than the reference reach in 2014 and 3.2% lower in 2016 (Table 3). Overall, water temperatures, including mean and maximum, did not differ between the manipulation reaches and reference reaches by more than the accuracy of the data loggers (Table 3 & Table A2).

Biotic Response

Across our three study locations, mean chlorophyll-*a* in the manipulation reaches was 1.16 times higher than in the reference reaches in 2014 and in 2016 the manipulation reaches were 0.43 times less than the reference reaches. Overall, there was a decrease, though not significant, in chlorophyll-*a* accrual on tiles in the manipulation reaches relative to the reference reaches with a 45.5% average decline in the ratio of reference to manipulation in 2016 relative to 2014 (Table 4; Figures 4b & 5). Considering each reach individually, the patchy decrease of in-stream light yielded a decline on periphytic chlorophyll-*a* in two out of three manipulation reaches. In Lookout 703 there was no significant difference in average accrued chlorophyll-*a* in the manipulation reach relative to the reference reach between 2014 and 2016 with the shading manipulation. In McRae 404, there was a 48.6% decrease in the chlorophyll-*a* ratio between reference and treatment reaches from 2014 to 2016, and in Lookout 701, we observed a 61.3% decrease in the chlorophyll-*a* ratio between reference and treatment reaches from 2014 to 2016. Within the manipulation reaches alone in 2016, median accrued chlorophyll-*a* was 6.4 (95% CI: (1.6, 26.3)) times less in shaded locations than in unshaded location of the same reach (Table 5; Figure 6b).

In 2014, mean invertebrate biomass in the manipulation reaches was 1.7 times higher than in the reference reaches and in 2016, the manipulation reaches decreased to 0.58 times less than the reference reaches. Because we pooled the macroinvertebrate samples from each reach, statistical analyses could not be conducted on individual reaches, but the ratio of reference to manipulation reach total biomass did declined in all three sites in 2016 relative to 2014 (Figure 4c). We saw the largest decrease in the ratio of total macroinvertebrate biomass in the manipulation reach to the reference reach in Lookout 703, with 83.0% less in 2016 than in 2014. In McRae 404, the ratio of total macroinvertebrate biomass in the manipulation reach with respect to the reference reach decreased by 48.6% from 2014 to 2016, and the ratio of total macroinvertebrate biomass decreased by 61.3% in Lookout 701 between 2014 and 2016. Across the three reach pairs, on average, there was a 64.3% decrease in total macroinvertebrate biomass when the shading manipulation was deployed (Table 4; Figure 5). There was a consistent decrease in macroinvertebrate biomass in the manipulation reach with respect to the reference reach across all functional feeding groups between 2014 and 2016. On average, across all three sites, relative biomass of the scraper functional feeding group in the manipulation reach with respect to the reference reach decreased by 88.1% in 2016 from 2014. Scrapers and shredders made up a larger relative proportion of the total vertebrate biomass in shaded locations than in unshaded locations within the manipulation reaches in 2016 (Figure 7). Conversely, predators and collector-gathers made up a larger proportion of relative total vertebrate biomass in unshaded locations than shaded locations within the manipulation reaches in 2016. Within the manipulation reaches, macroinvertebrate shaded samples taken directly under tarps in 2016, macroinvertebrate biomass was 5.72 (95% CI: (0.5, 60.2)) times less in shaded locations than in unshaded sections of the same manipulation reach (Table 5, Figure 6c).

Across all three reach pairs patchy stream shading reduced trout biomass significantly (by an average of 23.5%) in manipulated reaches relative to the references reaches (Table 4; Figures 4d & 5). In 2014, mean trout biomass in the manipulation reaches was 1.25 times larger than in the reference reaches, and in 2016 the mean biomass in the manipulation reaches was .024 times less than the reference reaches. The decreases in trout biomass differed between study sites, with the largest decreases in light yielding the largest relative declines in trout biomass. In McRae 404, light was reduced by 76.2%, we observed a 34.9% decline in the ratio of trout biomass between 2014 and 2016. In Lookout 703, there was a 17.3% in the manipulation reach with respect to the reference reach, and in Lookout 701m shading decreased trout biomass by 18.5% in manipulated reaches relative to reference reaches. Sculpin were only present in McRae 404 and the ratio of sculpin biomass between 2014 and 2016 decreased by 30.1%.

Young-of-the-year (YOY) biomass ratios between manipulation and reference reaches decreased by an average of 47.2% across all sites from 2014 to 2016 in association with patchy shading, though not significantly (Table 4, Figure 4e). In Lookout 703, the ratio of YOY biomass in the manipulation reach with respect to the reference decreased by 13.3% from 2014 to 2016. In McRae 404, this ratio decreased by 33.3%, and in Lookout 701 it declined by 94.8%. There was no clear trend in summer YOY growth rate ratios between 2014 and 2016, but when growth and abundance were included together in an estimate of YOY summer population productivity, we found that estimated productivity decreased in two out of three sites in association with the shading manipulation. And, on average, across all three sites, the YOY productivity ratio between manipulation and reference reaches decreased by 77.7% in the manipulation reach with respect to the reference reach between 2014 and 2016 (t=1.5, P=0.247, Appendix: Figure A2).

Salamander biomass ratio was lower in 2016 relative to 2014 in two of three reach pairs. In Lookout 703, the ratio of salamander biomass decreased by 70.9% between 2014 and 2016 in the manipulation reaches with respect to reference reaches. In McRae 404 there was a decrease of 73.5% in the ratio. Surprisingly, in Lookout 701 the ratio of salamander biomass in the manipulation reaches relative to reference reaches increased substantially (by 285.2%) in 2016 than in 2014. With the large positive response in Lookout 701, overall, there was a 46.9% increase in the ratio of salamander biomass in the manipulation reach to the reference reach from 2014 to 2016 (Table 4; Figures 4f & 5).

Total vertebrate biomass decreased with shading in 2 of 3 reach pairs, resulting in a 29% decline in the mean manipulation to reference reach ratio. In Lookout 703 total vertebrate biomass in the manipulation reach with respect to the reference reach decreased by 49.2% from 2014 to 2016. The total vertebrate biomass ratio decreased by 61.5% in McRae 404, between 2014 and 2016. In Lookout 701 total vertebrate biomass in the manipulation reach with respect to the reference reach was 114% larger in 2016 than in 2014, a result that was driven by the change in salamander biomass between years (Table 4; Figure 5). Overall, mean total vertebrate biomass was 1.47 times larger in the manipulation reaches than the reference reaches in 2014 and in 2016 the manipulation reaches were 0.32 times less than the reference reaches.

Forest Age Class Caparisons

In analysis of the two second-growth reaches at Lookout 701 and Lookout 703 reach pairs, were conducted to account for potential forest structure effects on steam system processes and morphology. In-stream biota responded consistently to decrease in patchy shade regardless of riparian forest type. With the patchy decreases in light throughout the manipulation reaches of both Lookout 703 and Lookout 701, we observed an 54.7% decline in the ratio of periphyton biomass between the second-growth manipulation reach at Lookout 703 and the second-growth reference reach at Lookout 701. The ratio of macroinvertebrate biomass between the Lookout 703 manipulation reach and the Lookout 701 reference reach also decreased by 70.9% between 2014 and 2016. The ratio of fish biomass in the Lookout 703 manipulation reach to the Lookout 701 reference reach decreased by 17.3% between 2014 and 2016. Salamander biomass decreased by 13.3% between 2014 and 2016 at the Lookout 703 manipulation reach and the Lookout 701 reference reach. The ratio of total vertebrate biomass decreased by 17% between 2014 and 2016 at these second-growth sites (Figure 8).

Discussion

Patchy, local shading along forested headwater streams reduced in-stream light and resulted in overall declines in periphyton accrued, macroinvertebrate biomass, and fish biomass at the reach scale across three replicate reach pairs. This result occurred independent of riparian forest age/structure with shade reducing fish and macroinvertebrate biomass in streams bordered by both second-growth and old-growth forests. These findings were consistent with our hypothesis that biota in headwater streams would respond to changes in light via bottom-up pathways. Further, we demonstrated that moderate and patchy changes in light can impact local- and reach-scale food web dynamics. While large uniform changes of in-stream light have been shown to strongly influence stream ecosystem processes and stream biota (Sabater et al. 2000, Wootton 2012), fewer studies have evaluated the effects of smaller changes in light on stream biota, and fewer still have assessed changes that result from differences in irregular patches of light and shade. Understanding how these terrestrial-aquatic linkages function and changes in riparian forests can affect in-stream processes and biota will contribute to our ability to properly manage forested systems in the Pacific Northwest.

Light has been well-established as an important driver of in-stream primary productivity (Hill et al. 1995, Julian et al. 2011, Warren et al. 2017). Our results were generally consistent and decreases in local light flux from patchy shading resulted in local decreases in periphyton accrual. In two of the three reach pairs assessed here, the areas of low production collectively lead to an overall reduction in mean chlorophyll-*a* ratios at a reach scale. At Lookout 703, chlorophyll-*a* sampled in 2016 in the manipulation reach was substantially lower in shaded locations than unshaded locations, however the ratio of manipulation to reference of reach average accrued chlorophyll-*a* was not significantly different between 2014 and 2016. While overall results from this study indicated that bottom-up processes dominate production in these systems, we suggest that the absence of significant response in benthic periphyton accrual in Lookout 703 is likely due in part to changes in top-down controls by macroinvertebrate consumers. The manipulation reach at Lookout 703 also had the highest initial macroinvertebrate biomass out of all study reaches, and shading at this site lead to substantial declines in the macroinvertebrate and fish biomass. The presence of a clear response in primary consumers, with a lack of a response in the biomass of primary producers to the shading manipulation is consistent with the results of Kiffney et al. (2003). They found that increases in stream light availability yielded mixed results with responses of periphyton biomass but substantial and consistent increases in stream macroinvertebrates that fed on benthic periphyton, specifically Chironomids. Top-down control of stream periphyton was identified as the most likely driver of this response as primary consumers increase with increased availability of food resources and then subsequently limit primary production. These primary producer-consumer relationships have also been explored by other studies as well, with mixed results, indicating the complexity of food web dynamics in these systems (Wootton and Power 1993, Quinn et al. 1997).

Macroinvertebrates decreased in all three sections of streams in response to the shading manipulation. This result was consistent with the hypothesis that decreases in light that in-turn lead to a decrease in the amount of periphyton growing on stream benthos would subsequently cause a decreased macroinvertebrate biomass. Previous research manipulating stream light has also demonstrated that algal community structure on the stream benthos can directly influence macroinvertebrate communities. For example, in a study that manipulated shading to create four levels of light in experimental channels, aquatic invertebrates (chironomidae) were 11 times greater in the two high light treatments (22 & 100% of max light) than the two lower light levels (<=10% of max) light (Kiffney et al. 2004). Recently logged streams, with substantially less canopy cover have been shown to contain significantly higher macroinvertebrate biomass than the unlogged or older logged sites (Fuchs et al. 2003). While, older logged and unlogged sites had comparable levels of canopy cover, and presented no difference with macroinvertebrate biomass or abundance (Fuchs et al. 2003). In another experimental channel study, the effects of shade on in-stream primary producers and primary consumers were explored by reducing available in-stream PAR at varying levels (declines of 0, 60, 90, & 98%) and found that shading was a direct mechanism for lower periphyton chlorophyll-*a* levels (Quinn et al. 1997). Periphyton responded to decreases in light with lower amounts of chlorophyll-*a*, particularly at 90 and 98% shading, even with more potential variability in chlorophyll-*a* levels with moderate shading. While total macroinvertebrate densities, and particularly Chironomids, declined with increases in shade, collector-browsing invertebrates only declined at the highest level of shading 98%. This study suggests that the somewhat weak relationship between invertebrates and primary production is indicative of food resources being derived from up-stream sources. Gjerløv and Richardson (2010) implemented a stream shading experiment in which they decreased light by more than 90% in two riffle sections of two streams, but in contrast to these earlier studies, they did not see a response in macroinvertebrates to stream light conditions. They attributed the lack of a response in macroinvertebrate to high levels of algal standing stocks at one of the two sites, which ultimately supports the fundamental importance of bottom-up processes in stream food webs.

Our results indicate that changes in stream light, which affect the availability of stream macroinvertebrate prey can substantially impact trout biomass in forested headwater streams. Across our three study locations, mean trout biomass remained constant between 2014 and 2016, with a 0.08 g m^{-2} increase. In the manipulation reaches there was a decreased of 1.01 g m^{-2} in mean trout biomass between

2014 and 2016. On average, mean estimated tout biomass in our 90-meter study reaches in these forested headwaters was between 4 and 5 g m^{-2}, therefore a decrease of 1.01 g m^{-2} would be a relatively substantial change to vertebrate predator biomass. This has been demonstrated in other studies, but most research tying changes in light to fish have focused on increase in light or have evaluated correlative studies between light availability and vertebrate biomass. Both food availability and habitat have been cited as important factors to consider when predicting vertebrate predator abundance in forested streams (Hawkins et al. 1983, Kiffney and Roni 2007). The relationship between aquatic vertebrate density, riparian canopy and physical habitat has been explored in Oregon streams. Total vertebrate biomass has been highly correlated with invertebrate density, and variation of invertebrate densities were dependent on canopy cover and substrate (Hawkins et al. 1983). Increased algal production was also shown to compensate for decreased habitat quality(Hawkins et al. 1983). Kiffney and Roni (2007) evaluated the relationship between stream vertebrates and relative stream light levels and found a strong positive relationship between light and stream vertebrate biomass. Kaylor et al. (2017) also found that reaches with higher light levels had higher fish biomass in both old-growth and previously harvested reaches. Of the few studies that have explored decreases on in-stream light in forested headwaters, to date none have identified a direct impact to higher aquatic trophic levels.

Salamanders account for a large amount of the aquatic vertebrate biomass in Pacific Northwest forested streams. Our results were mixed with respect to salamander biomass and patchy decreases in light. We saw expected results in two of our three sites, but in the third we saw an increase in salamander biomass in association with stream shading. Studies assessing the influence of riparian canopy cover and abiotic stream characteristics have been mixed. Gradient, substrate type, amount woody debris, and other stream habitat characteristics, have been identified as important factors associated with salamander biomass and abundance (Dudaniec and Richardson 2012, Clipp and Anderson 2014). Leuthold et al. (2012) explored the impact of near stream clear-cut timber harvest on salamanders in southern Oregon two years after forest harvest, and found no significant effect of the forest management on Pacific giant salamanders. Substrate explained the majority of variability in salamander biomass in this study. Other studies have found that aquatic food availability is highly associated with salamander biomass and abundance in forested streams. Due to the ability of salamanders to use the complexity and three-dimensional structure of the stream benthos, the probability of detection is a concern (MacKinzie et al. 2003, Kroll 2009). To facilitate better capture efficiencies, we sampled aquatic vertebrates later in the summer (end of August), when stream flows are lower and detection of salamanders and trout is higher. However, at the largest study reach pair, Lookout 701, with a high proportion of large cobble substrate with deep water levels, it was difficult to visually identify salamanders. This reach pair had an increase in the ratio of salamander biomass in the manipulation reach with respect to the reference reach between 2014 and 2016.

Many physical characteristics of forested stream habitats, such as woody debris, temperature, pool geomorphology, surface flow, and riparian vegetation have been identified as important factors influencing fish and salamander abundance and productivity in these forested streams (Torgersen et al. 1999, Warren et al. 2010, Huryn et al. 2014). However, food resources can also limit fish production in riverine ecosystems (Wipfli and Baxter 2010). Juvenile salmonid densities have been correlated with algal production (Wootton 2012, Kaylor et al. 2017). Wootton (2012) explored the response of algae, invertebrates and vertebrates to a large change in light availability in five sections of stream. Algal standing stocks increased by 60% and subsequently, there was a 7-fold increase in aquatic invertebrates as well as a 77% increase in juvenile salmonid densities. Salmonid densities and algal production were strongly correlated. Chlorophyll-*a*, macroinvertebrates, fish and total vertebrate biomass across reaches with old-growth and second-growth riparian forests, have also been shown to respond to variable light environments, specifically to an increase in canopy cover. This relationship supported the conceptual model that bottom-up processes directly influence primary production and invertebrate prey availability

(Kaylor et al. 2017). Forest stand age effects were considered because each study reach pair consisted of a section of stream bordered by old-growth and one bordered by second-growth. We found that in-stream biota responded to the manipulation regardless of riparian forest stand age. Stream habitat characteristics can be impacted by riparian forest stand age (Meleason et al. 2003). In our three study reach pairs, there was consistently higher volumes of large wood in reaches surrounded by old-growth forests than second-growth (Table 1). While all other habitat metrics were not as consistent between old-growth and second-growth forest types.

Temperature is one of the many abiotic factors that influence in-stream processes and organism alike. Solar radiation reaching the stream has been shown to directly influence in-stream biotic biomass and productivity, especially when changes to riparian vegetation such as timber harvest occurs (Beschta and Beschta 1997, Danehy et al. 2005). Biota in many headwater streams are sensitive to temperature and changes in irradiance that could impact stream temperature. A substantial decline in stream temperature associated with increased shading could lead to decreases in primary production rates and thereby the growth of macroinvertebrates and fish. Similarly, increases in stream light can lead to increases in stream temperature which may cause thermally stressful conditions for many cold-water adapted species that dominate the biota found in headwater streams. Even localized variation of temperature along sections of streams, such as patches of cooler water, can impact the distribution of fish, demonstrating not only that temperature is important but that habitat heterogeneity can provide important habitat for salmonids (Torgersen et al. 1999). We did not detect a significant change in water temperature with the shading manipulation in place. We did observe a slight decrease in the ratio of maximum water temperature in the manipulation reach with respect to the reference reach between 2014 and 2016 across all reach pair locations, though it was only a 2.1% decrease in the ratio of daily maximum temperature. Overall, the limited response in temperature to patchy shading in our results supports the conclusion that light is a primary driver of changes observed in the manipulated reaches in response to stream shading.

The development of riparian forests in the Pacific Northwest into later successional stages will cause inconsistent, patchy changes to light reaching the stream benthos. Understanding how these changes influence in-stream primary production and biota will be important to preserving forested stream ecosystem function and biodiversity. The amount of light reaching a forested headwater stream is influenced by the structure of the riparian vegetation, particularly the over-story canopy (Chazdon and Pearcy 1986, Warren et al. 2013, 2017). The structure of riparian forests is a product of the composition, age, and disturbance history of vegetation surrounding the stream, with complex riparian forest structure resulting in spatially and temporally variable light environments (Keeton et al. 2007, Warren et al. 2013, Kaylor et al 2016). Streams with young and mid-succession second-growth riparian forests often have a high density of younger trees, resulting in a more uniform canopy structure, and ultimately a heavily shaded stream. Late-succession forests have more complex canopy structure as a result of periodic small-scale disturbances and natural mortality of large trees that open canopy gaps (Franklin and Van Pelt 2004, Keeton et al. 2007). This difference in canopy structure between old-growth and second-growth riparian forests leads to differences in the amount and distribution of stream light availability. As natural and anthropogenic processes alter forest age and structure over time and space, light environments in forested headwaters will vary on localized scales throughout landscapes. Results this study indicates that these local, patchy changes in the amount of light reaching a forested headwater stream may significantly influence not only the biomass of primary producers, but also the amount of macroinvertebrates and vertebrate predators that the system can support.

Figures

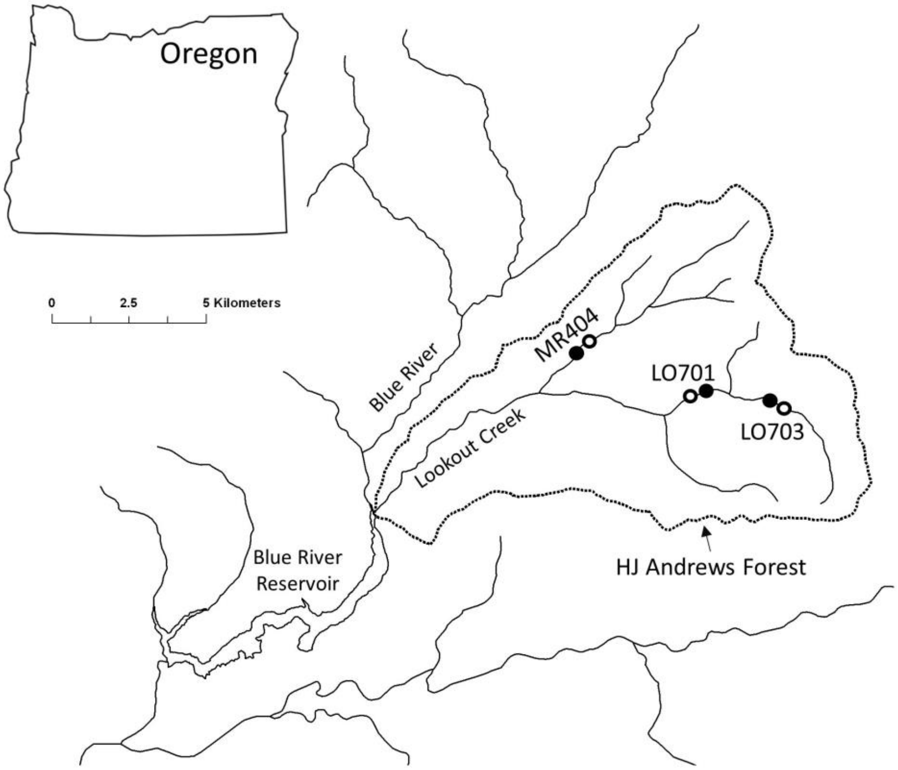


Figure 1: Map of the HJ Andrews Experimental Forest, near Blue River, Oregon, and locations of study sites. Circles indicate locations of the study reach pairs, with open circles representing the reference reaches and the filled circles representing the manipulation reaches. Exact coordinates of the six study reaches listed in appendix, Figure A3.

Figure 2: A photograph of deployed tarps in the second-growth reach of McRae 404 and an example aerial-view diagram of tarps deployed along a manipulation reach. Near 50% of linear stream in each 90-meter manipulation reach was shaded with tarps. We deployed tarps with a centerline perpendicular to stream flow and slopes parallel to stream flow to allow terrestrial litter inputs to fall into the stream as manipulation goal was to only manipulate solar flux reaching the stream benthos.

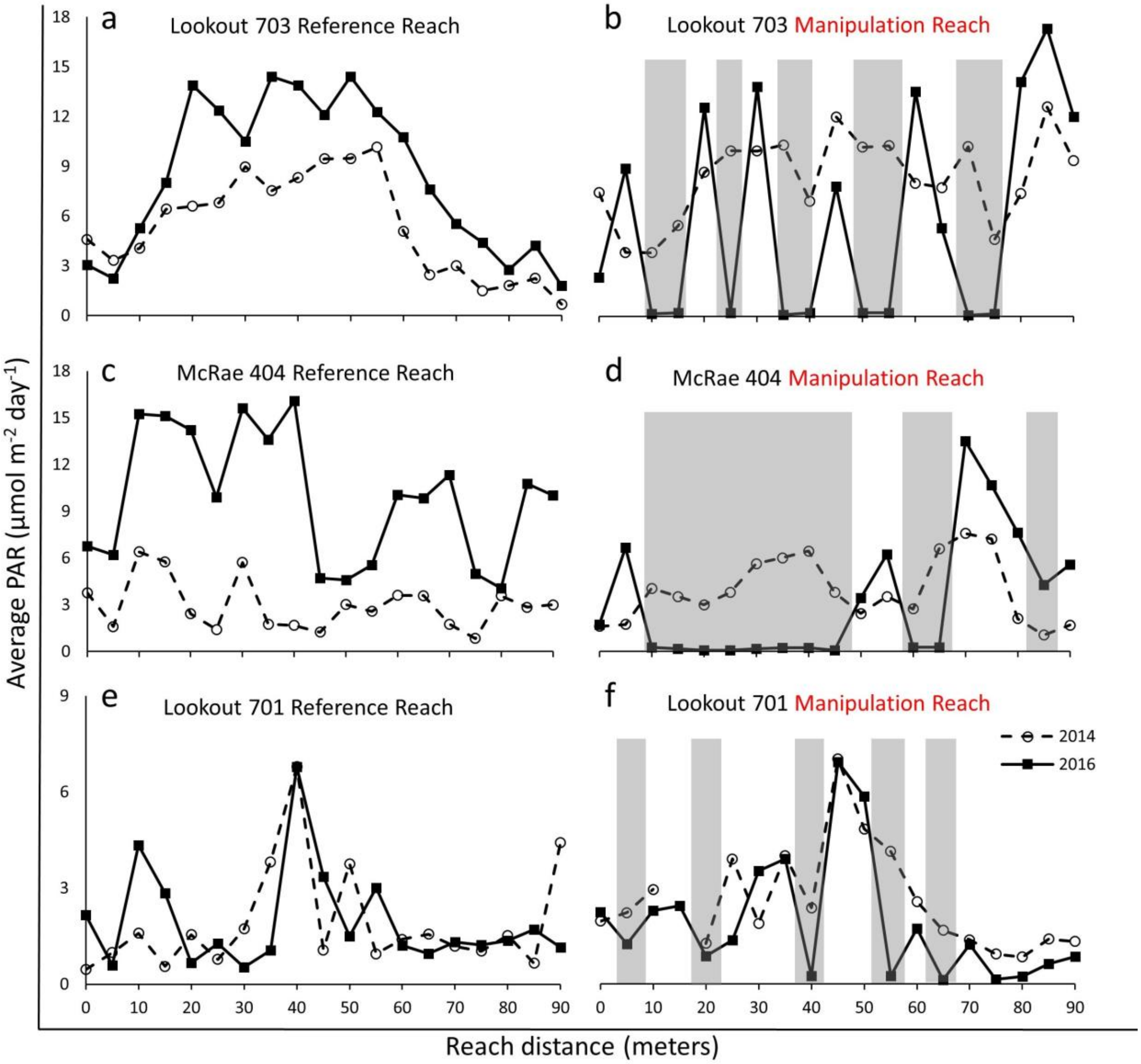


Figure 3: Profile of light (PAR) along each stream reach. Grey lines represent the 2014 light profile and black lines represent the 2016 light profile. Light values were collected with 3 replicates every 5 meters along each study reach in both years. Shading (via tarps) is represented by grey rectangles in the manipulation reaches (panels b, d, & f). Shading was deployed during the summer of 2016 and can be seen to decrease light directly where tarps were placed.

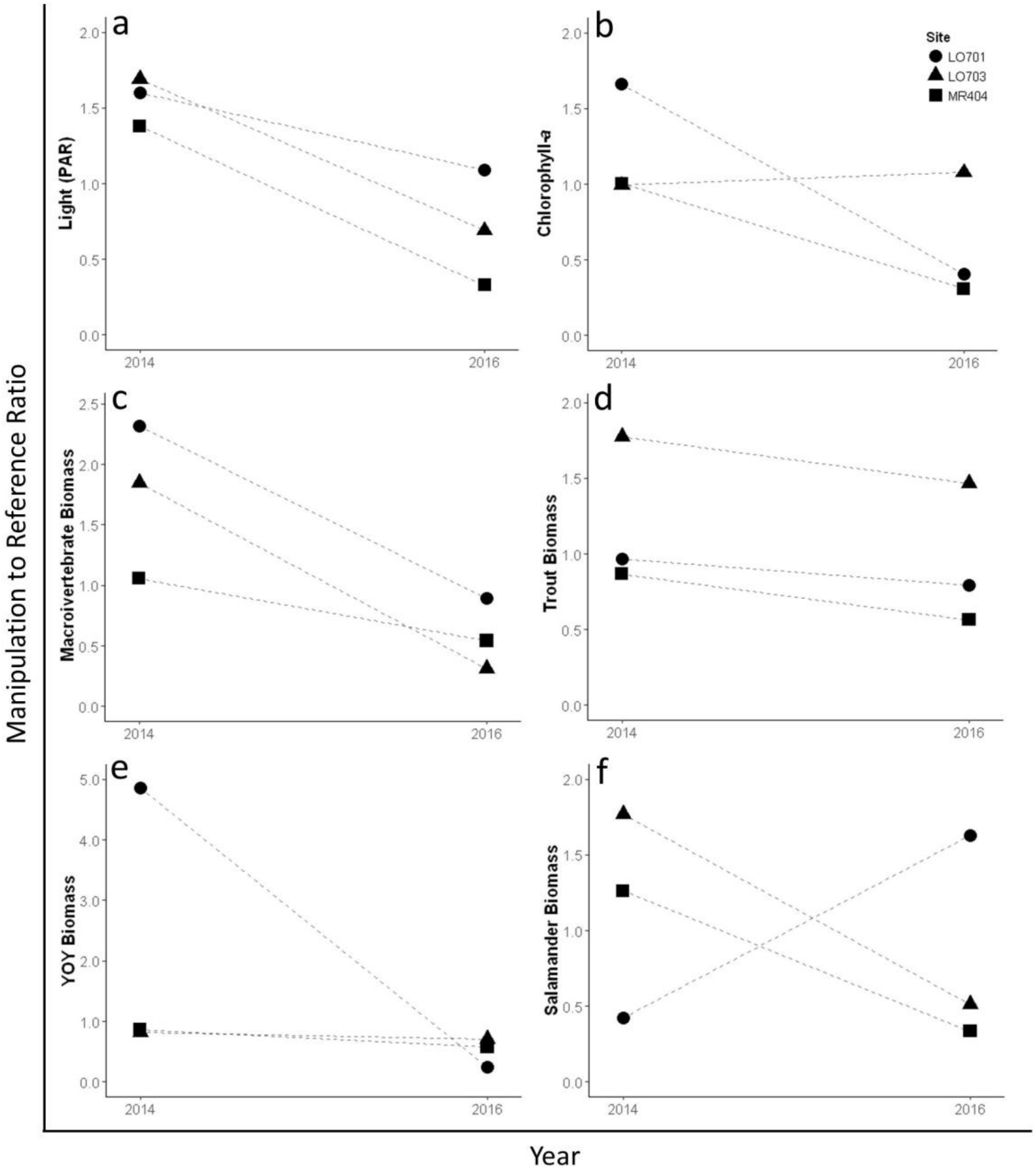


Figure 4: Manipulation to reference ratio in 2014 and 2016 for light as well as each food web metric at the three study reach pairs. Circles, triangles, and squares represent the Lookout 701, Lookout 703, and MR404 reach pairs respectively. LO701 = Lookout 701, MR404 = McRae 404, and LO703 = Lookout 703.

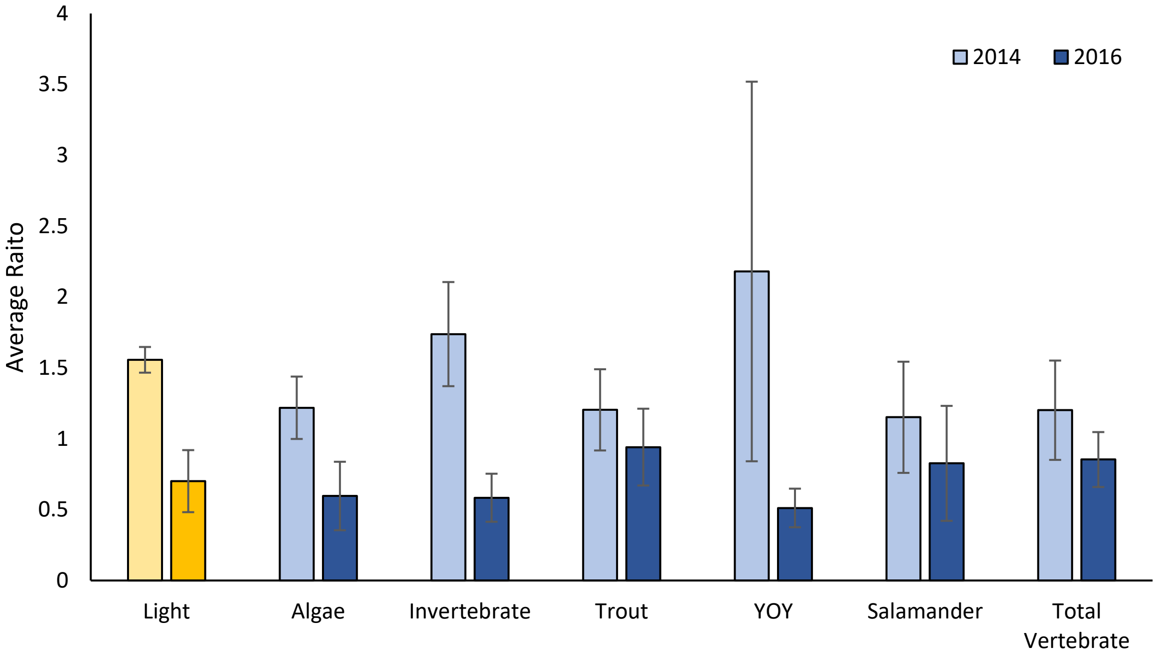


Figure 5: Reach scale averages of the ratio of manipulation to reference for light (PAR), algae (chlorophyll-*a*), macroinvertebrate biomass, trout biomass, YOY biomass, salamander biomass, and total vertebrate biomass. Error bars are ±one standard error calculated from individual ratios from each site.

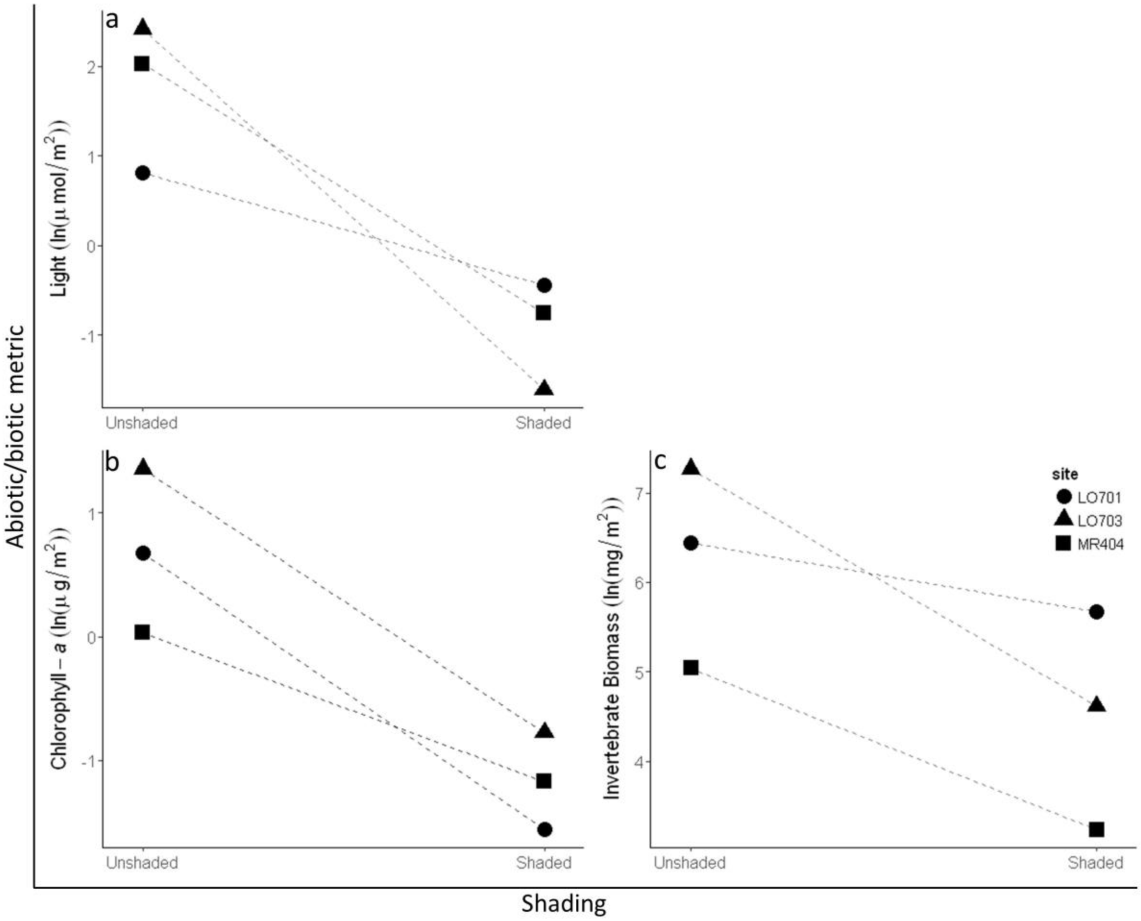


Figure 6: Comparisons of unshaded and shaded locations within each manipulation reach in 2016 while the tarps were deployed. LO703 = Lookout 703, MR404 = McRae 404, and LO701 = Lookout 701.

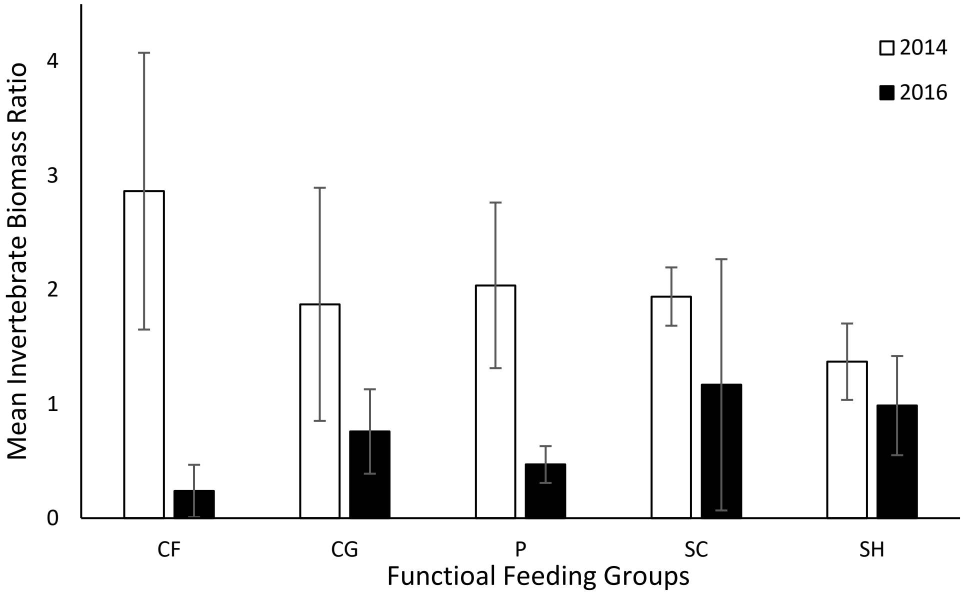


Figure 7: Mean manipulation to reference ratios of macroinvertebrate biomass per functional feeding groups. Macroinvertebrate biomass consistently decreased across all levels of community structure in the manipulation reaches, with respect to the reference reaches, when the shading manipulation was in place in 2016. CF = collector-filter, CG = collector-gatherer, P = predator, SC = scraper, SH = shredder.

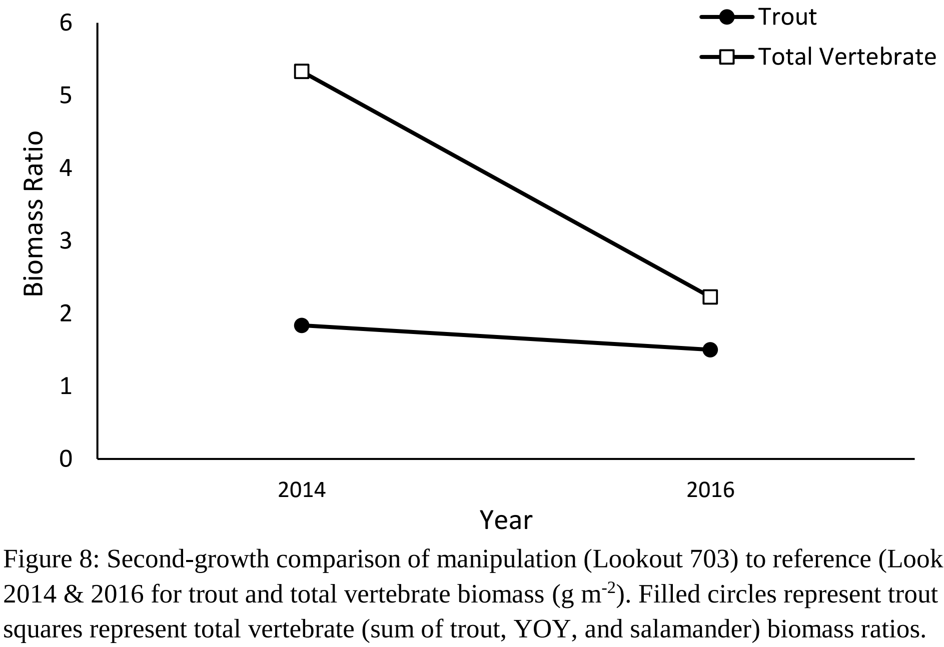


Figure 8: Second-growth comparison of manipulation (Lookout 703) to reference (Lookout 701) ratios between 2014 & 2016 for trout and total vertebrate biomass (g m^{-2}). Filled circles represent trout biomass ratios and filled in squares represent total vertebrate (sum of trout, YOY, and salamander) biomass ratios.

Tables

									2014	2016
Site	Reach type	Reach length (m)	Forest age class	Canopy cover (%)	Gradient (%)	Large wood (m^3 90m^{-2})	% Pool area (m^2)	Mean bankfull width (m)	Mean wetted width (m)	Mean wetted width (m)
LO703	Manipulation	90	SG	67.3	6.4	0.7	15.4	7.4	4.4	4.1
	Reference	90	OG	71.0	6.4	2.0	16.8	7.8	4.2	4.7
MR404	Manipulation	90	SG	46.2	4.0	0.3	19.2	8.6	3.8	4.5
	Reference	90	OG	66.0	7.6	6.8	41.0	10.4	4.0	5.3
LO701	Manipulation	90	OG	89.5	7.1	2.7	40.2	9.9	4.9	6.1
	Reference	90	SG	79.8	6.0	0.9	42.4	9.0	5.6	5.0

Table 1: Habitat characteristics of three streams and study reaches. Forest types, old-growth and second-growth, are referred to as OG and SG respectively. Large wood is reported in volume per 100 meters of reach area and percent pool area is calculated for reach area.

Year	Site	PAR	Chlorophyll-*a*	Invertebrate Biomass	Trout Biomass	YOY Biomass	Salamander Biomass	Sculpin Biomass	Total Vertebrate Biomass
2014	LO703	1.69	0.99	1.85	1.77	0.82	1.77	0	1.75
	MR404	1.38	1.00	1.06	0.87	0.86	1.26	2.73	1.30
	LO701	1.60	1.66	2.31	0.97	4.86	0.42	0	0.55
2016	LO703	0.69	1.08	0.31	1.47	0.71	0.51	0	0.89
	MR404	0.33	0.31	0.54	0.57	0.58	0.33	1.91	0.50
	LO701	1.09	0.40	0.90	0.79	0.25	1.63	0	1.17

Table 2: Manipulation reach to reference reach ratio for all in-stream metrics. LO703 = Lookout 703, MR404 = McRae 404, and LO701 = Lookout 701. PAR (µmol m^{-2} sec^{-1}), Chlorophyll-*a* (µg m^{-2}), Invertebrate Biomass (mg m^{-2}), Trout Biomass (g m^{-2}), YOY Biomass (g m^{-2}), Salamander Biomass (g m^{-2}), Sculpin Biomass (g m^{-2}), Total Vertebrate Biomass (g m^{-2}).

Year	Site	Reach	Average Daily Temperature (°C)	Average Max Daily Temperature (°C)
2014	LO703	Manipulation	9.3	9.8
		Reference	9.1	9.6
	MR404	Manipulation	13.7	14.7
		Reference	13.7	14.4
	LO701	Manipulation	9.8	10.1
		Reference	10.2	10.5
2016	LO703	Manipulation	8.4	9.2
		Reference	8.7	9.2
	MR404	Manipulation	12.2	14.2
		Reference	12.9	14.0
	LO701	Manipulation	8.9	9.8
		Reference	9.7	10.1

Table 3: Average stream temperature for all study reaches in both years of data collection. Temperature was collected from July through the beginning of September at the bottom of each study reach. LO703 = Lookout 703, MR404 = McRae 404, and LO701 = Lookout 701.

Metric	n	Estimate	Std. Error	t-value	DF	P-value	Lower.CI	Upper.CI
Light	3	-0.43	0.0	-4.95	2	0.038	-0.80	-0.06
Chlorophyll-*a*	3	-0.31	0.16	-1.90	2	0.197	-1.01	0.39
Invertebrate Biomass	3	-0.58	0.16	-3.58	2	0.069	-1.27	0.12
Trout Biomass	3	-0.13	0.02	-6.26	2	0.025	-0.22	-0.04
YOY Biomass	3	-0.83	0.67	-1.24	2	0.341	-3.73	2.06
Salamander Biomass	3	-0.16	0.28	-0.58	2	0.623	-1.38	1.05
Total Vertebrate Biomass	3	-0.17	0.20	-0.87	2	0.476	-1.04	0.69

Table 4: Statistical comparisons based on paired t-tests of the mean manipulation to reference ratio for each metric in 2014 and 2016. Estimated difference is between the mean 2014 and 2016 ratios for each metric listed. Lower.CI and Upper.CI are 95% confidence intervals for the estimated mean difference. DF = degrees of freedom.

Metric	n	Estimated Difference	Std. Error	t-value	DF	P-value	Lower.CI	Upper.CI
Light (PAR)	3	-2.69	0.6	-4.5	2	0.046	-5.25	-0.12
Chlorophyll-a	3	-1.86	0.33	-5.64	2	0.03	-3.27	-0.44
Invertebrate Biomass	3	-1.74	0.55	-3.19	2	0.086	-4.1	0.61

Table 5: Statistical comparisons based on paired t-tests of the median value for each metric in shaded and unshaded locations within the manipulation reaches in 2016. Estimated difference is between the median unshaded and shaded sampling locations for the natural-log of amount of each metric: light (PAR), chlorophyll-*a*, and invertebrate biomass. Lower.CI and Upper.CI are the 95% confidence intervals for the estimated median difference between unshaded and shaded sites. DF = degrees of freedom.

Year	Site	CF	CG	P	SC	SH
2014	LO703	1.70	1.02	1.16	1.45	1.28
	MR404	1.60	0.69	1.48	2.08	0.84
	LO701	5.28	3.90	3.47	2.30	1.99
2016	LO703	0.70	0.60	0.78	0.03	0.17
	MR404	0.02	0.21	0.37	0.11	1.65
	LO701	NA	1.46	0.25	3.37	1.13

Table 6: Manipulation to reference ratio of macroinvertebrate biomass for all functional feeding groups (FFG). CF = collector-filter, CG = collector-gatherer, P = predator, SC = scraper, SH = shredder. LO703 = Lookout 703, MR404 = McRae 404, and LO701 = Lookout 701. NA = no invertebrates is identified FFG detected in sample, therefore ratio not calculated.

Bibliography

Arar, E. J., and G. B. Collins. 1997. Method 445.0 In Vitro Determination of Chlorophyll a and Pheophytin in Marine and Freshwater Algae by Fluorescence. U.S. Environmental Protection Agency, Washington, DC.

Arismendi, I., M. Safeeq, J. B. Dunham, and S. L. Johnson. 2014. Can air temperature be used to project influences of climate change on stream temperature? *Environmental Research Letters* 9(8):84015.

Battin, T. J., L. A. Kaplan, S. Findlay, C. S. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold, and F. Sabater. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience* 1:95–100.

Bechtold, H., A. Marcarelli, C. Baxter, and R. Inouye. 2012. Effects of N, P, and organic carbon on stream biofilm nutrient limitation and uptake in a semi-arid watershed. *Limnology and Oceanography* 57:1544–1554.

Beschta, R. L., and R. L. Beschta. 1997. Society for Range Management Riparian Shade and Stream Temperature : An Alternative Perspective Published by : Society for Range Management Stable URL : http://www.jstor.org/stable/4001341 Riparian Shade and Stream Temperature : An Alternative Perspective. *Society for* 19(2):25–28.

Boston, H. L., and W. R. Hill. 1991. Photosynthesis-light relations of stream periphyton communities. *Limnology and Oceanography* 36(4):644–656.

Brett, M. T., M. J. Kainz, S. J. Taipale, H. Seshan, M. T. Brett3-, M. J. Kainzb, S. J. Taipalea, and D. M. Karl. 2009. Phytoplankton, Not Allochthonous Carbon, Sustains Herbivorous Zooplankton Production. *Proceedings of the National Academy of Sciences of the United States of America* 106(50):21197–21201.

Brown, G. W., and J. T. Krygier. 1970. Effects of clear-cutting on stream temperature. *Water Resources Research* 6(4):1133–1139.

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.

Chazdon, R. L., and R. W. Pearcy. 1986. Photosynthetic responses to light variation in rain-forest species: carbon gain and photosynthetic efficiency during lightflecks. *Oecologia* 69(4):524–531.

Clipp, H. L., and J. T. Anderson. 2014. Environmental and anthropogenic factors influencing salamanders in riparian forests: A review. *Forests* 5(11):2679–2702.

Cole, L., and M. Newton. 2015. Relationships between radiation and canopy closure estimates in streamside buffers in Western Oregon. *Forest Science* 61(June):559–569.

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.

Danehy, R. J., C. G. Colson, K. B. Parrett, and S. D. Duke. 2005. Patterns and sources of thermal heterogeneity in small mountain streams within a forested setting. *Forest Ecology and Management* 208(1–3):287–302.

Dudaniec, R. Y., and J. S. Richardson. 2012. Habitat associations of the Coastal Giant Salamander (dicamptodon tenebrosus) at its northern range limit. *Herpetological Conservation and Biology* 7(1):1–15.

Franklin, J. F., and R. Van Pelt. 2004. Spatial aspects of structural complexity in old-growth forests. *Journal of Forestry* 102(May):22–28.

Fuchs, S. A., S. G. Hinch, and E. Mellina. 2003. Effects of streamside logging on stream macroinvertebrate communities and habitat in the sub-boreal forests of British Columbia, Canada. *Canadian Journal of Forest Research* 33(8):1408–1415.

Gjerløv, C., and J. S. Richardson. 2010. Experimental increases and reductions of light to streams: Effects on periphyton and macroinvertebrate assemblages in a coniferous forest landscape. *Hydrobiologia* 652(1):195–206.

Groom, J. D., L. Dent, and L. J. Madsen. 2011a. Stream temperature change detection for state and private forests in the Oregon Coast Range. *Water Resources Research* 47(1):1–12.

Groom, J. D., L. Dent, L. J. Madsen, and J. Fleuret. 2011b. Response of western Oregon (USA) stream temperatures to contemporary forest management. *Forest Ecology and Management* 262(8):1618–1629.

Guo, F., M. J. Kainz, D. Valdez, F. Sheldon, and S. E. Bunn. 2016. High-quality algae attached to leaf litter boost invertebrate shredder growth. *Freshwater Science* 35(August):0.

Hall, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. *Ecosystems* 19:73–86.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Desity of Fish and Salamanders in Relation to Riparian Canopy and Physical Habitat in Streams of the Northwestern United States. *Fisheries and Aquatic Sciences* 40(8):1173–1185.

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(4):1297–1309.

Hoellein, T. J., D. A. Bruesewitz, and D. C. Richardson. 2016. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. *Limnology and Oceanography* 58(6):2089–2100.

Huryn, A. D., J. P. Benstead, and S. M. Parker. 2014. Seasonal changes in light availability modify the temperature dependence of ecosystem metabolism in an arctic stream. *Ecology* 95(10):2840–2850.

Jaffé, R., D. McKnight, N. Maie, R. Cory, W. H. McDowell, and J. L. Campbell. 2008. Spatial and temporal variations in DOM composition in ecosystems: The importance of long-term monitoring of optical properties. *Journal of Geophysical Research: Biogeosciences* 113:1–15.

Johnson, S. L. 2003. Stream temperature: scaling of observations and issues for modelling. *Hydrological Processes* 17(2):497–499.

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(6):913–923.

Julian, J. P., M. W. Doyle, and E. H. Stanley. 2008. Empirical modeling of light availability in rivers. *Journal of Geophysical Research* 113(G3):1–16.

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.

Kahlert, M., and B. G. McKie. 2014. Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environmental science. Processes & impacts* 16:2627–34.

Kaylor, M. J., and D. R. Warren. 2017a. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. *Ecosphere* 8(6):1–19.

Kaylor, M. J., and D. R. Warren. 2017b. Quantifying biotic and abiotic changes in headwater streams after 40 years of post logging riparian forest regeneration. *Canadian Journal of Fisheries and Aquatic Sciences* In Press.

Kaylor, M. J., D. R. Warren, and P. M. Kiffney. 2017. Long-term effects of riparian forest harvest on light in Paci fi c Northwest (USA) streams 2(July 2016):1–13.

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(3):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(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(July 2015):542–555.

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(4):1088–1103.

Kroll, A. J. 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. *Forest Ecology and Management* 257:1188–1199.

Leuthold, N., M. J. Adams, and J. P. Hayes. 2012. Short-term response of Dicamptodon tenebrosus larvae to timber management in southwestern Oregon. *Journal of Wildlife Management* 76(1):28–37.

Lockwood, R. N., and J. C. Schneider. 2000. Stream Fish Population Estimates by Mark-and-Recapture and Depletion Methods. Page *Manual of fisheries survey methods*. Fisheries. Michagan Department of Natural Resources.

MacKinzie, D. I., J. D. Nicholas, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.

Matheson, F. E., J. M. Quinn, and M. L. Martin. 2012. Effects of irradiance on diel and seasonal patterns of nutrient uptake by stream periphyton. *Freshwater Biology* 57(8):1617–1630.

Mayer, M. S., and G. E. Likens. 1987. The Importance of Algae in a Shaded Headwater Stream as Food for an Abundant Caddisfly The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). *Source Journal of the North American Benthological Society J. N. Am. Benthol. Soc* 6(4):262–269.

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

Meleason, M. A., S. V. Gregory, and J. P. Bolte. 2003. Implications of riparian management strategies on wood in streams of the Pacific Northwest. *Ecological Applications* 13(5):1212–1221.

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(7):1280–1301.

Merritt, R. W., and K. W. Cummins. 1996. *An introduction to the aquatic insects of North America*. Third edition. Kendall/Hunt, Dubuque, Iowa.

Noel, D. S., C. W. Martin, and C. A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. *Environmental Management* 10(5):661–670.

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(5):665–683.

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 …* 19(4):609–620.

Sievers, M., R. Hale, and J. R. Morrongiello. 2017. Do trout respond to riparian change? A meta-analysis with implications for restoration and management. *Freshwater Biology* 62(3):445–457.

Torgersen, C. E., D. M. Price, and H. W. Li. 1999. Multiscale thermal refugia and stream habitat associations of Chinook Salmon in northeastern Oregon. *Ecological Applications* 9(1):301–319.

Tranvik, L. J. 1992. Allochthonous dissolved organic carbon-matter as an energy-sourcee for pelagic bacteria and the concept of the microbiual loop. *Hydrobiologia* 229(1):107–114.

Warren, D. R., S. M. Collins, E. M. Purvis, M. J. Kaylor, and H. A. Bechtold. 2017. Spatial variability in light yields colimitation of primary production by both light and nutrients in a forested stream ecosystem. *Ecosystems* 20.

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(4):547–558.

Warren, D. R., W. S. Keeton, P. M. Kiffney, M. J. Kaylor, H. A. Bechtold, and J. Magee. 2016. Changing Forests – Changing Streams: Riparian forest stand development and ecosystem function in temperate headwaters. *Ecosphere* 7(8):1–19.

Warren, D. R., M. M. Mineau, E. J. Ward, and C. E. Kraft. 2010. Relating fish biomass to habitat and chemistry in headwater streams of the northeastern United States. *Environmental Biology of Fishes* 88(1):51–62.

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.

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.

Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences of the United States of America* 90(February):1384–1387.

Appendix

Supplemental chlorophyll-*a* methods

After collection, tiles and stream water were transported back to the laboratory in a cooler. Periphyton was then scrapped off each tile using a wire brush and slurries from each tile scraping. Periphyton/DI water slurries were filtered using Whatman 47 mm GF/F glass fiber filters, which were subsequently frozen for 24 to 48 hours. Chlorophyll-*a* was extracted from filtered periphyton samples with 15 ml of 90% acetone. Samples were then brought to room temperature in the dark for two to four hours. Chlorophyll-*a* concentration was then measured using a handheld flourometer and values were recorded.

After chlorophyll-*a* was quantified with the BenthoTorch measurements, tiles suspended in stream water were transported back to the laboratory in a cooler to be analyzed with ash free dry mass (AFDM) methods. Periphyton was scraped off tiles with wire brushes and washed with deionized water, the resulting slurry was filtered through a Whatman 47 mm pre-ashed micron GF/F glass fiber filters. The samples of filtered periphyton were then dried for 24 hours at 60 degrees centigrade and weighed to determine dry weight (g). Samples were then placed in a muffle-furnace at 500 degrees centigrade for two hours and re-weighed to determine ashed-mass (g cm^{-2}). To quantify how patchy decreases in light influenced accrued periphyton, we averaged the three replicate samples every 10 meters along each stream reach. We also calculated the reach average accrued chlorophyll-*a* to compare responses at reach scales. The average reach-scale chlorophyll-*a* ratios, of manipulation to reference reach, were compared between the two study years; 2014 before the shading manipulations, and 2016 during the shading manipulations. We used these values to compare localized, within-reach responses of algae in shaded and unshaded sites. To assess the influence of decreases in light on local, within reach-scale, chlorophyll-*a* accrual, we compared the average chlorophyll-*a* directly under tarps to between the tarps, as shaded and unshaded, among the manipulation reaches of all three reach pairs in 2016.

Additional Figures

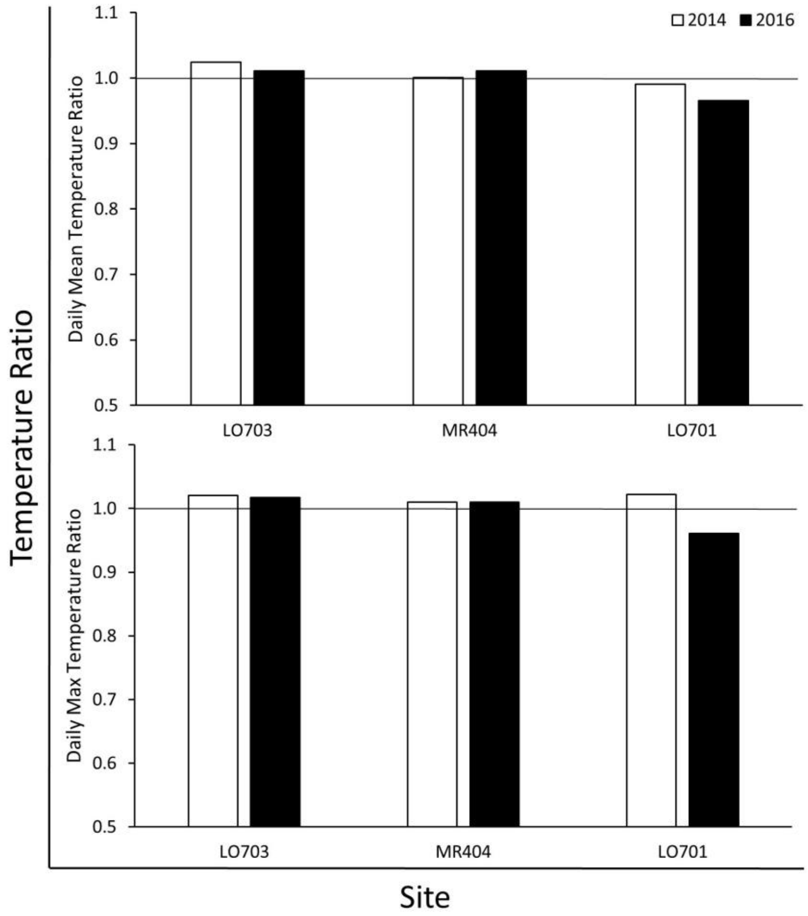


Figure A1: Temperature reference to manipulation ratios for all sites and both years. Values above horizontal line (at 1) indicated that the manipulation reach had higher temperatures than the reference reach and values below horizontal line indicated that the manipulation reach had cooler temperatures than the reference reach. LO701 = Lookout 701, LO703 = Lookout 701, and MR404 = McRae 404.

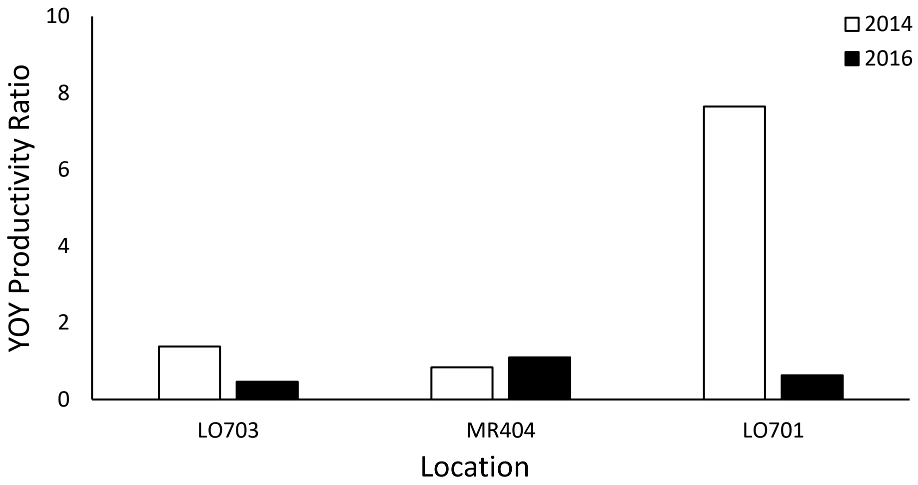
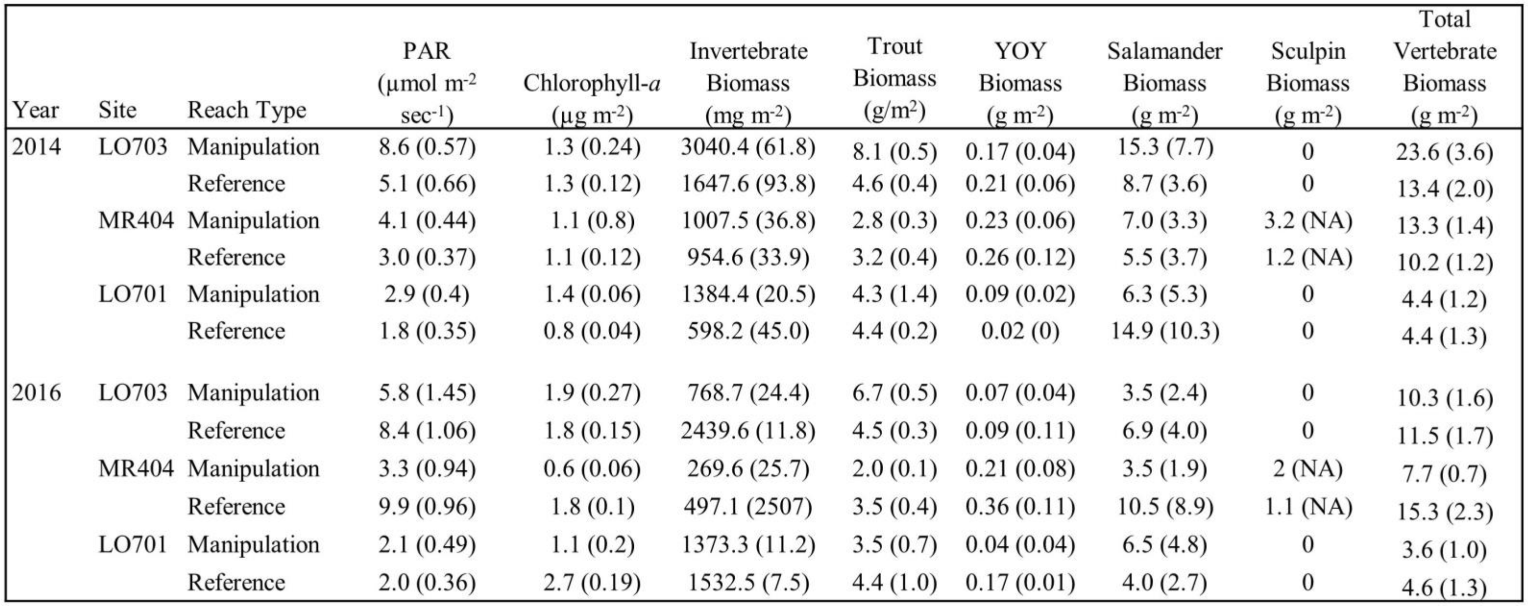


Figure A2: Young-of-the-year (YOY) productivity ratio - the manipulation reach with respect to the reference reach - as growth rate (g day^{-1}) relative to abundance. In Lookout 703 (LO703) and Lookout 701 (LO701), the productivity ratio decreased, however in McRae 404 (MR404) it stayed relatively constant.

Additional Tables



Year	Site	Reach Type	PAR (µmol m^{-2} sec^{-1})	Chlorophyll-*a* (µg m^{-2})	Invertebrate Biomass (mg m^{-2})	Trout Biomass (g/m^{2})	YOY Biomass (g m^{-2})	Salamander Biomass (g m^{-2})	Sculpin Biomass (g m^{-2})	Total Vertebrate Biomass (g m^{-2})
2014	LO703	Manipulation	8.6 (0.57)	1.3 (0.24)	3040.4 (61.8)	8.1 (0.5)	0.17 (0.04)	15.3 (7.7)	0	23.6 (3.6)
		Reference	5.1 (0.66)	1.3 (0.12)	1647.6 (93.8)	4.6 (0.4)	0.21 (0.06)	8.7 (3.6)	0	13.4 (2.0)
	MR404	Manipulation	4.1 (0.44)	1.1 (0.8)	1007.5 (36.8)	2.8 (0.3)	0.23 (0.06)	7.0 (3.3)	3.2 (NA)	13.3 (1.4)
		Reference	3.0 (0.37)	1.1 (0.12)	954.6 (33.9)	3.2 (0.4)	0.26 (0.12)	5.5 (3.7)	1.2 (NA)	10.2 (1.2)
	LO701	Manipulation	2.9 (0.4)	1.4 (0.06)	1384.4 (20.5)	4.3 (1.4)	0.09 (0.02)	6.3 (5.3)	0	4.4 (1.2)
		Reference	1.8 (0.35)	0.8 (0.04)	598.2 (45.0)	4.4 (0.2)	0.02 (0)	14.9 (10.3)	0	4.4 (1.3)
2016	LO703	Manipulation	5.8 (1.45)	1.9 (0.27)	768.7 (24.4)	6.7 (0.5)	0.07 (0.04)	3.5 (2.4)	0	10.3 (1.6)
		Reference	8.4 (1.06)	1.8 (0.15)	2439.6 (11.8)	4.5 (0.3)	0.09 (0.11)	6.9 (4.0)	0	11.5 (1.7)
	MR404	Manipulation	3.3 (0.94)	0.6 (0.06)	269.6 (25.7)	2.0 (0.1)	0.21 (0.08)	3.5 (1.9)	2 (NA)	7.7 (0.7)
		Reference	9.9 (0.96)	1.8 (0.1)	497.1 (2507)	3.5 (0.4)	0.36 (0.11)	10.5 (8.9)	1.1 (NA)	15.3 (2.3)
	LO701	Manipulation	2.1 (0.49)	1.1 (0.2)	1373.3 (11.2)	3.5 (0.7)	0.04 (0.04)	6.5 (4.8)	0	3.6 (1.0)
		Reference	2.0 (0.36)	2.7 (0.19)	1532.5 (7.5)	4.4 (1.0)	0.17 (0.01)	4.0 (2.7)	0	4.6 (1.3)

Table A1: Abiotic and biotic measurements for all 3 reach pairs before shading manipulation in 2014 and in 2016 during shading manipulation. LO701 = Lookout 701, LO703 = Lookout 701, and MR404 = McRae 404. Standard error is in parentheses next to PAR, chlorophyll-*a*, and invertebrate biomass. The lower bound of 95% confidence interval is in parentheses next to trout, YOY, salamander, sculpin, and total vertebrate biomasses.

		Manipulation to Reference Ratio	
Year	Site	Daily Mean Temperature	Daily Maximum Temperature
2014	LO703	1.02	1.02
	MR404	1.00	1.02
	LO701	0.99	1.01
2016	LO703	1.01	1.01
	MR404	1.01	1.02
	LO701	0.97	0.96

Table A2: Mean daily temperature and mean daily maximum temperature manipulation to reference reach ratios for all sites and both study years. LO701 = Lookout 701, LO703 = Lookout 701, and MR404 = McRae 404.

Site	Reach Type	Position
LO703	Manipulation	44°13.801‘N, 122°07.866‘W
	Reference	44°13.755‘N, 122°07.772‘W
MR404	Manipulation	44°15.225‘N, 122°10.178‘W
	Reference	44°15.254‘N, 122°10.062‘W
LO701	Manipulation	44°14.027‘N, 122°09.010‘W
	Reference	44°14.011‘N, 122°09.249‘W

Table A3: Location, in DMS coordinates, for the bottom (meter 90) of each of our study sites.