

Aquatic food web response to patchy shading along forested headwater streams

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Abstract: In forested streams, changes in age and structure of riparian vegetation have been shown to directly influence the amount of light reaching the stream benthos. The potential for light to directly impact primary productivity in forested streams is generally understood, but most field experiments exploring reach-scale in-stream light dynamics have evaluated large changes in riparian vegetation. Fewer studies have quantified influences of smaller changes in irradiance, particularly how patchy in-stream light developed with complex riparian forests affects stream biota. We applied patches of shade, covering ~50% of three manipulation reaches, which were each paired with an unmanipulated reference reach. We quantified changes in stream light availability, benthic periphyton, and aquatic macroinvertebrate, fish, and salamander biomass using a before–after control–impact study design. Patchy shading decreased localized and reach-scale light and reduced periphyton, macroinvertebrate, fish, and salamander biomass in manipulation sites relative to the reference reaches. Results suggest that moderate changes in stream light, such as those that occur through stand development and small-scale disturbance processes, can impact stream biota through bottom-up processes.

Résumé : Il a été démontré que, dans les cours d'eau forestiers, les variations de l'âge et de la structure de la végétation riveraine influencent directement la quantité de lumière qui atteint le benthos du cours d'eau. Le potentiel d'influence directe de la lumière sur la production primaire dans les cours d'eau forestiers est généralement compris, mais la plupart des expériences sur le terrain qui examinent la dynamique de la lumière dans les cours d'eau à l'échelle du tronçon s'attardent à des variations importantes de la végétation riveraine. Moins d'études ont quantifié les influences de variations plus faibles de l'éclairement énergétique, plus particulièrement l'effet sur le biote du cours d'eau de la lumière irrégulière associée à des forêts riveraines complexes. Nous avons appliqué des parcelles d'ombre couvrant ~50 % de trois tronçons expérimentaux, chacun étant jumelé à un tronçon non traité de référence. Nous avons quantifié les variations de la disponibilité de lumière dans le cours d'eau, du périphyton benthique et de la biomasse de macroinvertébrés aquatiques, de poissons et de salamandres selon un schéma d'étude avant–après témoin–incidence. L'ombrage parcellaire a entraîné une diminution de la lumière localement et à l'échelle du tronçon, et de la biomasse du périphyton, des macroinvertébrés, des poissons et des salamandres dans les sites traités par rapport aux sites de référence. Les résultats indiqueraient que des variations modérées de la lumière dans les cours d'eau, comme celles qui découlent du développement de peuplements et de perturbations à petite échelle, peuvent avoir une incidence sur le biote du cours d'eau par l'entremise de processus ascendants. [Traduit par la Rédaction]

Introduction

Forested stream ecosystems are directly and indirectly influenced by plant communities in adjacent riparian zones. 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 stream light availability that can influence 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 (McCutchan and Lewis 2002; Brett et al. 2009; Guo et al. 2016). Given the importance of autotrophic carbon, factors that affect stream primary

production have the potential to impact controls on bottom-up drivers of the larger stream food web.

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 via changes in temperature, food availability, structure, and nutrients (Noel et al. 1986; Wilzbach et al. 2005; Wootton 2012). However, the nature of 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). The wholesale loss or removal of riparian forests along streams is relatively uncommon across North America with today's forest management regulations, but more moderate changes in the canopy may become increasingly

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common. Invasive pests that kill riparian trees and stand development dynamics in riparian forests are expected to change light availability reaching streams by creating a more patchy, heterogeneous light environment (Warren et al. 2016). While relatively small in magnitude compared with clear-cutting, these changes in light have the potential to influence stream food webs. For example, in an assessment of buffer width effects on stream ecosystem processes, Kiffney et al. (2003) found that reaches with larger buffer widths allowed less light to reach the stream, resulting in lower periphyton accumulation compared with reaches with smaller riparian buffers. Shading studies in experimental stream channels have further demonstrated the importance of light for primary production (Quinn et al. 1997; Kiffney et al. 2004; Matheson et al. 2012). However, in situ studies assessing shading impacts on stream primary production or biota are less common. A study conducted in British Columbia, Canada, covered a 5 m riffle section with shade cloth in each of 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 (Gjerlov and Richardson 2010). That research demonstrated the possible link between modification of local light conditions and in-stream primary production in a natural stream setting, but it did not assess impacts of their effect on higher trophic levels in the food web.

When whole food web responses are considered, changes in light may manifest through multiple trophic levels (Wootton 2012), or they may appear only in select consumers 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 gross primary production (Bilby and Bisson 1992). Wootton (2012), for example, found that logging one side of a forested stream resulted in a 40% decrease in canopy cover and a 42-fold increase in light reaching the stream. This resulted in increased algal production, algal standing stocks, and macroinvertebrate and juvenile salmonid densities. In a correlative study of forested Oregon streams, Kaylor and Warren (2017a) also found that the biomass of periphyton, macroinvertebrates, fish, and total vertebrates were positively correlated with canopy cover. The potential importance of light was also highlighted in a meta-analysis of the effects of riparian forest harvest and stream cleaning (removal of large wood) on salmonids. Streams that were not cleaned during timber harvest generally exhibited a positive response in fish biomass and density after logging when light levels increased (Mellina and Hinch 2009). A more recent review of the response of fish to a variety of riparian changes (including forest harvest, livestock grazing, and restoration efforts) found inconsistent responses in trout populations to changing riparian conditions (Sievers et al. 2017); however, this review did find a consistent negative response in trout abundance associated with riparian afforestation, which increases stream canopy cover. This result is consistent with conceptual models developed to project changes in fish biomass over time following canopy closure responding primarily to generalized patterns in stream light over time (Mellina and Hinch 2009; Warren et al. 2016). However, the empirical afforestation result from Sievers et al. (2017) was based on only a few studies, and the authors highlight the need for experimental studies quantifying shading and afforestation effects on streams.

In this study, we implemented in situ manipulations of stream light to explicitly investigate how patchy shading along natural streams (mimicking a pattern in stream light that commonly develops in streams with late-succession riparian forests) affects periphyton and stream consumers. 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, macroinvertebrates, fish, and sala-

manders responded in the manipulated reach relative to the reference reach in a before–after control–impact (BACI) study design. Our hypotheses were derived from earlier correlative (Kaylor and Warren 2017a) and experimental studies (Kaylor and Warren 2017b) in this system. With decreased light reaching the stream benthos, we expected to see a reduction in the growth of in-stream autotrophs through the summer and with this a decrease in algal-consuming 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 H.J. 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 (Fig. 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 1600 m and encompasses the 6400 hectares of the Lookout Creek watershed. The HJA consists of a mixture of forest types, including late-successional forests (~500 years old), unmanaged mature forests (~100–150 years old), and second-growth forests (<70 years old) regenerating from previous timber harvest. Primary forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja 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 and coastal giant salamanders (*Dicamptodon tenebrosus*) are the dominant vertebrate predators in these lower-order streams. Sculpin (*Cottus* spp.) are also present at limited densities in the lower reaches of McRae Creek.

Our study consisted of three stream pairs: two on Lookout Creek and one located on McRae Creek (Fig. 1). Each pair had a reference reach in which light was not altered and a manipulation reach in which light was decreased through artificial shading. All reaches were 90 m in length with a 200–250 m buffer separating reaches within a reach pair. Each of the pairs was located on third-order stream sections with bankfull widths ranging from 7.4 to 10.4 m (Table 1). In all reach pairs, one of the reaches was bordered by old-growth riparian forest on both stream banks, and the other was bordered by second-growth riparian forest on one stream bank and old-growth riparian forest on the other stream bank.

Shading manipulation

We used a BACI study design. Pretreatment data were collected in all six reaches in summer 2014 (June–September). Shading manipulations were applied to one reach in each pair in May 2016 and were left in place until October 2016. Post-treatment data were collected in all reaches in summer 2016 (July–September). In each reach pair, the shading manipulation was applied to the reach with higher initial light (based on 2014 surveys; Table 1). This resulted in shading being applied to the reach bordered by second growth in the McRae Creek reach pair (hereinafter McRae 404; named for the harvest unit associated with the second-growth reach) and the upstream Lookout Creek reach pair (hereinafter Lookout 703) but the old-growth reach in the downstream Lookout Creek reach pair (hereinafter Lookout 701). Brown opaque tarps were used to shade patches along each study stream. Tarps were positioned with the high peaked center line perpendicular to the stream and tethered to adjacent trees and rocks. This design effectively shaded streams and allowed inputs of leaf

Fig. 1. Map of the H.J. 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 filled circles representing the manipulation reaches.

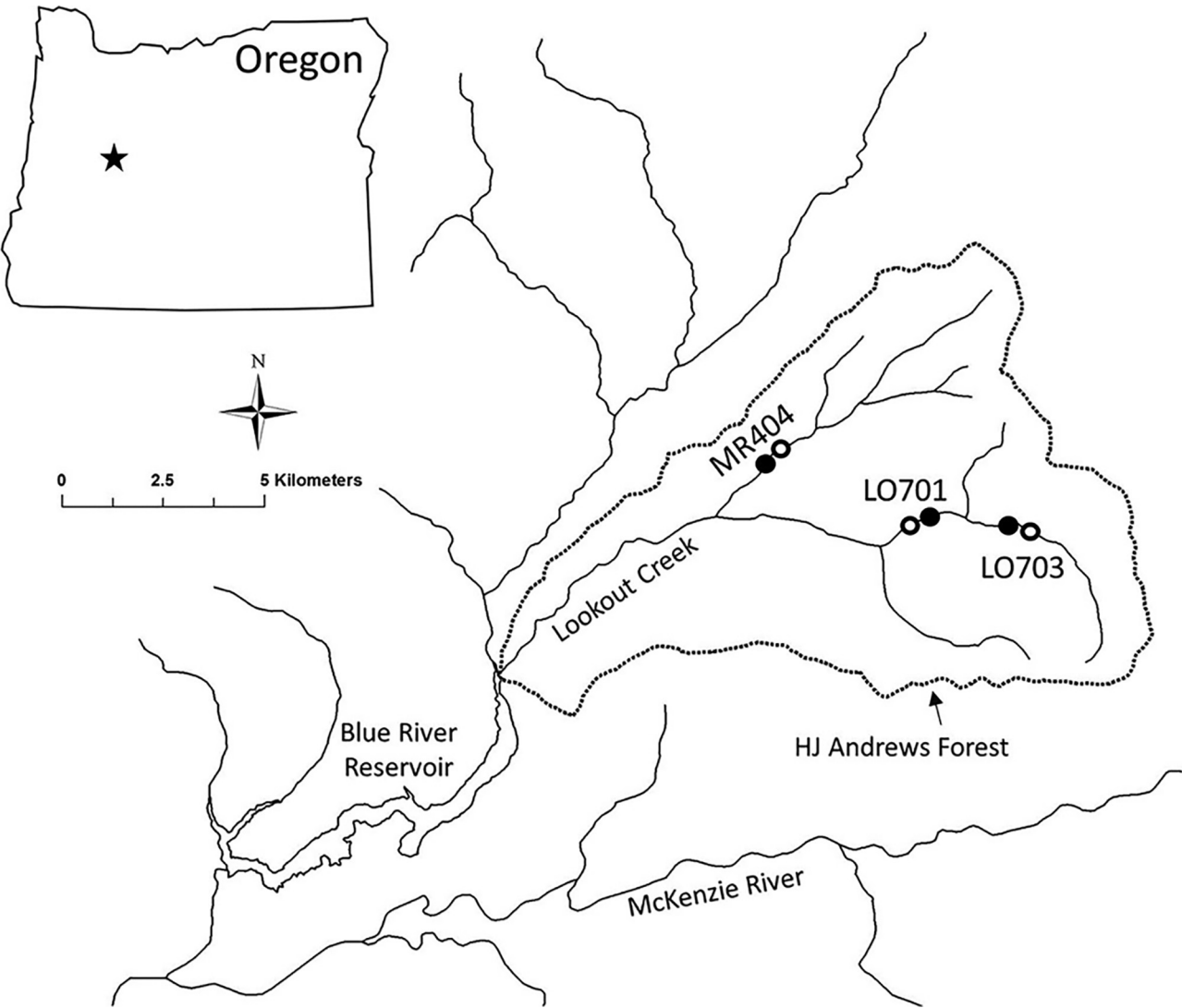


Table 1. Habitat characteristics of three streams and study reaches.

Site	Reach type	Reach length (m)	Forest age class	Canopy cover (%)	Gradient (%)	% Pool area	Bankfull width (m)	2014		2016	
								Wetted width (m)	Temp. (°C)	Wetted width (m)	Temp. (°C)
LO703	Manipulation	90	SG	67.3	6.4	15.4	7.4	4.4	9.3	4.1	8.4
	Reference	90	OG	71.0	6.4	16.8	7.8	4.2	9.1	4.7	8.7
MR404	Manipulation	90	SG	46.2	4.0	19.2	8.6	3.8	13.7	4.5	12.2
	Reference	90	OG	66.0	7.6	41.0	10.4	4.0	13.7	5.3	12.9
LO701	Manipulation	90	OG	89.5	7.1	40.2	9.9	4.9	9.8	6.1	8.9
	Reference	90	SG	79.8	6.0	42.4	9.0	5.6	10.2	5.0	9.7

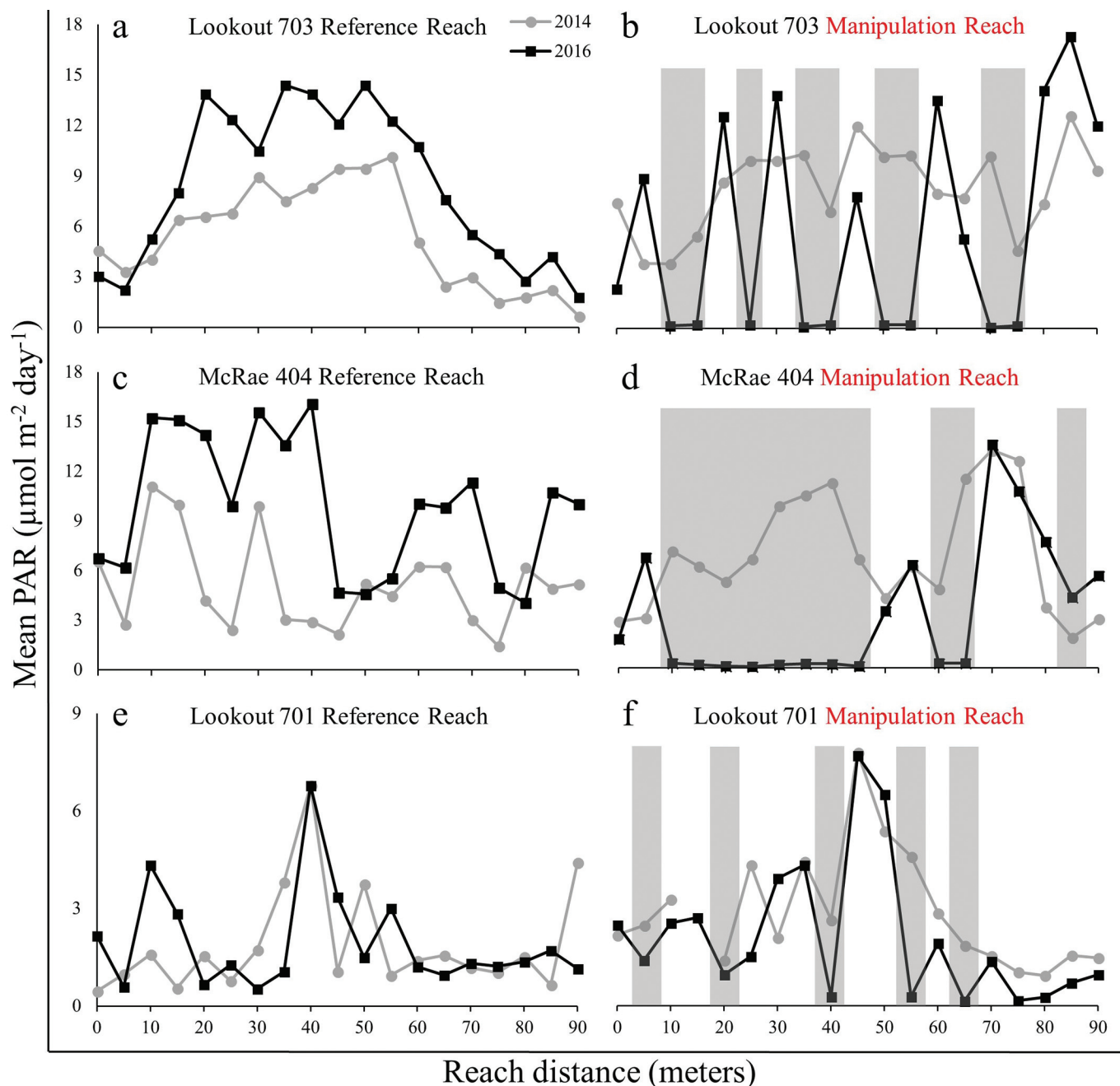
Note: Forest types are old-growth (OG) and second-growth (SG). Percent pool area is calculated over total reach area. Bankfull and wetted widths are for the mean across each 90 m reach, and temperature is reported as daily mean temperature.

litter and terrestrial invertebrates to fall into the stream (see online Supplementary material, Fig. S1¹). Collectively, the shading manipulation covered approximately 50% of each stream manipulation reach (Fig. 2). Specific tarp placement throughout stream reaches was determined during deployment based on logistical limitations and access. Tarp peaks were generally between 3 and

5 m above the stream, and tarp edges ranged from 1 to 3 m above the stream. The reference reach in each reach pair did not receive any shading manipulations; however, we walked through all three reference reaches in May 2016 without deploying the tarps to mimic stream disturbance associated with setting up the shading manipulation.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0464>.

Fig. 2. Profile of light (photosynthetically active radiation, 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 three replicates every 5 m along each study reach in both years. Shading (via tarps) is represented by grey rectangles in the manipulation reaches (panels b, d, and f). Shading was deployed during the summer of 2016 and can be seen to decrease light directly where tarps were placed. The onset of wildfire smoke in 2014 resulted in variability between PAR measurements, though the patterns along stream distance remained the same, and this was accounted for in the manipulation-to-reference ratios.



Quantifying abiotic variables

Light

To quantify stream light availability, we used arrays of photo-degrading fluorescein dye, deployed every 5 m along each study reach in the summers of both 2014 and 2016 (Table 1). An array of fluorescein vials consisted of three 3.5 mL vials zip-tied to a metal flag and deployed in the stream thalweg for 24 h. Fluorescein methods have been used to estimate benthic light availability in the HJA, and detailed methodology can be found in these studies (Kaylor et al. 2017; Warren et al. 2017). The resulting fluorescein

degradation for each location was converted to photosynthetically active radiation (PAR, in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) using an established standard curve for these streams developed in an earlier study (see Warren et al. 2017). PAR values from arrays deployed throughout each 90 m reach were averaged to produce one value for each reach, and this mean value was used in comparisons between manipulation and reference reaches in each pair in 2014 and 2016. We also compared the average light flux with the stream benthos between areas directly under the tarps (shaded locations) and unshaded locations within each of the manipulation reaches in 2016.

Stream habitat and temperature

Physical stream characteristics were sampled at transects set every 10 m along each of the six study reaches for a total of 10 transects for each study reach. In summer of 2014, at each transect, we quantified bankfull width, wetted width, thalweg depth, canopy cover, and volume of large wood (fallen wood within the bankfull channel >10 cm diameter and >1 m length). We also quantified length, width, maximum depth, and outflow depth of each pool within each study reach (Table 1). These same habitat variables were also measured in summer of 2016.

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 upstream and downstream ends of each reference reach and from early May (when tarps were deployed) through the end of September at the upstream and downstream ends of each manipulation reach. Temperature data loggers (HOBO Pro v2) encased in white PVC pipe to eliminate direct sunlight were fully submerged and placed on the stream benthos in the thalweg of the stream and recorded measurements every 15 min. We evaluated the change in mean daily average and mean daily maximum temperature between 2014 and 2016 by comparing the estimated mean change in the manipulation with reference ratio across all three reach pairs with paired *t* tests.

Quantifying biotic variables

Periphyton

We estimated periphyton biomass accrual during the summer in 2014 and 2016 through quantification of net benthic chlorophyll *a* growth on 15 cm × 15 cm unglazed ceramic tiles (225 cm²). In 2014, one tile was deployed in the stream thalweg every 10 m in each study reach (*n* = 10 per reach) for 6 weeks in midsummer. During this first year of the study, chlorophyll *a* on tiles was quantified using laboratory fluorometric methods and phaeophytin correction outlined in Environmental Protection Agency method 445.0 (Arar and Collins 1997). 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. Given the potential for tiles to flip or become covered with sediment or litter, in 2016 we deployed three replicate 15 cm × 15 cm ceramic tiles at the same 10 m intervals that were assessed in 2014 (*n* = 30 per reach for three weeks). In 2016, in situ chlorophyll *a* measurements were conducted using a BenthosTorch (BBE Moldaenke GmbH), a portable field instrument that provides real-time estimates of benthic algae concentrations (Kahlert and McKie 2014). Accrued chlorophyll *a* measurements were averaged across all 30 samples in each reach to produce a single value (as µg·cm²) in 2016. We also compared average accrued chlorophyll *a* directly under the tarps (shaded samples) with average chlorophyll *a* in unshaded locations within the manipulation reaches in 2016. Although different methodologies were used to estimate chlorophyll *a* accrual in 2014 and 2016, the BACI study design addresses this by comparing ratios between reference and manipulated sites within a year and then analyzing changes in the within-year ratios between the premanipulation year (2014) and the manipulation year (2016).

Macroinvertebrates

Macroinvertebrates in 2014 and 2016 were sampled using a Surber sampler (500 µm, 0.25 m²). In 2014, six Surber samples were collected at regular intervals from riffle habitats in each study reach. In 2016, three Surber samples were collected at regular intervals from riffle sections of the three reference reaches. To compare the more localized changes in macroinvertebrate biomass (g·m⁻²) and community composition within the shaded reaches, we collected a total of six Surber samples in each manipulation reach; three samples were collected from riffle sections under tarps and three from riffle sections outside 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 pooled into a single sample for identification and biomass analyses. In 2016, within each manipulation reach, samples from unshaded reach sections (outside tarps) were pooled separately from samples collected within shaded reach sections (under tarps). Sorting and biomass calculations were conducted on macroinvertebrate samples the winter following each field season. We summed the biomass of individuals within a subsample and divided this summed value by the proportion of the total sample that was subsampled. This value was then divided by the total area sampled to obtain biomass estimates per square metre (g·m⁻²). Macroinvertebrate samples collected in 2014 were analyzed on the Oregon State University campus (see Kaylor and Warren 2017a). 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). To quantify how experimental decreases in light influenced invertebrate biomass, we compared the manipulation-to-reference ratio of macroinvertebrate biomass between the two study years. We average the two pooled subsamples from the manipulation sites in 2016 to obtain the value used in the 2014 versus 2016 reach pair analyses. Because we pooled the macroinvertebrate samples from each reach, statistical analyses could not be conducted on reaches within each reach pair. Focusing on localized effects of the 2016 shading experiment, we also evaluated differences within each of the manipulation reaches between unshaded and shaded sections of each stream.

Vertebrates

In 2014 and 2016, populations of fish and salamanders were surveyed using a backpack electrofisher (Smith-Root model LR-20B). Vertebrate surveys were conducted between late July and early August (no sampling prior to 20 July to minimize mortality of young-of-year (age 0+; hereinafter referred to as YOY) trout that emerge in late spring to early summer in these systems). Single-pass mark-recapture methods were conducted over two consecutive days to obtain population size and biomass estimates of fish and salamanders in each reach (catch and mark on day one and recapture on day two). Block nets were left at the upstream and downstream end of each reach overnight to ensure a closed system. Marking consisted of small clips on the caudal fin of fish and the tail of salamanders, after anesthetization with AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand). Electrofishing is a common method for collecting fish in headwater streams, and this method is established as an effective method to capture and quantify coastal giant salamanders in western headwaters as well (Roni 2002; Cossel et al. 2012). The Chapman modification of the Lincoln-Peterson mark-recapture estimation was used to estimate vertebrate trout and salamander population sizes (Chapman 1951). Length (mm) and mass (g) were recorded for all individual salamanders and fish caught during mark-recapture surveys. Biomass (g·m⁻²) estimates were calculated by multiplying the mean mass (g) by the estimated number of individuals in the population divided by reach wetted area. The YOY trout age class was clearly identifiable in each site and in each year based on length-frequency histograms. To estimate YOY trout relative growth in each reach, a second sampling event targeting YOY was conducted in September. The difference in mean size from event one to event two was divided by the number of days between sampling events to obtain a relative growth rate (Kaylor and Warren 2017a).

To quantify how patchy decreases in light influenced the biomass of in-stream vertebrate predators, we compared the ratio of vertebrate biomass in the manipulation reach with 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

Table 2. Statistical comparisons based on paired *t* tests of the mean manipulation-to-reference ratio for each metric in 2014 and 2016.

Metric	<i>n</i>	Estimated difference	Lower CI	Upper CI	Std. error	<i>t</i>	df	<i>p</i>
Light (PAR)	3	-0.43	-0.80	-0.06	0.0	-4.95	2	0.038
Chlorophyll <i>a</i>	3	-0.31	-1.01	0.39	0.16	-1.90	2	0.197
Invertebrate biomass	3	-0.58	-1.27	0.12	0.16	-3.58	2	0.069
Trout biomass	3	-0.13	-0.22	-0.04	0.02	-6.26	2	0.025
YOY biomass	3	-0.83	-3.73	2.06	0.67	-1.24	2	0.341
Salamander biomass	3	-0.16	-1.38	1.05	0.28	-0.58	2	0.623

Note: 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.

as total vertebrate biomass (all three groups summed). The ratio of YOY relative growth ($\text{g}\cdot\text{day}^{-1}$) in the manipulation reach to the reference reach was also compared.

Statistical analysis

We evaluated the same metrics across all dates and sites; however, because sampling methods were not entirely consistent between years (e.g., chlorophyll *a* accrual), we compared manipulation-to-reference ratios within reach pairs and evaluated the differences in those ratios between years. We used paired *t* tests to assess the null hypothesis that there was no difference in mean manipulation-to-reference ratio of the three reach pairs between the two study years (2014 and 2016) for all reach-scale metrics: mean light (PAR), mean chlorophyll *a*, macroinvertebrate biomass, trout biomass, YOY biomass, salamander biomass, and total in-stream vertebrate biomass. 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 paired *t* tests to assess the local scale difference in 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 for this analysis of 2016 data in the manipulation reaches. Owing to the assumption violation and because this analysis is also based on raw data, unlike the ratio comparisons between years, data were natural logarithm-transformed. These within-manipulation reach comparisons were therefore conducted on the estimated median difference between shaded and unshaded locations for the amount of light (PAR), algae biomass (chlorophyll *a*), and macroinvertebrate biomass.

Results

Abiotic response

The experimental shading was successful in creating a patchy light environment in manipulation reaches with areas of both decreased local PAR flux and areas of higher light availability (Fig. 2). Across all three reach pairs, mean light flux in the manipulation reaches significantly declined by an average of 55% ($p = 0.038$) from 2014 to 2016 (Table 2; Fig. 3). The change in light between the reference and manipulation reaches was the greatest at McRae 404 (76.2% decline in the manipulation-to-reference ratio from 2014 to 2016) followed by Lookout 703 (59.2% decline) and Lookout 701 (32.1% decline; see Fig. S2¹). Within the manipulation reaches in 2016, light fluxes to the streambed below the tarps were 94.3% ($p = 0.046$, 95% CI: (0.12, 5.25)) lower on average than in unshaded locations on the same reach (Table S1¹).

Our analysis of mean daily average temperature showed no significant response in the reference-to-manipulation ratio in 2014 to 2016 ($p = 0.612$, 95% CI: (-0.03, 0.02)). Mean daily maximum temperature also showed no significant change between 2014 and 2016 with the shading in place ($p = 0.227$, 95% CI: (-0.02, 0.01)). Additionally, during the shading treatment in 2016, there was no significant difference in the mean daily average ($p = 0.652$, 95% CI:

(-0.11, 0.12)) or maximum ($p = 0.816$, 95% CI: (-0.17, 0.15)) temperature between the upstream and downstream ends of the three manipulation reaches, demonstrating that there was no detectable localized effect on in-stream temperature.

Biotic response

Across our three reach pairs, in 2014 mean chlorophyll *a* accrual on tiles in the manipulation reaches was 1.16 times greater than in the reference reaches, but in 2016, mean chlorophyll *a* accrual in the manipulation reaches had decreased to just 0.43 times that of the reference reaches. When using the ratio of chlorophyll *a* accrual on tiles between manipulation and reference reaches in each pair, we found an overall decline in mean chlorophyll *a* accrual of 50.3% on tiles from 2014 to 2016, though the result was not statistically significant ($p = 0.201$; Table 2; Fig. 3). Considering each reach pair individually, the stream shading experiment yielded a decline in periphyton chlorophyll *a* accrual for two of the three sites (Fig. S2¹). In McRae 404, there was a 48.6% decrease in average accrued chlorophyll *a* in the manipulation-to-reference reach ratio between 2014 and 2016. In Lookout 701, there was a 61.3% decrease in the chlorophyll *a* manipulation-to-reference ratio from 2014 to 2016, but in Lookout 703 there was no detectable difference in the ratio between years. Within the manipulation reaches alone in 2016, mean accrued chlorophyll *a* was significantly (87.6%) lower in shaded locations than in unshaded locations ($p = 0.030$, 95% CI: (0.44, 3.27); Table S1¹).

In 2014, mean macroinvertebrate biomass in the manipulation reaches was 1.7 times higher than in the reference reaches, but this ratio decreased to 0.58 in 2016, resulting in a 66.4% decrease in the mean manipulation-to-reference ratio ($p = 0.068$; Table 2; Fig. 3). We saw the largest decrease in the manipulation-to-reference ratio of total macroinvertebrate biomass in Lookout 703, with an 83.0% decline in the biomass ratio from 2014 to 2016. In McRae 404, the manipulation-to-reference ratio of total macroinvertebrate biomass decreased by 48.6% from 2014 to 2016, and Lookout 701 decreased by 61.3% between 2014 and 2016 (Fig. S2¹). On average, across all three sites, the manipulation-to-reference biomass ratio of the scraper functional feeding group — which is generally associated with periphyton consumption and which we therefore expected to respond strongly to the shading — decreased by 88.1% from 2014 to 2016. Shredder manipulation-to-reference biomass ratio — which is generally associated with consumption of coarse particulate organic matter in streams and which we therefore expected to be somewhat insulated from the shading effects — also decreased from 2014 to 2016, by an average of 28.1%. Overall, there were no clear trends associated with functional feeding groups with a decline in the macroinvertebrate biomass manipulation-to-reference ratios occurring across all functional feeding groups (Fig. S3¹). Within manipulation reaches, macroinvertebrate biomass collected in shaded locations (directly under tarps) in 2016 was 81.2% lower on average than in unshaded sections of the same manipulation reach, though this was not a statistically significant decline ($p = 0.086$, 95% CI: (-0.061, 4.1);

Fig. 3. Reach-scale means of the ratio of manipulation to reference for light (PAR), algae (chlorophyll *a*), macroinvertebrate biomass, trout biomass, young-of-year (YOY) biomass, salamander biomass, and total vertebrate biomass. Error bars are \pm one standard error calculated from individual ratios from each site.

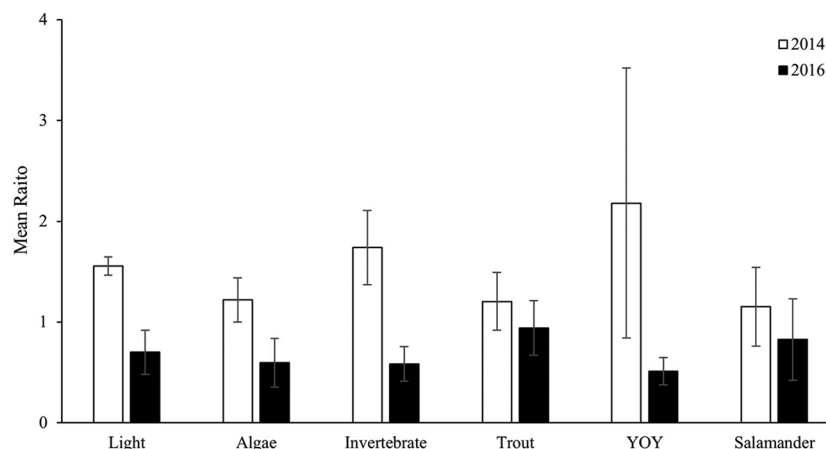


Table S1¹). No clear trend was found in biomass of functional feeding groups between shaded and unshaded locations.

Across all three reach pairs, patchy stream shading reduced the manipulation-to-reference ratio of trout biomass significantly, by an average of 21.9% across all three sites ($p = 0.023$; Table 2; Fig. 3). Decreases in trout biomass differed among study sites, with the largest decreases in light yielding the largest relative declines in trout biomass. In McRae 404, where light was reduced by 76.2%, we observed a 34.9% decline in the manipulation-to-reference ratio of trout biomass from 2014 to 2016. The manipulation-to-reference ratio decreased by 17.3% in Lookout 703 and by 18.5% in Lookout 701 from 2014 to 2016 (Fig. S2¹). Sculpin were only present in McRae 404, and the ratio of sculpin biomass between 2014 and 2016 decreased by 30.1%.

YOY biomass ratios between manipulation and reference reaches decreased by an average of 74.2% across all pairs from 2014 to 2016 in association with patchy shading, though not significantly due to large variability among sites and error associated with the population estimates of YOY ($p = 0.339$; Table 2; Fig. 3). In Lookout 703, the manipulation-to-reference ratio of YOY biomass 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% (Fig. S2¹). There was no clear trend in summer YOY relative growth rate ($\text{g} \cdot \text{day}^{-1}$) 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.

Salamander recapture rates were low, and therefore the mark-recapture population estimates for coastal giant salamanders in this study had very wide confidence intervals in some cases. The salamander manipulation-to-reference biomass ratio was lower in 2016 relative to 2014 in two of three reach pairs. In Lookout 703 and McRae 404, the ratio of salamander biomass decreased by 70.9% and 73.5%, respectively, from 2014 to 2016 in the manipulation reaches. Surprisingly, in Lookout 701 the ratio of salamander biomass in the manipulation reaches relative to reference reaches increased substantially (by 285.2%) from 2014 to 2016 (Fig. S2¹). Across all three sites, however, the mean manipulation-to-reference ratio decreased by 28.2%, though this was not statistically significant ($p = 0.623$; Table 2; Fig. 3).

Discussion

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), but few studies have evaluated

the effects of smaller changes in light on stream biota. We found that reduced light associated with the addition of patchy areas of shade along forested headwater streams resulted in overall declines in periphyton accrual, macroinvertebrate biomass, and fish biomass at the reach scale across three replicate reach pairs. These findings were consistent with our hypothesis that biota in these light-limited headwater streams would respond negatively to increasing shade through associated bottom-up drivers of secondary production. While we no longer have the wholesale removal of riparian forests along streams in the Pacific Northwest, that does not mean that these forests are static or that contemporary management does not affect light (Warren et al. 2016). Riparian forests recovery from past clearing, contemporary management with streamside buffers, and natural disturbances alter stream light, but they create moderate and patchy change in stream light. The response of stream food webs to the smaller decreases in light imposed in this experiment highlight the potential importance of these more moderate changes in light and stress the connections between stream ecosystems and the age, stage, structure, and management of riparian forests.

Decreases in local light flux from patchy shading resulted in local decreases in periphyton accrual. In two of the three reach pairs assessed in this study, the localized areas of low periphyton chlorophyll *a* situated under tarps collectively lead to an overall reduction in mean chlorophyll *a* at the reach scale. We suggest that the absence of significant response in benthic periphyton accrual in Lookout 703 is likely due at least in part to changes in top-down controls by macroinvertebrate consumers. The manipulation reach at Lookout 703 had the highest initial macroinvertebrate biomass out of all study reaches, and following shading at this site, we observed the greatest decline in the macroinvertebrate biomass, which may have in turn released periphyton from grazing pressures. Primary producer–consumer relationships have been explored by other studies with mixed results, (Wootton and Power 1993; Quinn et al. 1997), highlighting the importance of assessing multiple trophic levels when evaluating stream primary production as a response variable. Because we decreased light in this study, the issue of photosaturation of primary production at high light (Hill et al. 1995) — a factor that could mute the response of stream autotrophic and of subsequent food web compartments in studies that increase light — is unlikely to be a factor affecting these results.

Macroinvertebrate biomass decreased in all three experimentally shaded reaches relative to paired reference reaches. This result was consistent with the hypothesis that decreases in light that in turn lead to a decrease in periphyton production resonate

up the food web to consumers, including macroinvertebrates. Previous research manipulating stream light has also demonstrated linkages to macroinvertebrate biomass and community structure. Streams flowing through recently logged sections of forest, with substantially less canopy cover, have been shown to contain consistently higher macroinvertebrate biomass and (or) abundance than the unlogged or older logged sites (Noel et al. 1986; Fuchs et al. 2003; Lecerf et al. 2012). In one of the only other studies applying shade patches over a section of stream, Gjerløv and Richardson (2010) decreased light by more than 90% over a single 5 m riffle section in two streams. Their results were highly variable between streams and revealed that macroinvertebrate abundance at one location was significantly lower in the manipulation reach when compared with the reference reach, and at the second location there was no response detected due to the shading manipulation. They attributed the lack of a response in macroinvertebrate densities to high initial levels of algal standing stocks at one of the two sites that did not decline enough during the study, which ultimately supports the fundamental importance of bottom-up processes in stream food webs. Kiffney et al. (2004) evaluated periphyton and macroinvertebrate responses to a range of stream buffer widths and found that the experimental treatments increased light and, in turn, stream macroinvertebrates (Chrononemidae). Macroinvertebrate biomass increased in response to 100% riparian clearing and in response to light manipulations that increased light to just 22% of maximum potential light fluxes (Kiffney et al. 2004).

In addition to reductions in reach-scale total macroinvertebrate biomass, we found that biomass of all macroinvertebrate functional feeding groups decreased in the manipulations reaches relative to reference reaches after the shading manipulation was applied. The scraper functional feeding group was predicted to decrease in accordance with reduced periphyton availability. Predator, collector–gatherer, and collector–filterer groups can be supported largely by autochthonous carbon when this resource is readily available (Collins et al. 2016; Rosi-Marshall et al. 2016), and decreases in periphyton availability as a food resource to macroinvertebrates may have accounted for observed reductions. However, the response of shredders was surprising given their feeding method is best adapted to consumption of litter and other coarse particulate organic matter (Merritt and Cummins 1996). Given the care we took in setting up the tarps to shed litter into the stream (and this was checked regularly throughout the summer), we do not believe that reduced litter inputs account for the shredder response. An alternative explanation is that reduced solar flux altered the palatability of litter, resulting in reduced shredder abundance. Lagrue et al. (2011) found that artificial shading applied to streams resulted in reduced leaf litter breakdown rates and that shredder density was lower on litter bags incubated in shaded versus unshaded sections. Ultimately, light flux reduction decreased macroinvertebrate biomass in our study reaches independent of feeding guild, which in turn decreased a potentially important food resource for stream fish.

Studies have linked changes in stream light flux to changes in fish abundance, but most of this research has focused on large increases in light or has evaluated relationships through correlations between light availability and fish biomass (Murphy and Hall 1981; Bilby and Bisson 1992; Kiffney and Roni 2007; Kaylor and Warren 2017a). Few empirical studies have evaluated fish responses to decreases in stream light availability, such as those associated with riparian forest regeneration. Kaylor and Warren (2017b) compared trout populations in stream reaches between the 1970s, shortly after clear-cut harvesting, and 2014, after nearly four decades of riparian regeneration. Trout biomass was initially elevated in reaches adjacent to clear-cuts relative to reference reaches bordered by old growth; however, after riparian regeneration, trout biomass decreased and was accompanied by similar reductions of chlorophyll *a* accrual and predatory invertebrate

biomass suggesting bottom-up drivers of these biotic responses. The three study streams in this current study were part of the Kaylor and Warren (2017b) study. The changes in shading implemented in this study through artificial shading were much smaller in magnitude than changes that typically occur with riparian regeneration after a natural or anthropogenic disturbance. As previously harvested riparian forests continue to grow and develop, understanding how moderate and patchy changes in stream light influence primary production and aquatic biota will be important to our understanding of how forested stream ecosystem function and biodiversity will change in the future. Results from this study indicate that further canopy closure over these streams may result in additional reductions of top predator biomass mediated through bottom-up processes. It is important to note that other stream systems may respond differently to increased shading, and other factors, such as temperature and allochthonous inputs, can also impact in-stream biota. For example, recovering riparian forests may reduce temperatures, allowing recovery of cold-water species in streams where temperatures exceed species' lethal tolerances. Our results suggest that moderate changes in stream light, which affect the availability of stream macroinvertebrate prey, can also substantially impact trout biomass in forested headwater streams within a single season.

Shading within these streams reduced carrying capacity for trout, and the mechanism for reductions in trout biomass is unclear. However, it is likely a result of fish movement out of the shaded reaches with less food. Our study reaches were relatively short (90 m), and they remained open for the entire manipulation period (with the exception of the 2 days when mark–recapture sampling was conducted) so fish could move freely within our study reaches and beyond — both upstream and downstream. Although we did not assess movement explicitly in this study, other researchers have demonstrated the dominant role of movement as a driver of single-season abundance and biomass changes for fish at the reach scale (Burgess and Bider 1980; Gowan and Fausch 2002).

Salamanders account for a large amount of aquatic vertebrate biomass in Pacific Northwest forested streams. The salamander biomass and abundance responses to our shading experiment were mixed. In two of our three sites, the estimated relative abundance and biomass of salamanders declined following stream shading. However, in the third reach, we observed an increase in estimated salamander biomass in association with stream shading. Gradient, substrate type, amount of woody debris, and other stream habitat characteristics have been identified as important factors associated with salamander biomass and abundance (Hawkins et al. 1983; 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 2 years after forest harvest and found no significant effect of the forest management on Pacific giant salamanders; however, substrate explained the majority of variability in salamander biomass in this study. Other studies have found that aquatic food availability is strongly associated with salamander biomass and abundance in forested streams. Although a number of studies have used electrofishing to capture and quantify Pacific giant salamanders in headwater ecosystems (Hawkins et al. 1983; Roni 2002; Cossel et al. 2012), the ability of these aquatic dwelling salamanders to utilize the complexity and three-dimensional structure of the stream benthos can lead to concern about the probability of detection (MacKenzie 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, reaches were dominated by cobble substrates and capture efficiencies were low at all locations, resulting in wide confidence intervals on population estimates. Therefore, although we found a trend in support of our hypothesis in two of the three sites, our

ability to apply a measure of significance to these changes or to the salamander increase that we observed in at Lookout 701 is limited by low capture probabilities.

The amount of light reaching a forested headwater stream is influenced by the structure of the riparian vegetation, particularly the overstory canopy (Chazdon and Pearcy 1986; Warren et al. 2013, 2017), and the structure of riparian forest canopies 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. 2017). The recovery of historically cleared riparian forests in the Pacific Northwest into later successional stages will cause inconsistent, patchy changes to light reaching the stream benthos (Heaston et al. 2017). Streams with young and midsuccession second-growth riparian forests often have a high density of younger trees, resulting 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 from this study indicate that these local, patchy changes in the amount of light reaching a forested headwater stream may substantially influence not only the biomass of primary producers, but also the amount of macroinvertebrates and vertebrate predators that the system can support.

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References

- Arar, E.J., and Collins, G.B. 1997. Method 445.0: In vitro determination of chlorophyll-*a* and pheophytin in marine and freshwater algae by fluorescence [online]. US Environmental Protection Agency, Washington, D.C. Available from https://cfpub.epa.gov/si/si_public_record_report.cfm?dirEntryId=309417.
- Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Packman, A.I., Newbold, J.D., and Sabater, F. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. *Nat. Geosci.* 1: 95–100. doi:10.1038/ngeo101.
- 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(3): 540–551. doi:10.1139/f92-064.
- Boston, H.L., and Hill, W.R. 1991. Photosynthesis-light relations of stream periphyton communities. *Limnol. Oceanogr.* 36(4): 644–656. doi:10.4319/lo.1991.36.4.0644.

- Brett, M.T., Kainz, M.J., Taipale, S.J., and Seshan, H. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proc. Natl. Acad. Sci. U.S.A.* 106(50): 21197–21201. doi:10.1073/pnas.0904129106. PMID:19934044.
- Burgess, S.A., and Bider, J.R. 1980. Effects of stream habitat improvements on invertebrates, trout populations, and mink activity [online]. *J. Wildl. Manage.* 44(4): 870–880. Available from <https://link.springer.com.ezproxy.proxy.library.oregonstate.edu/article/10.1023/A%3A1016010723609>.
- Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses [online]. *Univ. Calif. Publ. Stat.* 1: 131–160. Available from <http://catalog.hathitrust.org/Record/005761134%0A>.
- Chazdon, R.L., and Pearcy, R.W. 1986. Photosynthetic responses to light variation in rainforest species: carbon gain and photosynthetic efficiency during lightflecks. *Oecologia*, 69(4): 524–531. doi:10.1007/BF00410358. PMID:28311611.
- Clipp, H.L., and Anderson, J.T. 2014. Environmental and anthropogenic factors influencing salamanders in riparian forests: a review. *Forests*, 5(11): 2679–2702. doi:10.3390/f5112679.
- Collins, S.M., Kohler, T.J., Thomas, S.A., Fetzer, W.W., and Flecker, A.S. 2016. The importance of terrestrial subsidies in stream food webs varies along a stream size gradient. *Oikos*, 125(5): 674–685. doi:10.1111/oik.02713.
- Cossel, J.O., Gaige, M.G., and Sauder, J.D. 2012. Electroshocking as a survey technique for stream-dwelling amphibians. *Wildl. Soc. Bull.* 36(2): 358–364. doi:10.1002/wsb.145.
- Cross, W.F., Benstead, J.P., Frost, P.C., and Thomas, S.A. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshw. Biol.* 50(11): 1895–1912. doi:10.1111/j.1365-2427.2005.01458.x.
- Dudaniec, R.Y., and Richardson, J.S. 2012. Habitat associations of the Coastal Giant Salamander (*Dicamptodon tenebrosus*) at its northern range limit [online]. *Herpetol. Conserv. Biol.* 7(1): 1–15. Available from <http://hdl.handle.net/1959.14/1072242>.
- Franklin, J.F., and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. *J. For.* 102(3): 22–28. doi:10.1139/cjfr-2017-0029.
- Fuchs, S.A., Hinch, S.G., and Mellina, E. 2003. Effects of streamside logging on stream macroinvertebrate communities and habitat in the sub-boreal forests of British Columbia, Canada. *Can. J. For. Res.* 33(8): 1408–1415. doi:10.1139/x03-070.
- Gjerløv, C., and Richardson, J.S. 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. doi:10.1007/s10750-010-0331-7.
- Gowan, C., and Fausch, K.D. 2002. Why do foraging stream salmonids move during summer? *Environ. Biol. Fishes*, 64(1–3): 139–153. doi:10.1023/A:1016010723609.
- Guo, F., Kainz, M.J., Valdez, D., Sheldon, F., and Bunn, S.E. 2016. High-quality algae attached to leaf litter boost invertebrate shredder growth. *Freshw. Sci.* 35(4): 1213–1221. doi:10.1086/688667.
- Hall, R.O., Tank, J.L., Baker, M.A., Rosi-Marshall, E.J., and Hotchkiss, E.R. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. *Ecosystems*, 19: 73–86. doi:10.1007/s10021-015-9918-1.
- Hawkins, C.P., Murphy, M.L., Anderson, N.H., 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. *Fish. Aquat. Sci.* 40(8): 1173–1185. doi:10.1139/f83-134.
- Heaston, E.D., Kaylor, M.J., and Warren, D.R. 2017. Characterizing short-term light dynamics in forested headwater streams. *Freshw. Sci.* 36(2): 259–271. doi:10.1086/691540.
- Hill, W.R., Ryon, M.G., and Schilling, E.M. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology*, 76(4): 1297–1309. doi:10.2307/1940936.
- Hoellein, T.J., Bruesewitz, D.A., and Richardson, D.C. 2016. Revisiting Odum (1956): a synthesis of aquatic ecosystem metabolism. *Limnol. Oceanogr.* 58(6): 2089–2100. doi:10.4319/lo.2013.58.6.2089.
- Jaffé, R., McKnight, D., Maie, N., Cory, R., McDowell, W.H., and Campbell, J.L. 2008. Spatial and temporal variations in DOM composition in ecosystems: the importance of long-term monitoring of optical properties. *J. Geophys. Res. Biogeosci.* 113: 1–15. doi:10.1029/2008JG000683.
- Julian, J.P., Doyle, M.W., and Stanley, E.H. 2008. Empirical modeling of light availability in rivers. *J. Geophys. Res.* 113(G3): 1–16. doi:10.1029/2007JG000601.
- Kahlert, M., and McKie, B.G. 2014. Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environ. Sci. Process. Impacts*, 16: 2627–2634. doi:10.1039/C4EM00326H. PMID:25277172.
- Kaylor, M.J., and Warren, D.R. 2017a. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. *Ecosphere*, 8(6): 1–19. doi:10.1002/ecs2.1845.
- Kaylor, M.J., and Warren, D.R. 2017b. Canopy closure after four decades of post-logging riparian forest regeneration reduces cutthroat trout biomass in headwater streams through bottom-up pathways. *Can. J. Fish. Aquat. Sci.* 75(4): 513–524. doi:10.1139/cjfas-2016-0519.
- 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): 1–13. doi:10.1086/690624.
- 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): 852–868. doi:10.1890/06-1172. PMID:17494402.

- Kiffney, P.M., and Roni, P. 2007. Relationships between productivity, physical habitat, and aquatic invertebrate and vertebrate populations of forest streams: An information-theoretic approach. *Trans. Am. Fish. Soc.* **136**(4): 1088–1103. doi:10.1577/T06-234.1.
- 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.
- 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. N. Am. Benthol. Soc.* **23**(3): 542–555. doi:10.1899/0887-3593(2004)023<0542:ELAACM>2.0.CO;2.
- Kroll, A.J. 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. *For. Ecol. Manage.* **257**: 1188–1199. doi:10.1016/j.foreco.2008.12.008.
- Laguerre, C., Kominoski, J.S., Danger, M., Baudoin, J.M., Lamothe, S., Lambrigt, D., and Lecerf, A. 2011. Experimental shading alters leaf litter breakdown in streams of contrasting riparian canopy cover. *Freshw. Biol.* **56**(10): 2059–2069. doi:10.1111/j.1365-2427.2011.02637.x.
- Lecerf, A., Baudoin, J.-M., Besson, A.A., Lamothe, S., and Laguerre, C. 2012. Is smaller necessarily better? Effects of small-scale forest harvesting on stream ecosystems. *Ann. Limnol. Int. J. Limnol.* **48**(4): 401–409. doi:10.1051/limn/2012028.
- Leuthold, N., Adams, M.J., and Hayes, J.P. 2012. Short-term response of *Dicamptodon tenebrosus* larvae to timber management in southwestern Oregon. *J. Wildl. Manage.* **76**(1): 28–37. doi:10.1002/jwmg.269.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., and Franklin, A.B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**(8): 2200–2207. doi:10.1890/02-3090.
- Matheson, F.E., Quinn, J.M., and Martin, M.L. 2012. Effects of irradiance on diel and seasonal patterns of nutrient uptake by stream periphyton. *Freshw. Biol.* **57**(8): 1617–1630. doi:10.1111/j.1365-2427.2012.02822.x.
- McCutchan, J.H., and Lewis, W.M. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnol. Oceanogr.* **47**(3): 742–752. doi:10.4319/lo.2002.47.3.0742.
- 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., and Cummins, K.W. 1996. An introduction to the aquatic insects of North America. 3rd ed. Kendall/Hunt, Dubuque, Iowa.
- 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**(2): 137–145. doi:10.1139/f81-018.
- Noel, D.S., Martin, C.W., and Federer, C.A. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. *Environ. Manage.* **10**(5): 661–670. doi:10.1007/BF01866770.
- Quinn, J.M., Cooper, A.B., Stroud, M.J., and Burrell, G.P. 1997. Shade effects on stream periphyton and invertebrates: An experiment in streamside channels. *N.Z. J. Mar. Freshw. Res.* **31**(5): 665–683. doi:10.1080/00288330.1997.9516797.
- Roni, P. 2002. Habitat use by fishes and Pacific Giant salamanders in small western Oregon and Washington streams. *Trans. Am. Fish. Soc.* **131**(4): 743–761. doi:10.1577/1548-8659(2002)131<0743:HUBFAP>2.0.CO;2.
- Rosi-Marshall, E.J., Vallis, K.L., Baxter, C.V., and Davis, J.M. 2016. Retesting a prediction of the River Continuum Concept: autochthonous versus allochthonous resources in the diets of invertebrates. *Freshw. Sci.* **35**(2): 534–543. doi:10.1086/686302.
- Sabater, F., Butturini, A., Martí, E., Muñoz, I., Romani, A., Wray, J., and Sabater, S. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *J. N. Am. Benthol. Soc.* **19**(4): 609–620. doi:10.2307/1468120.
- Sievers, M., Hale, R., and Morrongiello, J.R. 2017. Do trout respond to riparian change? A meta-analysis with implications for restoration and management. *Freshw. Biol.* **62**(3): 445–457. doi:10.1111/fwb.12888.
- Tranvik, L.J. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. *Hydrobiologia*, **229**(1): 107–114. doi:10.1007/BF00006994.
- Warren, D.R., Keeton, W.S., Bechtold, H.A., and Rosi-Marshall, E.J. 2013. Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. *Aquat. Sci.* **75**(4): 547–558. doi:10.1007/s00027-013-0299-2.
- 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): 1–19. doi:10.1002/ecs2.1435.
- Warren, D.R., Collins, S.M., Purvis, E.M., Kaylor, M.J., and Bechtold, H.A. 2017. Spatial variability in light yields colimitation of primary production by both light and nutrients in a forested stream ecosystem. *Ecosystems*, **20**(1): 198–210. doi:10.1007/s10021-016-0024-9.
- 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**(1): 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): e51839. doi:10.1371/journal.pone.0051839. PMID: 23284786.
- Wootton, J.T., and Power, M.E. 1993. Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. U.S.A.* **90**: 1384–1387. doi:10.1073/pnas.90.4.1384. PMID:11607368.