

RESEARCH ARTICLE

Fish and aquatic salamander responses to the creation of riparian canopy gaps along forested headwater streams

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Many headwaters across temperate North America have uniform mid-succession riparian forests recovering from historic land clearing. These young riparian stands contrast with late-succession forests, which have complex structural characteristics including canopy gaps. Canopy gaps provide structural diversity that can be important for terrestrial species, and they are also hypothesized to be important features for aquatic environments. The light patches below gaps create productivity hotspots in streams and therefore create potential for increased stream apex predator abundances through bottom-up food web drivers. However, increasing light may also affect stream temperature, a consideration for coldwater fish (salmonids). We established an experimental before-after control-impact study to explicitly assess how creating canopy gaps in the riparian forest affects the abundance and biomass of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and Pacific giant salamanders (*Dicamptodon tenebrosus*) in paired reference and treatment reaches at five replicate streams. Gaps were designed to resemble those in old-growth forests in the treatment reach of each system although wood was explicitly left out of the stream. At four of five sites, we found small and generally consistent positive responses in adult cutthroat trout and total vertebrate biomass to localized increases in light but only 2 years after treatment. Results suggest that opening riparian canopies adjacent to streams via gaps is a viable tool to enhance structural complexity of riparian forests without negatively impacting stream vertebrates; however, a single gap alone had small effects on aquatic vertebrates. More or larger gaps would likely be needed to notably enhance aquatic apex predators.

Key words: canopy gap, coastal cutthroat trout, forest-stream interactions, HJ Andrews Experimental Forest, Pacific giant salamander, riparian forest

Implications for Practice

- Cutting localized patches of trees adjacent to streams to increase structural complexity in otherwise uniform riparian stands does not negatively impact coldwater fish or aquatic salamanders.
- Creating localized canopy gaps in the riparian zone increased stream light and generally lead to small increases in apex predator abundances.
- Although we found small increases in total vertebrate biomass as a result of creating canopy gaps, the magnitudes of increases were insubstantial, suggesting that a greater frequency of gaps in the catchment or larger gaps would be needed to have population-level effects.

Introduction

In headwater streams, the abundance of fish and other apex predators is influenced by a combination of key habitat features (Bisson et al. 1992; Reeves et al. 1995; Roni & Quinn 2001) and the abundance of food resources (Chapman 1966; Boss & Richardson 2002; Kaylor & Warren 2017). In forested systems, although the majority of carbon resources are derived from terrestrial inputs (Webster & Meyer 1997; Bernot et al. 2010), a number of studies have found that autochthonously derived carbon is a disproportionately important basal food resource given

the high quality of benthic biofilms relative to leaves and other terrestrial carbon (McCutchan & Lewis 2002; Lau et al. 2009; Guo et al. 2016). Along most forested temperate headwaters, shading by riparian forests can lead to low standing stocks of biofilms (Hill et al. 1995; Warren et al. 2016) and aquatic invertebrates (Kaylor & Warren 2017). Large-scale removal of streamside vegetation has been shown to release stream biofilms from light limitation and lead to increases in benthic biofilm standing stocks that translate to increases in stream vertebrates (fish and salamanders) via greater invertebrate production (Bilby & Bisson 1992; Wilzbach et al. 2005; Wootton 2012). However, as we consider the future of riparian forests across North America, increases in light along streams may be more commonly linked to smaller canopy openings (canopy

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gaps)—rather than large-scale clearing— due to natural stand development processes in many forests (Franklin et al. 2002).

Canopy gaps in riparian forests are created by small-scale disturbances and generally become more common as young dense stands transition to mature and ultimately late-successional forests with increased structural complexity (Denslow & Spies 1990; Keeton 2006). Given the prevalence of gaps in late-succession forests, the creation of riparian canopy gaps has been explicitly suggested as a restoration strategy to increase both aquatic and terrestrial riparian habitat complexity, which aligns with the management concept of emulating natural disturbances (Franklin et al. 2002; Kreutzweiser et al. 2012; Tulod et al. 2019). Complex forest structure provides habitat for terrestrial biota (Palmer & Bennett 2006; Olson et al. 2007), and correlative studies have suggested that light exposure in streams beneath canopy gaps can be an important driver of biofilm production at the base of aquatic food webs with implications for aquatic apex predators (Kaylor & Warren 2017). However, the potential for individual gaps to enhance productivity of stream predators through increased light exposure and subsequent increases in basal resources and invertebrate production has not been explicitly evaluated in a rigorous experimental context.

Although there is evidence that increasing light can enhance bottom-up drivers of the stream food web, tree removal and associated logging activities in riparian forests can negatively impact fish (Mellina & Hinch 2009), and therefore cutting gaps in the riparian zone—whether for target aquatic species or terrestrial species that benefit from greater structural complexity—may lead to a decline in fish, salamanders, or other aquatic biota. Anthropogenic activities that increase light exposure to streams are often controversial because increases in direct sunlight are linked to increases in stream temperature (Groom et al. 2011; Swartz et al. 2020) which can increase bioenergetic demand for prey resources (Railsback & Rose 1999), leading to stressful conditions for fish and other biota adapted to cold-water environments (Bear et al. 2007; Leach et al. 2012). Indeed, a key assumption underlying many of the current restrictions on riparian forest harvest in the United States and around the world is that maximizing stream shade will maximize habitat benefits for stream ecosystems and stream biota (salmonids in particular). This assumption is grounded largely in concerns over increases in stream temperature that can occur when a substantial amount of the riparian corridor is removed (Gomi et al. 2006; Janisch et al. 2012). In fish bioenergetic models, fish growth increases with increasing temperature until a maximum growth level is reached, at which point production declines sharply (Harvey et al. 2014; Railsback 2022). Given the precipitous decline in production, when temperatures exceed a thermal threshold, any increase in temperature can be a restoration concern to managers (Parkinson et al. 2016; Mandeville et al. 2019). However, if increases in temperature are moderate and remain below key thermal tolerances, they may not necessarily lead to local declines in coldwater fish (Leach et al. 2012), and increases in light do not always yield increases in stream temperature (Groom et al. 2011; Swartz et al. 2020). If moderate or localized increases in stream light availability, or increases in the complexity of riparian forest structure for terrestrial or aquatic species, are to become restoration objectives, the

question of how a gap affects aquatic biota—positively or negatively—must be addressed.

The goal of this study was to understand the response of stream apex predators (fish and salamanders) to canopy gaps that create patches of elevated light in shaded forested streams. We used a before-after control-impact (BACI) experimental study design replicated across five separate streams to test how canopy gaps influence fish and salamander densities at the reach scale. We did not anticipate detrimental temperature increases like those found in response to large clear-cut riparian treatments (Brown & Krygier 1970; Beschta et al. 1987) but expected the light increase to elevate benthic biofilms and invertebrate resources in the aquatic food web. Further, based on comparisons between biota in streams with gaps (old-growth) versus dark mid-succession riparian forests in our study region (Kaylor & Warren 2018), we expected our experimental canopy gaps to have a small positive impact on fish and salamander populations in our study reaches.

Methods

Study Design and Location

This study took place in five replicate streams in the western Cascade Mountains of central Oregon within the McKenzie River watershed. In each stream we established a set of two paired reaches. One reach was designated as a reference reach and the other was designated as an experimental reach where we would implement a canopy gap treatment. All reaches were surveyed before and after gaps were cut in the treatment reaches establishing a replicated BACI study design. All five streams had 40–60-year-old regenerating closed-canopy riparian forests that were harvested to the edge of the stream during previous forest management. Two of the streams are located on private land owned by Weyerhaeuser Company (W-113 and W-100), and three are on U.S. Forest Service (USFS) land in the Willamette National Forest (McTE, Loon Creek, and Chucksney Mountain Creek). McTE, one of the USFS sites, is located within the HJ Andrews Experimental Forest, a Long-Term Ecological Research site. The western Cascade Mountains of Oregon are characterized by a Mediterranean climate with high precipitation during cool winter months and very low or no precipitation during warm summer months which creates summer low flow conditions. The study systems are second- and third-order fish bearing headwater streams that ranged from 2.2 to 5.4 m in bankfull width (Table 1). At the initiation of the study all sites had closed canopies (Swartz et al. 2020; Swartz 2022), with tree communities that were composed predominantly of red alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*) with sporadic western red cedar (*Thuja plicata*); the Weyerhaeuser Co. sites also contained bigleaf maple (*Acer macrophyllum*).

Study sites in each stream encompassed two 90-m reaches separated by a buffer section of 20–150 m between reaches. The reach pair with the small buffer section has a steep drop just below the downstream end the upstream reach isolating the upstream reach and making movement between reaches unlikely. There were no large tributary inputs within or between

Table 1. Site characteristics of the five streams, including elevation, coordinates, mean bankfull width, gap size, baseflow discharge, azimuth and aspect, and gradient.

Stream	Elevation (m)	Latitude	Longitude	Mean Bankfull Width (m)	Gap Size (m ²)	Baseflow Discharge (L/second)	Azimuth and Aspect	Mean Gradient (%)
McTE	867	44.254544	−122.16672	2.2	1,374	5.0	SW—221.6°	14
W-113	537	44.192892	−122.51074	3.3	713	9.1	SE—118.2°	11
Loon	721	43.953624	−122.18333	4.1	514	12.5	NE—58.5°	10
Chucksney	833	43.953624	−122.11355	5.2	1,113	21.0	NE—29.1°	18
W-100	441	44.198130	−122.49298	5.4	1,164	43.9	SE—136.9°	03

the study reaches. At four of the five stream sites the experimental canopy gap was created in the riparian zone of the downstream reach. Gaps were cut at the upstream reach at Chucksney Mountain Creek (hereafter “Chucksney”) due to concerns about slope stability in the downstream reach. At Chucksney, the buffer sections between the reference and treatment reaches were over 100 m long. By using a BACI study design we can compare reach differences between the pre- and post-treatment years to reduce inherent stream-to-stream environmental variability (e.g. gradient, geology, substrate, etc.) as well as environmental variation between pre- and post-treatment periods (Stewart-Oaten et al. 1986; Heffner et al. 1996; Bal-digo & Warren 2008).

Data were collected during the summer in 2016, 2017, 2018, and 2019. Pre-treatment data at McTE, Loon, and Chucksney were collected in 2016. We do not have summer 2017 pre-treatment data at Loon, Chucksney, and McTE. In 2017, a large fire in the Willamette National Forest limited access to Loon and Chucksney during the summer 2017 field season (the wildfire fire did not impact our reaches directly, but it eliminated mid- and late-summer access). Pre-treatment data were collected at W-113 and W-100 creeks in summer 2017. Post-treatment data were collected at all five streams in 2018 and 2019. With the BACI study design, we focused on changes in the differences between paired reference and treatment reaches before the gaps versus after the gaps. Although pre-treatment data collection occurred over two different years, we evaluated within-stream reach pair differences for 2016 or 2017 and compared those within-stream reach pair differences after the treatments. By using reference reaches and focusing on within-stream differences before and after treatments, we accounted for year-to-year variability.

Canopy Gap Treatments

Gaps were centered on a tree next to the stream at approximately 30 m along each reach. Wood from the gaps was explicitly left out of the stream to focus only on responses from light without confounding effects of wood additions. Our goal was to create gaps that were comparable to naturally occurring gaps from tree-fall or small-scale disturbance events found in late-successional forests within these systems, which have gap diameter to tree height ratios ranging from 0.4 to 1.0, with smaller gaps occurring more frequently (Spies et al. 1990; Gray & Spies 1996). We intended to create gaps in the 0.4–1.0 gap

diameter to tree height ratio range (approximately 314–1,963 m² given the site potential tree height in this region) (Canham et al. 1990). Due to safety considerations in initiating the gaps and trees getting hung up in felling, some additional, unplanned trees had to be cleared. Therefore, actual gap sizes varied across sites from approximately 514–1,374 m² (0.45–0.74 gap ratios) with a mean of 962 m² (mean gap ratio 0.61), which also falls within the gap area distribution found in other temperate forests (Foster & Reiners 1986).

Vertebrate Sampling

Vertebrate surveys occurred in late July to early August each year using a backpack electrofisher (Smith-Root model LR-20B) and following multiple pass depletion survey methods. Between passes, all fish and salamanders were held in aerated coolers (large fish and salamanders were held separately from smaller fish to avoid predation during holding). AQUIS was used to anesthetize fish prior to handling. Fish total length and both the vent and total length of salamanders were recorded to the nearest millimeter. Weight was recorded to the nearest 0.01 g. Fish and salamanders were fully recovered before being released back into the reach in which they were captured.

Population Estimates

Abundances for adult (age 1+ and older) coastal cutthroat trout (*Oncorhynchus clarkii clarkii*; “CT”), age 0+ juvenile coastal cutthroat trout (“young-of-year” or “YOY” trout), Pacific giant salamanders (*Dicamptodon tenebrosus*; “DC”), and sculpin (*Cottus* spp.; “SC”), which were present only at site W-100, were estimated from multiple-pass depletion surveys and application of the Fisheries Stock Assessment Methods package in R (FSA, version 0.0.3; <https://github.com/fishR-Core-Team/FSA>). FSA is based on the program Microfish (version 3.0; Van Deventer & Platts 1989), which calculates population estimates from multiple pass depletion surveys using maximum likelihood estimation (Carle & Strub 1978).

Fish and salamander abundances in each reach were quantified as densities (individuals/m²) calculated using abundance estimates from the multiple pass depletion surveys divided by wetted area (m²) of the stream reach during the survey. Population estimates for YOY and adult cutthroat trout, salamanders, and sculpin were analyzed separately because capture probabilities can differ between these groups. The YOY fish were clearly identifiable

based on length-frequency histograms (Fig. S1). When calculating total density or biomass, we added the individual estimates from each group together. The upper and lower confidence intervals for the density estimates were calculated using the upper and lower 95% confidence intervals (CIs) from the maximum likelihood population estimate analysis. Fish population estimates from small streams often produce 95% CIs that are asymmetric because the lower bound of the confidence interval is adjusted based on the known number of fish sampled (e.g. the estimated lower confidence bound is smaller than the actual number of fish sampled and is therefore adjusted up to the total catch).

As with the density estimates, fish and salamander biomass in each reach was quantified per unit area of each reach (g/m^2). Biomass estimates were calculated by multiplying the average weight (g) of the given group (YOY, 1+ cutthroat, salamanders, or sculpin) within a reach by the estimated abundance of that group (n) and then dividing by reach area (per m^2). Confidence intervals around biomass density estimates were calculated using the upper and lower bounds of the 95% CIs from the population estimates for each group in each stream.

Adult and YOY Cutthroat Trout Summer Growth

In the first summer after the gap treatments (2018, Post-1), we returned to four streams in September and resampled (single pass) each reach to estimate summer growth of individually tagged adult fish and of the overall YOY population in Chucksney, Loon, W-100, and W-113 (Table S1). McTE was part of another study in which diet samples were taken via gastric lavage, so adult cutthroat were not pit tagged for growth to avoid both confounding the growth estimates and stressing individuals with both measurements (pit tagging and diet sampling). During the mid-summer population surveys a minimum of 15 cutthroat trout of at least 90 mm total length from each stream received a 9 mm HPT9 Passive Integrated Transponder tag (PIT; Biomark, Boise, ID, U.S.A.) for individual identification. Single-pass recapture surveys were conducted 5–9 weeks after the initial survey to catch and measure fish to determine the change in weight over the summer. Both reaches in a stream were surveyed for growth on the same day so the number of days for fish growth was comparable within paired reaches (Table S1). During the second survey all fish captured in the single pass were scanned for PIT tags with a hand-held reader, and individuals with a PIT tag were weighed and measured for total length.

In this study, we defined summer growth rate as the overall daily change in weight between sampling periods normalized to the initial weight of the individual. Normalized summer growth was calculated by dividing the change in weight between the two sampling events by the initial weight of the individual. Because the period between mark and recapture events was not identical across all streams, we also divided the weight-normalized summer growth by the number of days between capture and recapture events to ensure data units were comparable between all sites. We acknowledge that adult trout “growth” in mountain streams may be negative through this time period, but this measure of growth, whether positive or negative, remains a valid assessment of individual responses through

summer in our different treatment sites. We calculated summer growth rate as:

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

where W_t is the mass of the fish when recaptured, W_{t-1} is the mass of the fish when first captured, and delta T (ΔT) is the number of days between capture events.

We also calculated condition factor for individuals using Fulton’s body condition (K), calculated as follows:

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

where W is wet weight (g) of each fish and L is total tail length (cm).

During the single-pass recapture event, we also captured, weighed, and measured all YOY within both reference and treatment reaches. Mean overall apparent YOY trout growth in each reach was estimated using the calculation above; however, because fish were too small to be individually marked in the initial survey, we use the mean length and weight of all YOY captured in the first event as our initial time value, and the mean length and weight of YOY captured in the second event as our time-2 value to determine apparent growth.

Statistical Analysis

In order to determine effects of the experimental canopy gaps on vertebrate density and biomass in our streams, we used the following linear mixed model using the nlme package (Pinheiro et al. 2016) in R statistical software:

$$Y_i = \beta_0 + \beta_1 \cdot \mathbb{I}_{i=\text{Trt}} + \beta_2 \cdot \mathbb{I}_{i=\text{Post-1}} + \beta_3 (\mathbb{I}_{i=\text{Trt}} \cdot \mathbb{I}_{i=\text{Post-1}}) + \beta_4 \cdot \mathbb{I}_{i=\text{Post-2}} + \beta_5 (\mathbb{I}_{i=\text{Trt}} \cdot \mathbb{I}_{i=\text{Post-2}}) + Z_i u_s + \varepsilon_i$$

where $\mathbb{I}_{i=\text{Trt}}$ is an indicator variable taking the value 1 if observation i is from a treatment reach and 0 otherwise (from a reference reach). $\mathbb{I}_{i=\text{Post-1}}$ is an indicator variable that takes the value 1 if the observation i is from Post-1 (the first year after the gaps were implemented), $\mathbb{I}_{i=\text{Post-2}}$ is an indicator variable that takes the value 1 if observation i is from Post-2 (the second year after the gaps were implemented), Z_i is a row vector that pulls out the random nested stream and reach effect, u_s , associated with observation i , and ε_i is the random error where ε_i and $\varepsilon_{i'}$ are independent. β_3 therefore represents the effect of the treatment the first year and β_5 represents the effect of the treatment in the second year.

In assessing adult growth and change in condition factor across the four replicate streams in the first year after the treatments, we used a linear mixed model to test for the effect of reach (reference or treatment) with a random effect for each stream. We also tested for significant differences among reaches for individual sites using Student’s t tests. For mean juvenile YOY apparent growth we do not have data from individuals, so we used paired t tests on reach means to assess the null

hypothesis that there is no difference in mean growth. We also used a paired *t* test to evaluate changes in mean condition between reference and treatment reaches before and after gaps were cut.

We used linear regression to evaluate potential relationships between gap size and biomass responses of trout and all vertebrates. Stream temperature responses to this gap experiment were assessed in (Swartz et al. 2020) and are summarized in Supplement S1. Using results from that earlier study, we also used linear regression to assess the relationship between changes in stream temperatures relative to biomass responses. Stream temperature data were not collected in Post-2, so responses relative to stream temperature were only evaluated for the first year after gap treatments.

Results

In all reaches, creating a gap substantially increased light exposure in the reach (Swartz et al. 2020); however, while we initially planned to create gaps of comparable size at each stream, local conditions and vagaries of the implementation process at each site ultimately led to a range of gap sizes across the five streams. The smallest gap was on Loon Creek where approximate canopy gap area was 514 m² in mid-summer and encompassed about 20 linear meters of stream (Table 1; Swartz et al. 2020). The largest gap was in McTE where the gap area

was 1,374 m² and encompassed about 55 linear meters of stream (Table 1; Swartz et al. 2020).

Vertebrate Density and Biomass

Considering just adult (1+ and older) cutthroat trout, four of the five sites showed increases in density and biomass after the gap treatment, and there was weak support for the effect of the gaps on adult biomass across all five replicate sites 2 years post-treatment (0.010 g m⁻², 95% CI: -0.003, 0.023; Table 2). The major outlier was Loon Creek which had a large decline in reach differences in the first year post-treatment increasing the variability among responses (Fig. 1). Stream W-113 had a large relative increase after the first year, while relative increases from the gap at McTE, Chucksney, and W-100 were small. Patterns in biomass estimates were similar to densities (Fig. 1), and for both metrics the range in reach densities across streams in the first year post-treatment (Post-1) was less than during the pre-treatment period (Fig. S3). In the second year post-treatment (Post-2), adult trout increases were larger compared to pre-treatment (Table 2) and were more consistent than during the first post-treatment year (Fig. 1). While the reach differences at Loon Creek declined in the first year after the gaps were imposed, in the second year after the treatments the difference in adult trout densities between reaches returned to pre-treatment levels, and reach densities at Loon remained highest among sties. The lack of increase may have been due to greater

Table 2. Statistical results of linear mixed model testing effects of the gap treatment (treatment) and the first and second year after the treatment (Post-1 and Post-2) on biomass (g/m²) and density (individuals/m²) for adult cutthroat trout (CT), age-0 cutthroat trout (YOY), Pacific giant salamanders (DC), and total vertebrates (All verts).

Species Group	Coefficient	Density				Biomass			
		Estimate	Lower 95% CI	Upper 95% CI	p Value	Estimate	Lower 95% CI	Upper 95% CI	p Value
CT	Intercept	0.002	0.001	0.003	<0.01	0.029	0.018	0.040	<0.01
	Post-1	0.000	-0.001	0.000	0.43	-0.004	-0.013	0.005	0.41
	Post-2	0.001	0.001	0.002	<0.01	0.010	0.000	0.019	0.06
	Treatment	0.000	-0.001	0.001	0.66	-0.003	-0.012	0.006	0.56
	Post-1:Treatment	0.000	-0.001	0.001	0.68	0.006	-0.007	0.018	0.41
	Post-2:Treatment	0.001	0.000	0.002	0.20	0.010	-0.003	0.023	0.14
YOY	Intercept	0.002	0.001	0.003	<0.01	0.003	0.000	0.006	0.10
	Post-1	0.000	-0.001	0.000	0.43	0.003	0.000	0.007	0.05
	Post-2	0.001	0.001	0.002	0.00	0.000	-0.003	0.004	0.78
	Treatment	0.000	-0.001	0.001	0.66	0.000	-0.004	0.003	0.78
	Post-1:Treatment	0.000	-0.001	0.001	0.68	0.000	-0.004	0.005	0.95
	Post-2:Treatment	0.001	0.000	0.002	0.20	-0.001	-0.005	0.004	0.77
DC	Intercept	0.004	-0.002	0.010	0.18	0.032	0.002	0.062	0.05
	Post-1	0.001	-0.003	0.006	0.54	0.005	-0.017	0.028	0.65
	Post-2	0.005	0.000	0.009	0.05	0.023	0.000	0.046	0.07
	Treatment	0.000	-0.004	0.005	0.87	0.006	-0.017	0.029	0.65
	Post-1:Treatment	-0.001	-0.007	0.004	0.63	-0.008	-0.040	0.025	0.64
	Post-2:Treatment	0.001	-0.005	0.007	0.64	0.015	-0.018	0.047	0.38
All verts	Intercept	0.010	0.004	0.016	0.01	0.072	0.038	0.107	0.00
	Post-1	0.003	-0.002	0.008	0.26	0.005	-0.021	0.030	0.73
	Post-2	0.006	0.001	0.012	0.03	0.029	0.003	0.054	0.04
	Treatment	-0.001	-0.006	0.004	0.77	-0.003	-0.028	0.023	0.86
	Post-1:Treatment	-0.001	-0.009	0.006	0.75	0.000	-0.036	0.037	0.99
	Post-2:Treatment	0.003	-0.005	0.010	0.52	0.032	-0.004	0.068	0.10

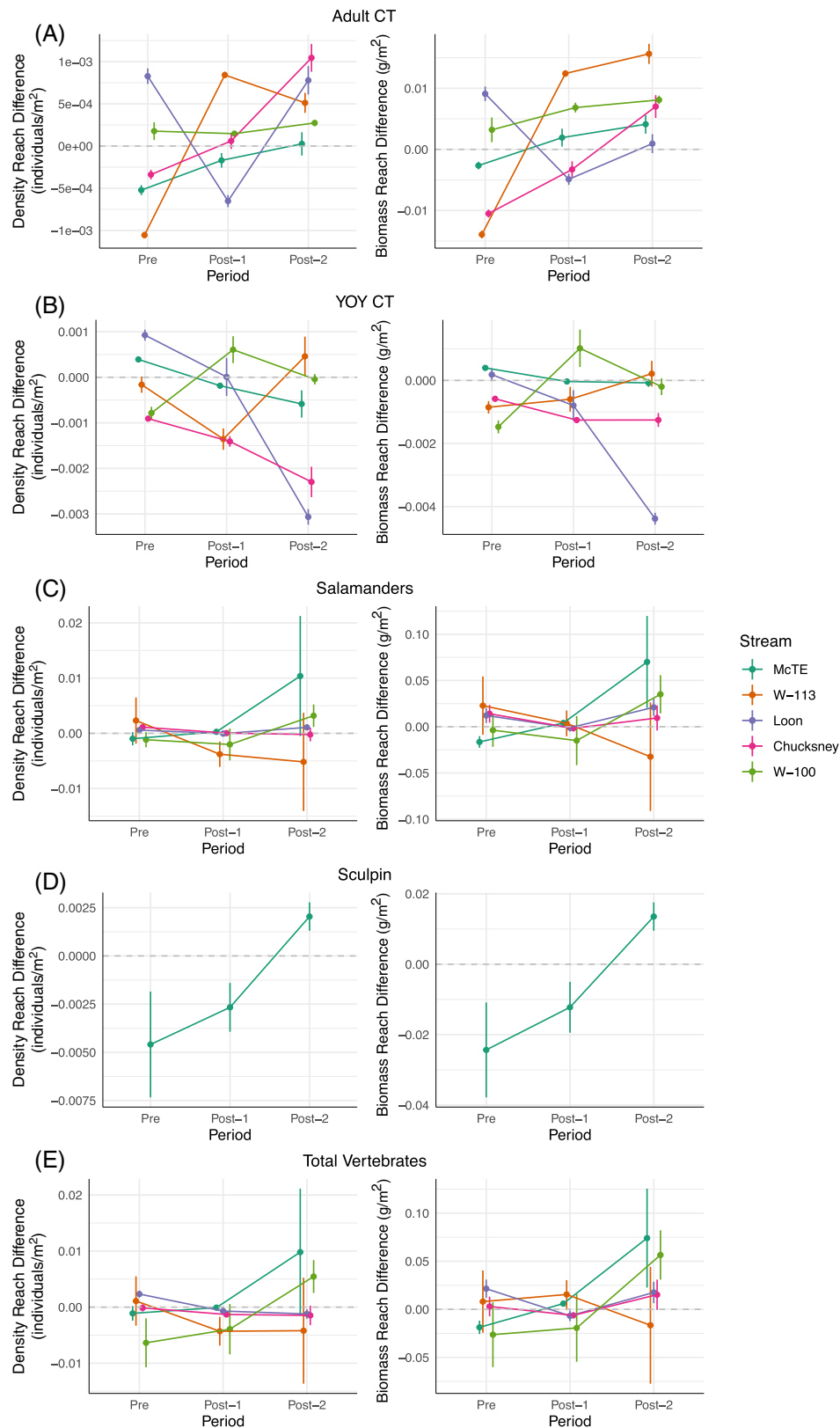


Figure 1. Density (individuals/m²) and biomass (g/m²) reach differences (treatment reach – reference reach) (\pm SE) at each stream for each species: (A) adult cutthroat trout (CT), (B) juvenile cutthroat trout (YOY), (C) Pacific giant salamanders (DC), and (D) sculpin (only present at W-100); and (E) total vertebrates. [Correction added on 25 October 2023, after first online publication: Figure 1 was updated to correct labeling and overlapping lines.]

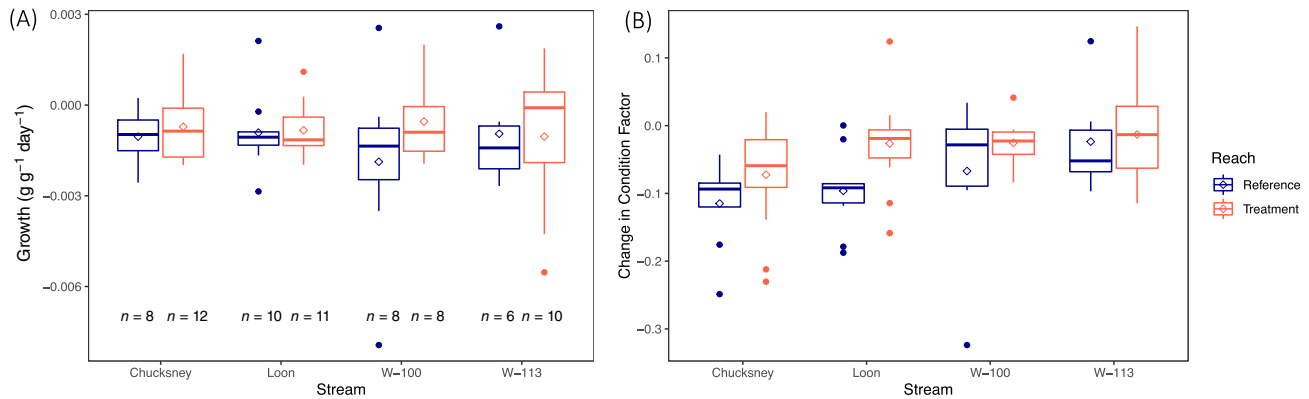


Figure 2. (A) Growth ($\text{g g}^{-1} \text{ day}^{-1}$) and (B) change in condition factor of recaptured adult cutthroat trout in reference and treatment reaches from August to September 2018 (post-treatment). The number of individuals recaptured are listed below boxplots in growth panel and the asterisk indicates a significant difference ($p < 0.05$) in reaches.

density and biomass in the gap reach during the pre-treatment period (Fig. S3).

The densities and biomass of YOY trout were variable among sites and time periods. Analyzing differences relative to reference sites largely normalized for year-to-year variability, but across nearly all sites summer 2018 (Post-1) was a very strong year for YOY populations (Figure S1 & S3). In the first year post-treatment, the change in relative density of YOY from the gaps was not significantly different across all sites combined (Table 2). Individually, one site (W-100) had a substantial relative increase in YOY density while the other four sites had relative declines (Fig. 1). In the second year after gaps were cut, there was similarly no clear overall response in YOY when considering all five replicate streams together (Table 2).

Sculpin were present only at one stream in this study (W-100). Sculpin increased slightly in the first year after the gap treatment; however, 2 years after treatment both density

and biomass increased substantially compared to the reference reach (Fig. 1).

Because salamander capture probabilities are low, error around their collective density estimates are high, and across the replicate sites there was no support for an effect of gaps on salamander density or biomass in either year post-treatment (Table 2). In the first year after the gap treatments (and pre-treatment), reach differences were small at all sites and reach pairs had overlap in the 95% CI of density and biomass of salamanders. Two years after the gap implementation (Post-2), salamander biomass and abundance in treatment reaches at W-100 and McTE increased substantially relative to reference reaches, while at Chucksney and Loon, salamanders in treatment reaches increased slightly, and at W-113, salamanders in treatment reaches decreased slightly relative to reference reaches (Fig. 1).

Total vertebrate estimates were highly variable (Fig. S3) and did not indicate responses to the treatments in the first summer (Post-1), but there was support for an overall effect of

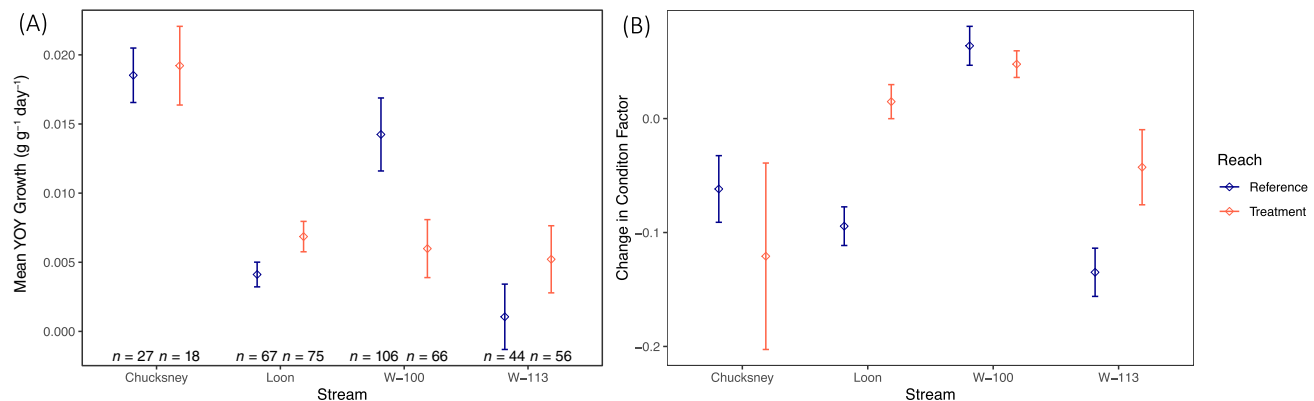


Figure 3. (A) Mean and bootstrapped 95% confidence intervals of YOY growth ($\text{g g}^{-1} \text{ day}^{-1}$) in each reach from August to September 2018. (B) Mean change in YOY condition factor in each reach in each reach in from August to September 2018.

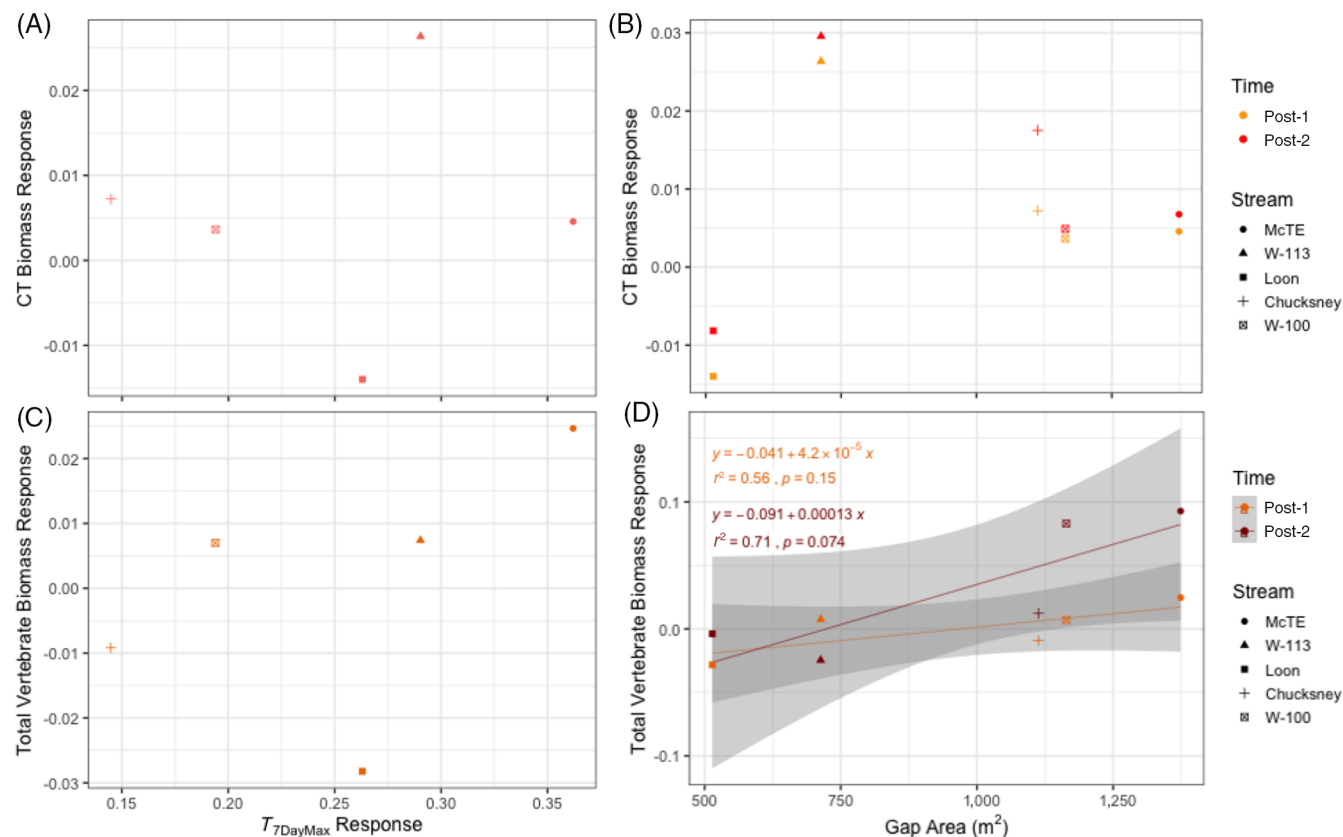


Figure 4. Stream temperature responses ($^{\circ}\text{C}$) and gap area (m^2) versus responses in (A, B) adult cutthroat trout biomass (g/m^2) and (C, D) total vertebrate biomass (g/m^2) at each of the paired stream sites. Post-2 stream temperature data were not available.

the gaps on total vertebrate biomass 2 years post-treatment (0.032 g m^{-2} , 95% CI: $-0.004, 0.068$) with relative reach increases at four of the five sites (Table 2). Total vertebrate biomass results were largely comparable to the density responses in the first year after gap treatments with the exception of W-113, which had a small relative increase in biomass despite a decline in density (Fig. 1), indicating fewer but larger individuals in the gap treatment reach. In the second summer, both McTE and W-100 exhibited continued increases in total vertebrates in the gap sites relative to treatment sites, while Loon, Chucksney, and W-113 had slight declines. Although total vertebrate density declined slightly in Chucksney in Post-2 at the gap reach relative to the reference reach, as with W-113 in Post-1, Chucksney had a slight relative increase in total vertebrate biomass, indicating fewer but larger individuals in this reach (Fig. 1).

Cutthroat Trout (Adult and YOY) Summer Growth and Condition

We quantified growth in a total of 73 adults in Chucksney, Loon, W-100, and W-113 during 2018. Across the full set of adults 12.3% showed an increase in mass over the 6-week study period, while 62.0% showed a relative decrease and 36.7% showed “no change” ($>2\%$ change between mark and recapture). There were no differences in mean growth for adult trout between gap and reference reaches in any of the four streams when evaluated

collectively or individually (Tables S2 & S3). Nearly all recaptured fish lost condition through the summer, but recaptured adult cutthroat trout lost significantly ($p = 0.02$) less condition in treatment reaches than reference reaches when evaluated at all four replicate reaches (Table S3). Loon was the only site where, when evaluated individually, the treatment reach was significantly greater (Table S2; Fig. 2B). Chucksney also had less condition loss in the treatment reach whereas in W-100 and W-113, recaptured fish in reference and gap treatment reaches lost a similar amount of mean condition. None of the four site pairs had cases in which the reference site fish had lower mean changes in condition.

The summer mean apparent growth rate of YOY trout in 2018 was greater in the treatment reaches at three of the four streams that were re-surveyed in fall (Loon, Chucksney, and W-113) than in the reference reaches at these streams (Fig. 3A), but collectively the effect of reach was not significant ($p = 0.98$; Table S4). There was also a clear density-dependent response in YOY apparent growth across sites (Fig. S4). Mean YOY change in condition was not significantly greater in treatment versus reference reaches ($p = 0.60$; Table S4), but was significantly greater at treatment reaches at Loon and W-113 based on 95% CIs. Mean change in condition was comparable among reaches at Chucksney and W-100, but the treatment reaches were slightly lower (Fig. 3B).

Gap Size Effects

Stream temperature changes were not related to the responses of either adult cutthroat trout or total vertebrates across the five study streams in the first summer after the treatment (Fig. 4A & 4C). The responses of adult cutthroat trout were also not related to gap size (Post-1 and Post-2 summers, respectively) in either the first or second summer post-treatment; however, when considering all of the apex predator biomass together, total vertebrate biomass responses were related to gap size across the five study sites ($r^2 = 0.56$, $p = 0.15$ and $r^2 = 0.71$, $p = 0.07$ for Post-1 and Post-2 summers, respectively).

Discussion

Across this replicated field experiment, results indicate that opening patches in the riparian canopy adjacent to the stream does not negatively impact aquatic vertebrates, and therefore may be a viable tool to enhance structural complexity of western Pacific Northwest riparian forests. We also found that creating individual gaps immediately adjacent to the stream yielded a small overall increase in total vertebrate and adult cutthroat trout biomass two years after treatment, and gap reaches had slightly greater cutthroat trout growth and condition at most sites after treatment. However, the magnitude of all of the biomass responses were small, suggesting that potential effects from a single gap are not likely to be large enough to make individual gaps alone a viable tool to substantially enhance apex predator density beyond the individual reach scale.

The small positive adult cutthroat trout responses at four of the five streams were consistent with our hypothesis and with other studies that imposed more extensive riparian manipulations of stream light and found substantial cutthroat trout increases (Murphy & Hall 1981; Kiffney et al. 2003; Wootton 2012). In Loon Creek, in the first summer after creating the gap there was a decline in adult cutthroat trout relative to the reference reach, which remained similar to its pre-treatment density. But the relative decline did not reflect a crash in population densities. In the second year post-treatment, both reaches at Loon had the highest adult trout densities compared to all of the other reaches in this study. During this period, trout density in the treatment reach was greater than in the reference, resulting in a relative difference between reaches during Post-2 that was comparable to that of the pre-treatment differences. So, although adult cutthroat trout at Loon showed an initial negative response to the gap, fish densities remained high in the system and by the second year post-treatment the density in the gap treatment relative to the reference returned to what it was prior to the gap. Loon was also the only stream where the summer change in condition factor was significantly greater for recaptured adult trout from the treatment reach compared to recaptured individuals in the reference reach following gap creation. We suggest that this improved condition following the canopy gap treatment here was likely due to the decline in density in the first year post-treatment.

Total vertebrate biomass responded only to the treatment the second summer after implementation, providing partial support for the hypothesis that increases in light drive greater stream

vertebrate biomass via enhanced basal resource availability. The 2-year responses suggest a need for continued monitoring as the magnitude of responses could change over time depending on how the gaps change (fill in, get larger, or remain similar sizes) and if species exhibit population level responses over time. Total vertebrate responses were inconsistently driven by dominance of salamanders, cutthroat trout, or sculpin populations among sites, and though consistent across sites, the first year post-treatment was more variable than the second summer. W-100 is the only site that contains sculpin (*Cottus* spp.), and the positive sculpin responses to the gap contributed to the large response in total vertebrates the second year at W-100. The strong positive sculpin response with more moderate responses by YOY and adult cutthroat (perhaps due to increased competition) to a canopy opening in this field experiment provides empirical support for a recent ecosystem modeling study that found sculpin were more responsive to riparian canopy modifications and associated changes in autochthonous resources than cutthroat trout (Benjamin et al. 2022). The large sculpin response that we observed may be in part due to foraging behavior as sculpin generally feed from the stream benthos (Falke et al. 2020) where changes in light may lead to increased periphyton and perhaps invertebrate production, whereas trout are opportunists feeding from the water column, surface, and stream benthos (Keeley & Grant 2001; Romero et al. 2005). Pacific giant salamanders (*Dicamptodon tenebrosus*) are primarily benthic dwellers, but are generalists and also commonly prey on stream vertebrates (Cudmore & Bury 2014). Recent diet analyses in systems with cutthroat trout and Pacific giant salamanders have indicated predation of both species on each other and themselves (Roon 2021). Therefore, community interactions within aquatic predator species in headwater ecosystems may contribute to how densities and biomasses of different species or age classes respond to increases in autochthonous resources in the stream food web when riparian canopies are manipulated.

YOY densities and biomasses were not consistently affected by the gap treatment in either the first or second year post-treatment. Over the course of the study, YOY populations varied between years with high populations across almost all streams and reaches in 2018. The high adult cutthroat trout densities and biomasses at all sites in the second summer relative to pre-treatment and the first summer post-treatment are likely influenced by the high YOY populations in 2018 (Post-1). Apparent growth of YOY increased at three of the four sites evaluated (growth data were not collected at McTE). At W-100, we suggest that more limited YOY growth was a result of density dependence as total vertebrates were abundant at this site. Indeed, growth rates of salmonids are commonly limited by competition of foraging resources yielding density-dependent responses (Huntsman et al. 2021; Jenkins et al. 1999; Matte et al. 2020), and this is often specifically found in juveniles (Grant & Imre 2005). Previous studies on large-scale removal or loss of all riparian forests have found consistently greater abundances and sizes of juvenile trout (Johnson et al. 1986; Swartz & Warren 2022); however our YOY density responses were variable. We suggest that the differences here are due to the relatively small size of our treatments. When all of the

riparian forest is lost or cleared, the impacts encompass the whole stream reach or beyond and there are often increases in temperature that may affect emergence time and growth (Holtby 1988; Swartz & Warren 2022); however, gap treatments encompass only a portion of the reach unlike large harvest treatments or severe wildfire events.

Summer adult cutthroat trout growth in forested headwaters in the Pacific Northwest can often be zero or negative (Harvey et al. 2014; Jensen 2017) as were growth rates of adults in this study, but growth rates in gap reaches after treatment were slightly less negative than reference reaches. Also, changes in condition of adults in gap reaches over the first summer post-treatment were greater than in paired reference reaches in this time period. Growth for adults was quantified only for recaptured individuals. This aspect of the study therefore does not account for potential immigration or emigration during summer; however, the sites are high gradient headwaters sampled over the summer low-flow period, so there is limited opportunity for upstream movement at all reaches except for those at W-100, which has higher discharge and where some potential movement is possible. Previous post-harvest studies have found increases in adult growth related to increases in stream temperature, and perhaps more importantly, increases in resource availability (Mellina & Hinch 2009; Leach et al. 2012). Although relative growth responses of recaptured individuals to gaps are small, they partially support our hypothesis that riparian canopy openings have a positive effect on adult cutthroat trout.

While temperature is also a potential driver of changes in stream ecosystem processes as well as conditions for coldwater biota, cutthroat trout and aquatic vertebrate responses were not related positively or negatively to stream temperature responses. The changes in stream temperature that were documented in response to the gaps were small and decreased with increasing stream size (Swartz et al. 2020). Temperature increases from gaps did not approach levels generally thought to negatively impact cutthroat trout and salamanders. Also, while fish growth rate is a function of stream temperature, it is also dependent on and potentially more sensitive to food availability (Beauchamp 2009; Railsback 2022). Therefore, fish responses to changes in light from canopy gaps depend on both the changes in temperature and changes in food resources that may occur in response to opening the riparian canopy.

Aquatic macroinvertebrates are a dominant food resource for both cutthroat trout and salamanders in headwater streams (Roon et al. 2022), and macroinvertebrate responses have been identified as a key bottom-up pathway leading to increases in salmon and trout following removal of streamside forest canopies (Bilby & Bisson 1992; Wootton 2012). However, aquatic food webs are complex and autochthonous resource increases do not always extend to aquatic predators, in part due to scraping invertebrates that either leave the aquatic system or are inedible (Power & Dietrich 2002; Roon 2021). In our study, snails (*Juga*) were present at two streams (W-100 and W-113) and are largely considered inedible to fish but graze heavily on stream periphyton. At W-100 and W-113 average density of snails increased 4-fold in gap reaches compared to the change in reference reaches (Mackness 2020), indicating increased grazing of periphyton

and greater abundance of energetic end points in the aquatic food web. In summer, cutthroat trout (and to a much lesser degree coastal giant salamanders) also rely on terrestrial macroinvertebrates as a key food resource in forested headwater streams (Roon et al. 2022). The removal of canopy cover via the creation of a gap does have the potential to locally reduce these inputs that would need to be offset by increased in-stream production in order to see a response in higher trophic levels. There was likely a decline in these inputs directly over the gaps; however, gap treatments did not encompass the whole reach leaving overhead canopy inputs in other areas of the system and upstream, and the areas next to the stream had strong regeneration of understory herbaceous vegetation. We therefore suggest that terrestrial inputs were not reduced to a degree proportional to the amount of canopy removal, or proportional to the area of biofilm growth responses.

Riparian buffers that restrict forest harvest in areas adjacent to fish-bearing streams are a key regulatory and conservation tool applied to forest management on federal, state, and private ownerships across Oregon, Washington, California, and British Columbia and Alaska—encompassing the range of many anadromous Pacific salmon (Richardson et al. 2012). As riparian forests in the Pacific Northwest continue to recover from previous harvest and are left to regenerate (Frainer & McKie 2021), understanding the driving mechanisms and interactions between riparian canopies and stream ecosystems is important for informing future management designed to balance the protection of stream biota with sustainable forest harvest and the restoration of complex forest structure in riparian zones. Conceptual papers have suggested that management in the riparian zone designed to mimic natural disturbances may be ecologically beneficial (Kreutzweiser et al. 2012; Kuglerová et al. 2014; Laudon et al. 2016) and have noted the need for rigorous experimental studies evaluating potential riparian manipulations. This experimental BACI study provides a direct assessment of aquatic apex predator responses to implementation of riparian canopy gaps as a management tool—whether to enhance structural complexity for terrestrial biota who respond positively to gaps (Przepióra et al. 2020; Tena et al. 2020; Kozel et al. 2021) or to restore complex light environments to stream ecosystems. We focused explicitly on creating patches of light availability similar to those from natural canopy gaps in old-growth forest stream systems, although the riparian forests upstream and downstream of the gap treatments remained different from those in old-growth systems. The small overall relative increase in trout and total vertebrates in response to these individual gaps suggests that one gap alone is not an effective tool to enhance in-stream apex predator production; however, the gap treatments are relatively low cost and logistically feasible to implement and may be more effective at larger scales. Larger gaps than those used in the present study may yield greater stream predator responses, but this must balance ecological tradeoffs (e.g. larger temperature responses). Or, a larger number of gaps along a reach may be more effective in creating a series of patches with elevated light and would also create greater structural complexity in the forest canopy along a riparian corridor. Further work is needed expanding beyond an individual reach to impose varying frequencies of similarly sized gaps

(within the range of naturally occurring in old-growth Douglas-fir forests) in the catchment or gaps of varying sizes.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Supporting information.

Table S1. Population and growth sampling dates in 2018 (Post-1).

Table S2. Statistical results of *t*-tests evaluating reach differences.

Table S3. Statistical results of the effect of the treatment reach on adult cutthroat summer growth and change in condition factor during 2018 (Post-1).

Table S4. Statistical results of the effect of the treatment reach on mean juvenile cutthroat trout summer growth and change in condition factor during 2018 (Post-1).

Figure S1. Length (mm) frequency histograms of all coastal cutthroat trout separated by age-0 and age-1+ at all stream reaches.

Figure S2. Length (mm) frequency histograms of all coastal cutthroat trout separated by age-0 and age-1+ at Chucksney, Loon, W-113, and W-100.

Figure S3. Density and biomass at each stream reach.

Figure S4. YOY growth as a function of (a) YOY density and (b) total vertebrate density indicating density dependence.

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