Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams

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

Key words: aquatic–terrestrial linkages; bottom-up controls; *Oncorhynchus clarkii clarkii*; riparian forests; trophic linkages.

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INTRODUCTION

Riparian zones are key areas of exchange between aquatic and terrestrial ecosystems. In many regions, riparian zones are dominated by forests, which exert strong controls on stream habitat and the quantity and quality of food resources at the base of food webs. Riparian vegetation influences stream primary production via controls on stream light (Gregory 1980, Bilby and

Bisson 1992, Hill et al. 1995), and terrestrial vegetation in the riparian zone subsidizes stream food webs by contributing nutrients, leaves, needles, and terrestrial invertebrates (Gregory et al. 1991). Riparian vegetation also stabilizes banks, reduces erosion, and provides streams with wood that can create pools and promote habitat heterogeneity (Montgomery et al. 1995). Given their strong influence on streams, differences in the community composition, age distribution, and structural characteristics of riparian forests have the potential to exert control on stream biota.

The availability and quality of stream habitat is commonly identified as a factor limiting abundance of stream fishes (Poff and Huryn 1998, Rosenfeld 2003). For salmonids, pools are key habitat elements that provide deep water cover (Berg et al. 1998) and thermal refuge (Matthews et al. 1994), and can minimize energetic costs of feeding (Fausch 1984, Rosenfeld and Boss 2001). In forested streams, pool creation, overhead cover, and habitat complexity are often associated with large wood (Beechie and Sibley 1997, Montgomery et al. 1995). The removal of large wood from streams, which was once a common practice associated with timber harvesting (Richardson et al. 2012), has been linked to reductions in pool area and fish abundance (Fausch and Northcote 1992, Mellina and Hinch 2009). In streams lacking large wood and structural complexity, the artificial addition of wood or other structures intended to promote pool formation and habitat complexity often increases salmonid abundance (Roni and Quinn 2001, Roni et al. 2002). Consequently, stream restoration efforts over the past 30 yr often involve large wood additions and physical manipulations to promote pool formation, structural heterogeneity, and habitat complexity, particularly in the Pacific Northwest ecoregion (Naiman et al. 2012). In addition, riparian zones are commonly managed to promote future large wood inputs to streams (Richardson et al. 2012). However, some studies have found little to no response in salmonid abundance following habitat restoration (Roni et al. 2002, 2008), suggesting that factors beyond habitat and wood may be limiting fish populations in some streams.

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

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

Riparian stand development processes and the legacies of forest management can affect stream habitat and productivity. Streams bordered by old-growth riparian forests typically exhibit greater large wood loading, large wood volume, and total pool area than streams where riparian harvesting occurred (Bilby and Ward 1991, Keeton et al. 2007, Warren et al. 2007). Light availability is highest following riparian clear-cutting or a stand-replacing event but as the riparian

forest regenerates, canopies close, typically reaching maximum cover when stands are 30–100 yr of age (Kaylor et al. 2017). In late stages of stand development (e.g., old growth), the formation of canopy gaps results in greater and more spatially variable light (Keeton et al. 2007, Kaylor et al. 2017). To evaluate the relative strength of habitat and productivity metrics in explaining fish and salamander biomass, we created a study design in which we selected adjacent stream sections with these contrasting riparian forest conditions.

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

MATERIALS AND METHODS

Study site

The nine reach pair sites evaluated in this study were located within the McKenzie River Basin in the western Cascade Mountains of Oregon (Fig. 1). Seven of the sites were located within the HJ Andrews Experimental Forest (HJA), a 6400-ha research forest encompassing the entire Lookout Creek drainage basin. Cook Creek and Fritz Creek were located outside of the HJA. Cook Creek is a tributary of Blue River

upstream of Blue River reservoir and Fritz Creek is a tributary of Deer Creek, which flows directly into the McKenzie River. The Mediterranean climate of this region is characterized by wet winters with high stream discharge and dry summers with annual minimal flows occurring between late August and early September.

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

The previously harvested cutblocks were cleared 40–60 yr prior to this study (Table 1). In all cases, timber was removed down to the stream bank with no riparian buffer. Trees were replanted within 5 yr post-harvest in seven of the nine cuts in accordance with forest management practices at the time. Stands in McRae Creek Tributary-West (MCTW) and Mack Creek were regenerated without any post-harvest planting. In 2014, the second-growth riparian forests were predominantly Douglas fir (*Pseudotsuga menziesii*) but red alder (*Alnus rubra*) was also a common canopy species in areas directly adjacent to streams and provided substantial stream shading. Old-growth forests were comprised of Douglas fir, western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Red alder was present adjacent to streams within old-growth forests as well, but it was not as common as in second-growth sections.

Coastal cutthroat trout and coastal giant salamanders (*D. tenebrosus*) were present in all 18 stream reaches and were the dominant vertebrates. Sculpin (*Cottus* spp.) were present in both reaches of MR404, but were not found in any
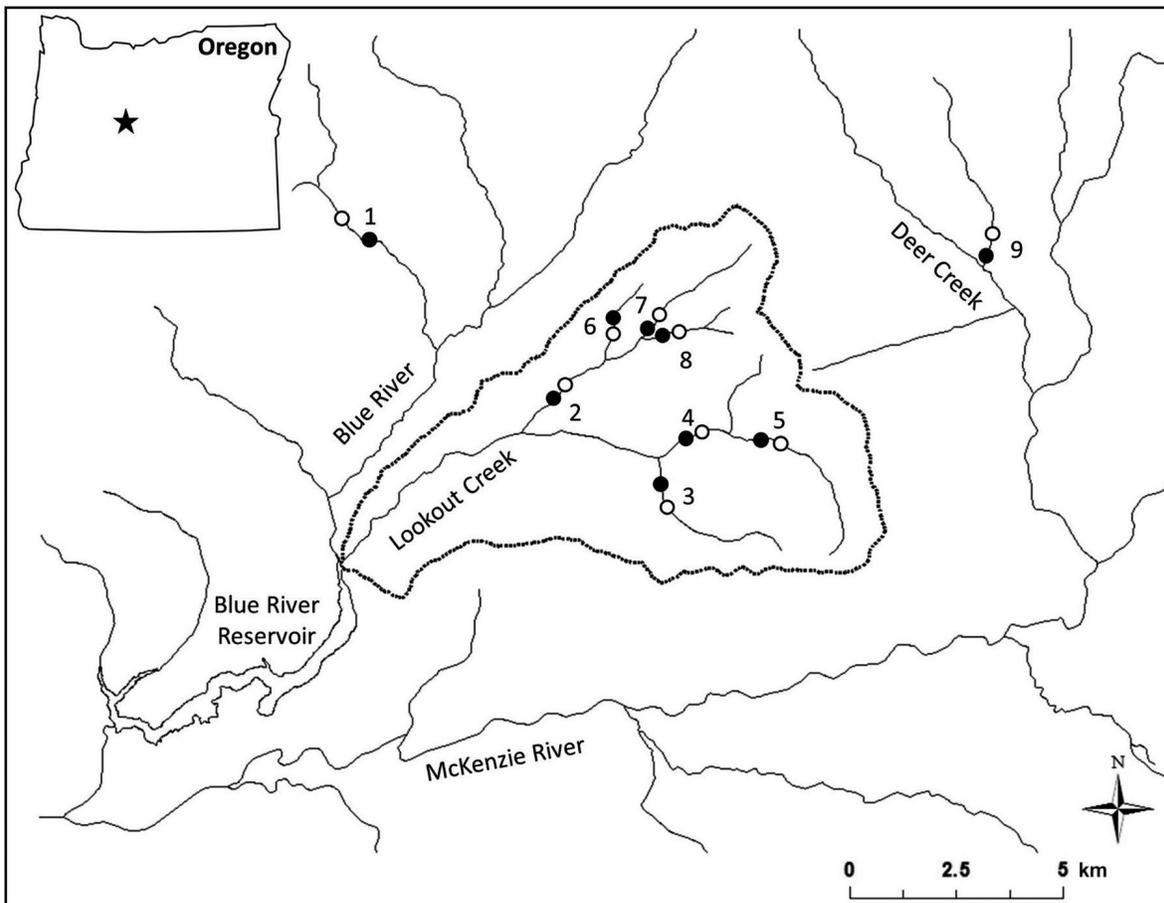
Fig. 1. Map of the nine reach pair locations in the McKenzie River Basin, Oregon. Each reach pair consists of a reach within old-growth forest (open circles) and a reach bordered by previously harvested riparian forest (closed circles). Pair 1 = Cook; 2 = MR404; 3 = Mack; 4 = LO701; 5 = LO703; 6 = MCTW; 7 = MR504; 8 = MCTE; 9 = Fritz.

other reaches. Tailed frogs (*Ascaphis truei*) were found in low abundance in some of the streams, but were not evaluated in this study.

Field sampling—abiotic variables

All data were collected in the summer of 2014 during low-flow conditions. Across all nine pairs, we collected a suite of physical habitat variables in each reach including canopy cover, bankfull width, wetted width, pool area, large wood abundance and volume, temperature, nutrient concentration, and stream gradient. Canopy cover was quantified using a convex spherical densiometer (Forestry Suppliers Model A). Measurements were taken in each cardinal direction at 11 regularly spaced locations in each

reach. All densiometer measurements were taken by the same individual to avoid user bias. Bankfull width and wetted width were measured at transects across the same 11 reach locations. The mean wetted width for each reach was multiplied by reach length to obtain total reach wetted area, which was used to standardize fish, salamander, and invertebrate abundance and biomass estimates per square meter of stream. Pools were identified during summer low-flow conditions as slow velocity habitats connected to the main channel. Pool area was calculated using the length and width of each pool, and percent pool area was calculated as the total pool area divided by total wetted reach area. We quantified all large wood pieces greater than 1 m in length and

Table 1. Physical attributes of stream reach pairs.

Sites	Riparian type	Harvest year	Stand area (ha)	Bankfull width (m)	Canopy openness (%)	Gradient (%)	Wood volume (m^3/100 m^2)	Pool area (%)	NO$_3$-N (µg/L)	Temperature (°C)
MCTE	OG	...	...	3.46	11.2	6.8	6.0	29.3	1.3	12.3
	PH	1958	9	3.06	5.1	7	1.4	10.3	5.8	12.6
MCTW	OG	...	...	4.1	8.6	6.7	10.8	24.4	4.0	13.1
	PH	1953	17	3.4	6.1	4.3	1.2	13.1	3.3	13.3
MR504	OG	...	...	6.9	22.4	6.8	2.6	37.9	3.0	11.2
	PH	1958	9	6.3	8.4	6.8	3.1	30.8	4.0	11.4
LO703	OG	...	...	7.8	34.0	6.4	2.0	16.8	48.9	9.1
	PH	1960	7	7.4	53.8	6.4	0.7	15.4	44.2	9.3
Fritz	OG	...	...	9.7	11.1	16	2.6	27.3	9.6	13.9
	PH	1960	7	7.8	2.6	13.8	2.8	29.9	11.3	14.2
Mack	OG	...	...	9.8	23.9	9.5	6.0	27.0	63.7	12.4
	PH	1965	4	9.3	32.2	9.9	1.5	21.4	58.0	12.7
LO701	OG	...	...	9.9	20.2	7.1	2.7	40.2	42.0	9.9
	PH	1959	12	9.0	10.5	6.0	0.9	42.4	38.5	10.3
Cook	OG	...	...	10.55	23.8	4.6	6.6	17.5	37.5	13.8
	PH	1971	7	8.6	4.8	4	0.6	21.2	31.9	13.9
MR404	OG	...	...	10.4	29.0	7.6	6.8	41.0	20.4	13.7
	PH	1953	20	8.6	32.7	4.0	0.3	19.2	20.6	13.6

Note: OG = old-growth riparian forest and PH = previously harvested riparian forest on at least one stream bank.

10 cm in diameter (Richmond and Fausch 1995, Young et al. 2006, Warren et al. 2009). We only measured the portion of wood pieces located within the bankfull channel for wood volume estimates. Total channel area (mean bankfull width multiplied by reach length) was used to standardize large wood volume among reaches. Temperature loggers (HOBO Pro v2, Onset Computer Corporation, Bourne, Massachusetts, USA) were deployed for 2 weeks during mid-summer to evaluate relative temperature among streams and differences between paired reaches. Due to a limited number of sensors, not all sensors were deployed for the same time interval. Sensors were deployed from 20 July 2014 to 3 August 2014 in Cook Creek and Fritz Creek and from 4 August 2014 to 24 August 2014 in all other streams. Water samples were collected in September 2014 at all reaches during a two-day period prior to the onset of autumn rain events in this region. Water samples were filtered (25-mm Whatman GF/F filters), frozen, and analyzed for nitrate-N (NO$_3$-N) and phosphate-P (PO$_4$-P) using a Dionex 1500 Ion Chromatograph (Sunnyvale, California, USA). Nitrogen is the limiting nutrient for stream autotrophy in the streams evaluated in this study (Gregory 1980, Warren et al. 2017). Phosphate-P was poorly correlated with all biotic response variables, and we therefore present only nitrate-N results.

Field sampling—biotic variables

Periphyton chl *a* accrual was quantified on 10 ceramic tiles (15 × 15 cm) per reach. Tiles were placed in the stream in mid-July and were retrieved after six weeks. Tiles were spaced at regular intervals and positioned within riffle sections of the stream at a depth of 10–25 cm. After six weeks, tiles were scraped using a wire brush and the slurry was filtered through 47-mm glass fiber filters (Whatman GF/F). Filters were placed in 20-mL glass vials and frozen for 24–48 h. 15 mL of 90% acetone was then added to vials to extract chl *a*. After 2–4 h of dark storage at room temperature, chl *a* was quantified using fluorometric methods (Arar and Collins 1997). Fluorescence of a subsample of the extraction solution was measured before and after the addition of 0.1 N HCl (0.15 mL/5 mL solution).

Benthic invertebrates were sampled in late July (15 July 2014 to 29 July 2014). Both reaches within a reach pair were always sampled on the same day. In each reach, six Surber samples (363 µm, 0.0625 m^2) were collected from riffle habitats at regular intervals. Substrate within the Surber sample quadrate was disturbed to a depth of

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

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

separately. Trout were distinguished as juvenile or adult based on length frequency histograms and, in general, trout <65 mm were classified as juveniles.

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

In addition to the primary fish and salamander surveys conducted in mid-summer, a second single-pass survey was conducted in late September 2014 to capture juvenile (age 0+) cutthroat trout and assess summertime relative growth rates for this age class. We did not sample Mack Creek in the second juvenile assessment as we did not want to interfere with long-term research efforts occurring annually at this site. In LO701, McRae Creek Tributary-East (MCTE), and Fritz Creek, juvenile trout were surveyed on two sampling dates but there were few surveyed fish in at least one of these surveys ($n < 5$). Therefore, we were only able to evaluate juvenile relative growth rates in five of the nine sites. Relative growth rates were determined by subtracting the mean weight at survey date 2 from the mean weight of survey date 1 and then dividing this number by the number of days between sampling events.

Statistical analysis

Data from the 18 stream reaches were used to explore relationships between habitat and biotic variables and the biomass of cutthroat trout, salamanders, and total vertebrates. We used three approaches: (1) We examined correlations (Pearson's correlation coefficient (r) and r-squared) between all explanatory and response variables among sites, blocked by riparian forest age class, (2) we examined correlations of all explanatory and response variables using reach pair

differences, and (3) we evaluated the relative support of sets of a priori models for cutthroat trout biomass, salamander biomass, and total vertebrate biomass across old-growth and previously harvested reaches using Akaike Information Criteria adjusted for small sample sizes (AICc, Hurvich and Tsai 1989).

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

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

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

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

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

regression ($n = 5$) to evaluate correlations between differences in explanatory variables and differences in juvenile trout relative growth rates between reaches within reach pairs.

RESULTS

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

Across old-growth and previously harvested reaches, correlations were generally consistent with a bottom-up-driven food web. There were strong positive correlations between chlorophyll a, invertebrate biomass, predatory invertebrate biomass, cutthroat trout biomass, and salamander biomass (Fig. 2). Chlorophyll a was positively correlated with both canopy openness (r^2 old growth

[OG] = 0.49; r^2 previously harvested [PH] = 0.81) and nitrate-N concentration (r^2 OG = 0.66; r^2 PH = 0.60). Invertebrate biomass (r^2 OG = 0.58; r^2 PH = 0.55) and predatory invertebrate biomass (r^2 OG = 0.67; r^2 PH = 0.62) were positively correlated with chl a. Both cutthroat trout biomass (r^2 OG = 0.67; r^2 PH = 0.82) and total vertebrate biomass (r^2 OG = 0.64; r^2 PH = 0.73) were, in turn, positively correlated with total invertebrate biomass. Salamander biomass was positively correlated with invertebrate biomass, but less so than for cutthroat trout or total vertebrate biomass (r^2 OG = 0.30; r^2 PH = 0.47).

Among all potential explanatory variables, cutthroat trout biomass was positively correlated with nitrate-N concentration (r OG = 0.71, r PH = 0.69), canopy openness (r OG = 0.68; r PH = 0.85), chl a (r OG = 0.88; r PH = 0.76), and invertebrate biomass (r OG = 0.82; r PH = 0.90) across both old-growth and previously harvested reaches (Fig. 3A, B). Cutthroat trout biomass was negatively correlated with temperature (r OG = -0.68; r PH = -0.77); however, this relationship was largely driven by the two coldest sites, LO701 and LO703, that were just downstream of a ground water-fed tributary, which also exhibited

Table 2. Biotic variables estimated in each reach.

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

Notes: OG = old-growth riparian forest and PH = previously harvested riparian forest on at least one stream bank. Parentheses for chl a, and cutthroat trout, salamander, and total vertebrate biomass represent 95% confidence intervals.

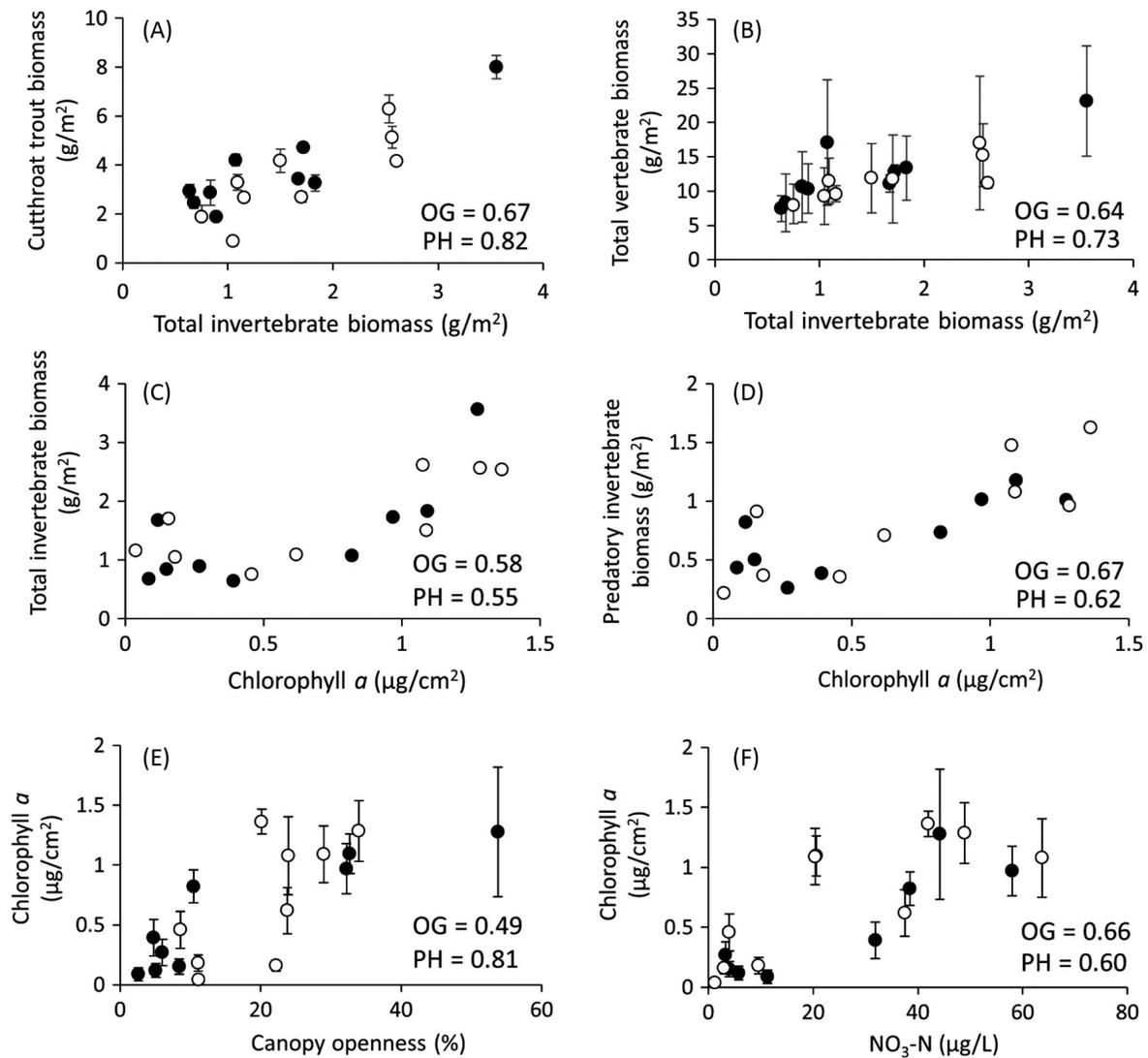† Total vertebrate biomass for MR404 includes sculpin (*Cottus* spp.).

Fig. 2. Relationships between total invertebrate biomass and cutthroat trout biomass (A), total invertebrate biomass and total vertebrate biomass (B), chl *a* and total invertebrate biomass (C), chl *a* and predatory invertebrate biomass (D), canopy openness and chl *a* (E), and nitrate-N and chl *a* (F). Open circles indicate previously harvested site reaches, while closed circles indicate old-growth reaches. Values in lower right corner of each panel indicate *r*-squared values, which were evaluated separately across old-growth (OG) and previously harvested (PH) reaches.

high nitrate-N concentrations, canopy openness, chl *a*, and invertebrate biomass relative to other sites. All Pearson's correlation coefficients for large wood volume, percent pool area, gradient, and bankfull width were less than 0.5 across both reach types (Fig. 3A, B; Appendix S1: Figs. S1 and S2). When reach pair differences (old growth less previously harvested) were evaluated, differences in temperature, large wood volume, percent pool area, gradient, bankfull width, and nitrate-N

concentration were all poorly correlated (all *r* values <0.40) with differences in cutthroat trout biomass (Fig. 3C). However, differences in canopy openness (*r* = 0.53; Fig. 4A), chl *a* (*r* = 0.64), and invertebrate biomass (*r* = 0.62) were all positively correlated with differences in cutthroat trout biomass (Fig. 3C).

Coastal giant salamander biomass was not as well correlated as cutthroat trout biomass was with nitrate-N concentration (*r* OG = 0.32;

(A) Old growth

(B) Previously harvested
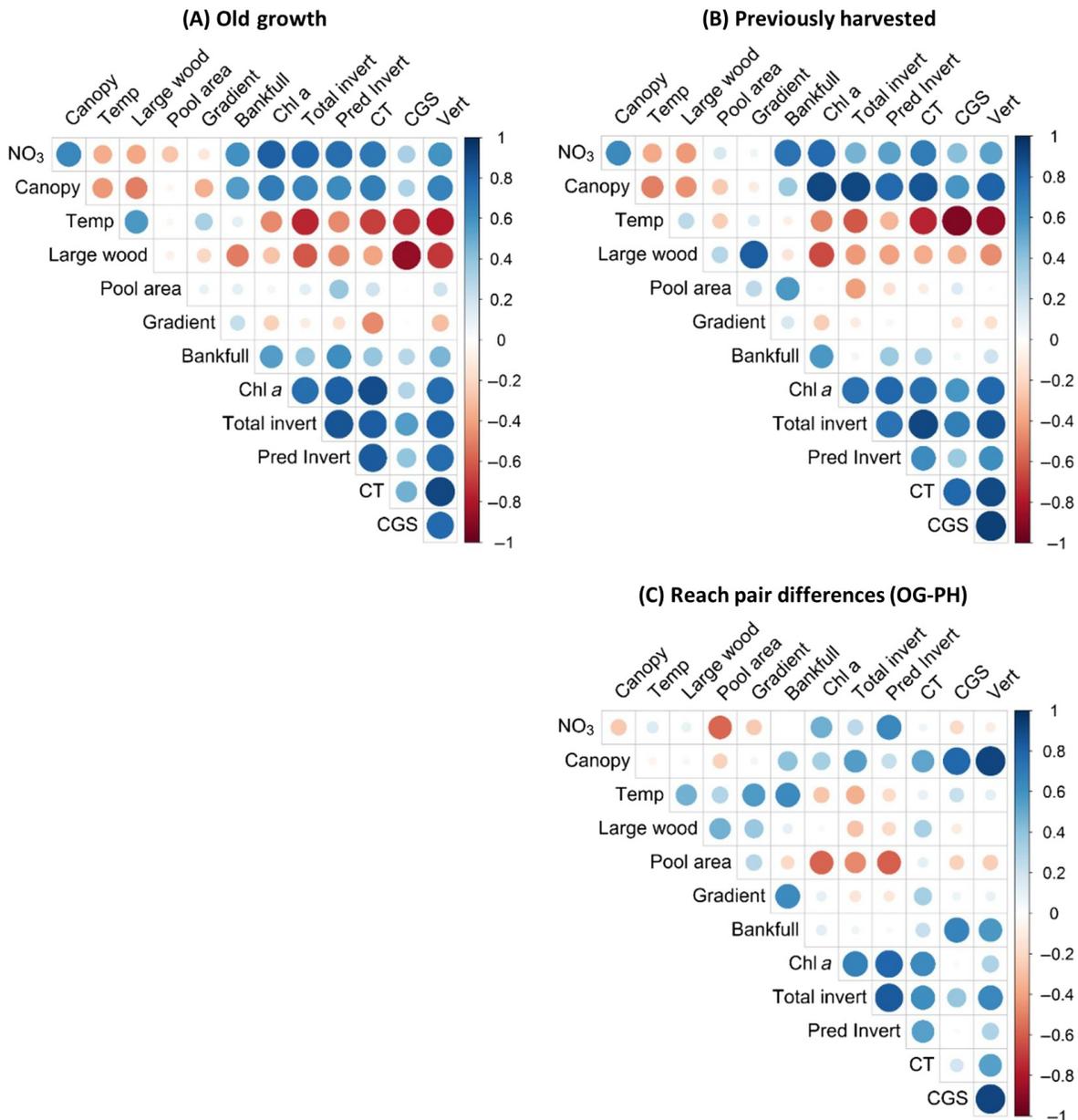
(C) Reach pair differences (OG-PH)

Fig. 3. Correlation matrix for reaches bordered by old-growth forests (A), reaches bordered by previously harvested forests (B), and reach pair differences (C). CT = cutthroat trout biomass (g/m^2); CGS = coastal giant salamander biomass (g/m^2); Vert = total vertebrate biomass (g/m^2); Chl = chlorophyll a content (µg/cm^2); Invert = total invertebrate biomass (g/m^2); PredInvert = predatory invertebrate biomass (g/m^2); Canopy = canopy openness (%); BF = bankfull width (m); LW = large wood volume (m^3/100 m^2); Grad = gradient (%); NO$_3$ = nitrate-N concentration (µg/L); Temp = mean daily mean temperature (°C). See Appendix S1: Figs. S1–S3 for correlation coefficients and P-values.

r PH = 0.41), canopy openness (r OG = 0.30; r PH = 0.59), chl a (r OG = 0.30; r PH = 0.59), or invertebrate biomass (r OG = 0.55; r PH = 0.68) across old-growth and previously harvested reaches (Fig. 3A, B). Temperature (r OG = −0.74; r PH = −0.93) and large wood volume (r OG = −0.87; r PH = −0.36) were strongly negatively correlated with salamander biomass (Fig. 3A, B).
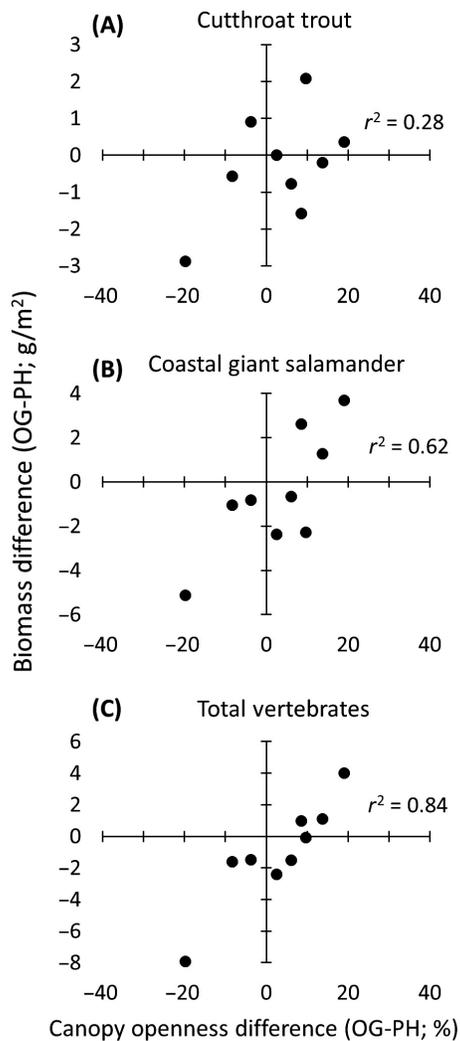
Fig. 4. Relationships between reach pair differences (old growth minus previously harvested) in canopy openness vs. trout biomass (upper), salamander biomass (middle), and total vertebrate biomass (lower).

Pearson's correlation coefficients for percent pool area, gradient, and bankfull width were all less than 0.3 across both reach types (Fig. 3A, B; Appendix S1: Figs. S1 and S2). When reach pair differences were evaluated, differences in bankfull width ($r = 0.66$) and canopy openness ($r = 0.79$; Fig. 4B) were positively correlated with differences in salamander biomass. Differences in all other variables, including temperature, chl a, and invertebrate biomass, were poorly correlated ($r < 0.40$) with differences in salamander biomass (Fig. 3C).

Total vertebrate biomass was positively correlated nitrate-N concentration (r OG = 0.60; r PH = 0.53), canopy openness (r OG = 0.67; r PH = 0.80), chl a (r OG = 0.76; r PH = 0.79), and invertebrate biomass (r OG = 0.80; r PH = 0.80), but negatively correlated with temperature (r OG = −0.78; r PH = −0.87) and large wood volume (r OG = −0.71; r PH = −0.47) across old-growth and previously harvested reaches (Fig. 3A, B). Pearson's correlation coefficients for percent pool area, gradient, and bankfull width were all less than 0.5 across both reach types (Fig. 3A, B; Appendix S1: Fig. S3). Differences in bankfull width ($r = 0.57$), canopy openness ($r = 0.92$; Fig. 4C), and total invertebrate biomass ($r = 0.64$) were positively correlated with differences in total vertebrate biomass, while differences in all other variables were weakly correlated ($r < 0.30$) with differences in total vertebrate biomass (Fig. 3C).

Canopy openness was lower in the previously harvested reach of six of the nine reach pairs, but greater in three of the nine pairs. The differences in canopy cover between reaches explained over 80% of the variability in the difference in vertebrate biomass between reaches. This correlation was stronger for total vertebrate biomass ($r^2 = 0.84$) than for salamanders ($r^2 = 0.62$) and cutthroat trout biomass ($r^2 = 0.28$; Fig. 4). Surprisingly, differences in canopy openness were only weakly correlated with differences in chl a ($r^2 = 0.12$). However, the difference in chl a was strongly positively correlated with the difference in invertebrate biomass ($r^2 = 0.73$). The difference in invertebrate biomass was, in turn, positively correlated with the difference in cutthroat trout biomass ($r^2 = 0.38$) and total vertebrate biomass ($r^2 = 0.41$), but less so for salamanders biomass ($r^2 = 0.15$). Despite substantial differences in large wood volume (range 0.5–9.7 m³/m²) and percent pool area (range −3.6% to 21.8%) between reaches within reach pairs, these metrics were not well correlated with differences in cutthroat trout biomass, accounting for less than 10% of the variation in differences in trout biomass, salamander biomass, and total vertebrate biomass (Appendix S1: Fig. S3). Differences in gradient, temperature, and nitrate-N were relatively small between reach pairs and were not well correlated with cutthroat trout biomass, salamander biomass, or total vertebrate biomass (all r^2 values <0.10).

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

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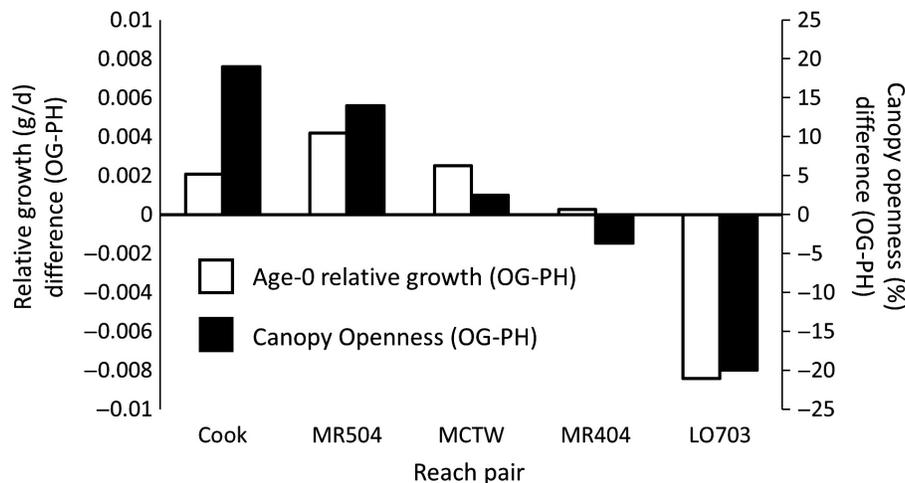

Fig. 5. Reach pair differences (old growth [OG] minus previously harvested [PH]) for juvenile (age-0+) relative growth rates (open bars; left y-axis) and canopy openness (filled bars; right y-axis).

and abundance in Cook Creek, MR404, and LO703 (Table 2). These trends are generally consistent when comparing vertebrate biomass and abundance between reaches within reach pairs (Table 2).

DISCUSSION

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

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

Although forested headwater streams are often predominantly heterotrophic with food webs deriving the majority of basal carbon from allochthonous resources (Fisher and Likens 1973, Vannote et al. 1980, Wallace 1997, Tank et al. 2010), autochthonous carbon can be a disproportionately important food resource for stream consumers in these systems (Bilby and Bisson 1992, McCutchan and Lewis 2002, Lau et al. 2009). The potentially disproportionate influence of autochthonous carbon production on stream secondary consumers is illustrated well by Bilby and Bisson (1992) in which carbon budgets were compared between a stream section bordered by old-growth riparian forest and a stream section where the riparian forest was recently harvested. The old-growth section received 300 $g \cdot m^{-2} \cdot yr^{-1}$ of allochthonous carbon and 100 $g \cdot m^{-2} \cdot yr^{-1}$ of autochthonous carbon (total carbon inputs = 400 $g \cdot m^{-2} \cdot yr^{-1}$), while the harvested reach received 60 $g \cdot m^{-2} \cdot yr^{-1}$ of allochthonous carbon and 175 $g \cdot m^{-2} \cdot yr^{-1}$ of autochthonous carbon

(total carbon inputs = 235 g·m^{-2}·yr^{-1}). Despite lower total carbon flux to the harvested section compared to the old-growth section, fish production was greater in the harvested reach, which they suggest is a result of higher biomass of high-quality autochthonous carbon at the base of the food web. In an assessment of carbon isotopes, McCutchan and Lewis (2002) found that 40–80% of secondary consumer production was supported by autochthonous production, whereas availability of this carbon source was disproportionally low (<2–40% of total available organic carbon). The disproportionate influence of autochthonous carbon on secondary production relative to its availability is likely due to the lower C: N ratio in periphyton compared to allochthonous litter (Cross et al. 2005). With more N per unit biomass, the energetic benefits of assimilation increase for the same amount of material consumed, making periphyton a higher-quality food source for consumers. Consequently, relatively small changes in light availability and primary production may have disproportionate influences on consumer communities.

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

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

sections where the riparian forest had been recently harvested and stream wood had been removed relative to upstream sections bordered by old-growth forest. They found that cutthroat trout biomass was greater in the recently harvested sections even though pool area and wood volume were both lower in harvested reaches.

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

CONCLUSIONS

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

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Supporting Information