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ARTICLE

Freshwater Ecology

Influence of riparian thinning on trophic pathways supporting stream food webs in forested watersheds

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Abstract

Resource managers seek to thin second-growth riparian forests to address multiple stream and riparian management objectives, including enhancing aquatic productivity via light-mediated trophic pathways in watersheds of the Pacific Northwest (USA). However, such increases in aquatic productivity depend on complex food web dynamics that link riparian forests and streams. To evaluate how riparian forest thinning influences stream food webs, we conducted a replicated, manipulative field experiment in three northern California watersheds composed of second-growth redwood forests and tracked responses across multiple trophic levels (periphyton, macroinvertebrates, amphibians, and fish) 1 year pre- and post-treatment. Riparian thinning treatments increased light to the stream channel, yet we observed mixed responses by stream food webs. Thinning did not change stream periphyton biomass on natural substrates but increased periphyton accrual on ceramic tiles. Periphyton accrual appeared to be partially muted by top-down effects from invertebrate scrapers, which were more abundant in thinned reaches. Prey in the diets of top predators—coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*)—did not change in biomass, composition, or structure in response to thinning and instead varied more seasonally and between predators. Stable isotope analysis indicated that shifts in carbon ($\delta^{13}C$) signatures of stream periphyton associated with thinning were reflected to varying extents by primary consumers but did not propagate up to top predators. Top predator biomass responses varied between species, where salamander biomass remained unchanged, but cutthroat trout biomass increased slightly in thinned reaches. However, trout biomass responses were not supported by diets or isotopes and correlated weakly with changes in light associated with thinning, suggesting little evidence that responses could be attributed directly to changes in autotrophic pathways. Furthermore, we found no evidence that local trophic responses to thinning propagated into downstream reaches. Taken together, we observed that

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trophic pathways supporting stream food webs remained largely intact immediately after riparian thinning treatments. Collectively, these results suggest that riparian thinning does not necessarily enhance aquatic productivity in forested streams, indicating that contextual factors driving realized ecological responses should be accounted for when considering thinning as a restoration strategy for stream–riparian ecosystems.

KEYWORDS
coast redwood forests, coastal cutthroat trout, coastal giant salamander, downstream propagation, forest restoration, macroinvertebrates, riparian thinning, stable isotopes, stream food webs, stream periphyton, trophic pathways

INTRODUCTION

Stream ecosystems in forested landscapes rely on a combination of aquatic and terrestrial energy sources derived locally from within the stream channel, laterally from the riparian forest, and from upstream and downstream locations transported by flow and species movements (Humphries et al., 2014; Power & Dietrich, 2002; Wipfli & Baxter, 2010). The relative importance of these energy sources varies both seasonally and spatially within stream networks, which can increase stability in these dynamic systems (Benjamin et al., 2022; Nakano & Murakami, 2001; Nelson et al., 2021). Traditionally, forested streams were assumed to rely primarily on subsidies of terrestrial leaf litter (Vannote et al., 1980; Wallace et al., 1997). Although abundant, these terrestrial inputs are of relatively low nutritional quality and so may contribute less energy to stream food webs than previously thought (Cross et al., 2005; Marcarelli et al., 2011; Power & Dietrich, 2002). Instead, growing evidence suggests that aquatic primary production of stream periphyton can support a significant amount of energy flow, even in heavily shaded forested watersheds (Bilby & Bisson, 1992; Kiffney et al., 2004; McCutchan & Lewis, 2002; Minshall, 1978; Thorp, 2002).

Terrestrial disturbances that alter riparian forest conditions can directly affect trophic pathways supporting stream food webs by shifting the relative availability of terrestrial and aquatic energy sources (Bilby & Bisson, 1992; Gregory et al., 1987; Kiffney et al., 2004; Warren et al., 2016). In the Pacific Northwest (USA), forest harvest is a widespread terrestrial disturbance that has received much attention. Historical timber harvest practices that clear-cut riparian forests frequently increased aquatic primary production (Gregory et al., 1987), leading to shifts in stream food webs toward increased reliance on autotrophic (light-mediated) energy sources (Bilby & Bisson, 1992; Gregory et al., 1987; Murphy & Hall, 1981). However, riparian forest harvest increased stream temperatures and fine sediment influxes, as well as reduced inputs of large wood, degrading aquatic habitats (Ashton et al., 2006; Benda et al., 2016; Moore et al., 2005; Murphy et al., 1981). As a result, forest practices now require greater protections for riparian zones (Moore et al., 2005). In response to these protections, riparian forests in much of the Pacific Northwest have regenerated, resulting in dense stands of riparian vegetation that heavily shade streams (Richardson et al., 2012; Warren et al., 2016).

Just as historical timber harvest practices motivated concerns over the loss of riparian vegetation, afforestation of riparian zones has raised new questions regarding the consequences of such stands for stream–riparian ecosystem dynamics (Lecerf et al., 2012; Warren et al., 2016; Wootton, 2012). For example, resource managers in the Pacific Northwest have suggested that thinning dense second-growth riparian forests may achieve multiple restoration objectives (Benda et al., 2016; Berg, 1995; Pollock & Beechie, 2014; Reeves et al., 2016). First, thinning may increase heterogeneity in dense, homogenous second-growth stands to accelerate the recovery of old-growth forest structures (Keyes & Teraoka, 2014; O'Hara et al., 2010; Russell, 2009; Soland et al., 2021; Teraoka & Keyes, 2011). Second, over long time spans, thinning may shift tree species composition away from early-seral species such as red alder (*Alnus rubra*) toward conifers, which can eventually serve as sources of large wood that can be important for structuring instream habitats (Benda et al., 2016; Pollock & Beechie, 2014). On shorter timescales, questions emerge about whether thinning may strike a balance between minor increases in stream temperature versus increases in light that may enhance aquatic productivity (Wilzbach et al., 2005). Some have even gone so far as to suggest that riparian forests should be managed specifically to enhance the productivity of salmonid fishes (Newton & Ice, 2015). However, more information on thinning effects is needed before it can be confidently applied as a restoration strategy.

Although questions regarding whether increases in light associated with thinning second-growth riparian forests will translate into enhanced aquatic productivity appear straightforward, substantial uncertainty remains. Whereas previous research has documented increased aquatic productivity associated with more dramatic changes in riparian canopies associated with clear-cutting (Bilby & Bisson, 1992; Wilzbach et al., 2005), far less is known about the effects of more subtle changes in riparian forests, such as with forest thinning. Although some recent studies have documented similar outcomes across ranges of riparian canopy changes (Heaston et al., 2018; Kaylor & Warren, 2017; Niles & Hartman, 2021; Wootton, 2012), others point to minimal trophic responses to contemporary forest management practices such as riparian buffers with minimal forest harvest near streams (Bateman et al., 2018; Kiffney et al., 2003).

Uncertainty in the outcomes of riparian forest management for aquatic systems can be partially attributed to the complexity of stream–riparian systems (Baxter et al., 2005; Gregory et al., 1991; Naiman et al., 2010; Nakano & Murakami, 2001): Responses depend on and can be mediated by the food web dynamics that link streams and riparian forests (Bascompte, 2010; Power & Dietrich, 2002; Whitney et al., 2020; Wootton, 2012). Management goals that focus on the productivity of target species such as salmonid fishes can be misleading (Bellmore et al., 2017; Whitney et al., 2020), as target species are part of complex ecological networks that require an understanding of species interactions and the trophic processes supporting them (Bascompte, 2010; Naman et al., 2022). Additionally, inherent spatial and temporal variation in environmental conditions and food web structure across stream networks can lead to context dependency in biological responses (Power & Dietrich, 2002; Whitney et al., 2020). As a result, a food web perspective that explicitly considers the trophic dynamics and structure of ecological networks provides a more holistic understanding of stream ecosystems and can more effectively address the underlying mechanisms driving whether riparian thinning enhances aquatic productivity in forested streams (Bascompte, 2010; Bellmore et al., 2017; Benjamin et al., 2022; Naiman et al., 2012; Naman et al., 2022).

In this study, we evaluated how riparian thinning affected the trophic pathways supporting stream food webs in three watersheds in second-growth coast redwood forests (*Sequoia sempervirens*) of northern California. We collected data in a manipulative field experiment following a replicated before–after control–impact (BACI) study design involving experimental thinning of riparian zones (Roon et al., 2021). The primary objective of this study was to evaluate how increases in light associated with thinning affected autotrophic (light-mediated) pathways supporting multiple trophic levels including basal resources; macroinvertebrate and amphibian primary consumers—coastal tailed frog (*Ascaphus truei*); and top predators—coastal giant salamander (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). To address this objective, we compared pre- and post-treatment data on light availability, stream periphyton, prey in diets of the top predators, stable isotopes to track broader pathways of energy flow, and biomass of top predators. Given that stream food webs are seasonally and spatially dynamic (Hawkins & Sedell, 1981; Humphries et al., 2014; Polis et al., 1997; Power & Dietrich, 2002), our second objective addressed how thinning influenced food webs across three seasons: spring, summer, and fall; and how local responses to thinning propagated into downstream reaches.

Within the broad objectives of this work, we tested a series of hypotheses and predictions based on conceptual models of how food web structure influences responses to thinning (Figure 1). First, we hypothesized that increased light from thinning would increase stream periphyton abundance (Hill et al., 1995). We then hypothesized that increases in periphyton abundance would shift the seasonal and spatial dynamics of food webs supporting top predators. Although periphyton is naturally abundant in spring before deciduous canopies leaf out (Hill et al., 2001), we predicted that thinning would extend the availability of periphyton into summer and fall, thereby increasing the abundance of resources for scraping macroinvertebrates (Bilby & Bisson, 1992; Gregory et al., 1987). This in turn would increase the prevalence of scrapers in the diets of top predators, thereby shifting energetic pathways supporting top predators toward autotrophic resources in summer and fall (Bilby & Bisson, 1992; Kaylor & Warren, 2017). Given their differences in habitat use and foraging behaviors, we predicted differential responses to thinning by top predators (Falke et al., 2020; Roni, 2002; Rundio, 2002). Coastal giant salamanders function as benthic predators, so we predicted that they would respond most directly to changes in the composition of benthic invertebrate assemblages (Falke et al., 2020; Parker, 1994; Rundio, 2002). In contrast, coastal cutthroat trout display multiple foraging behaviors where they function primarily as drift feeders in high flows, but then, as flows recede trout shift toward search-foraging and increasingly rely on inputs of terrestrial invertebrates, so we predicted they would respond less strongly to thinning (Falke et al., 2020; Harvey & Railsback, 2014; Li et al., 2016; Rundio, 2002). Moreover, reductions in canopy density with thinning could adversely affect cutthroat trout via decreased terrestrial invertebrate inputs (Benjamin et al., 2022). Finally, we predicted that local responses to thinning could propagate downstream via increased invertebrate drift,

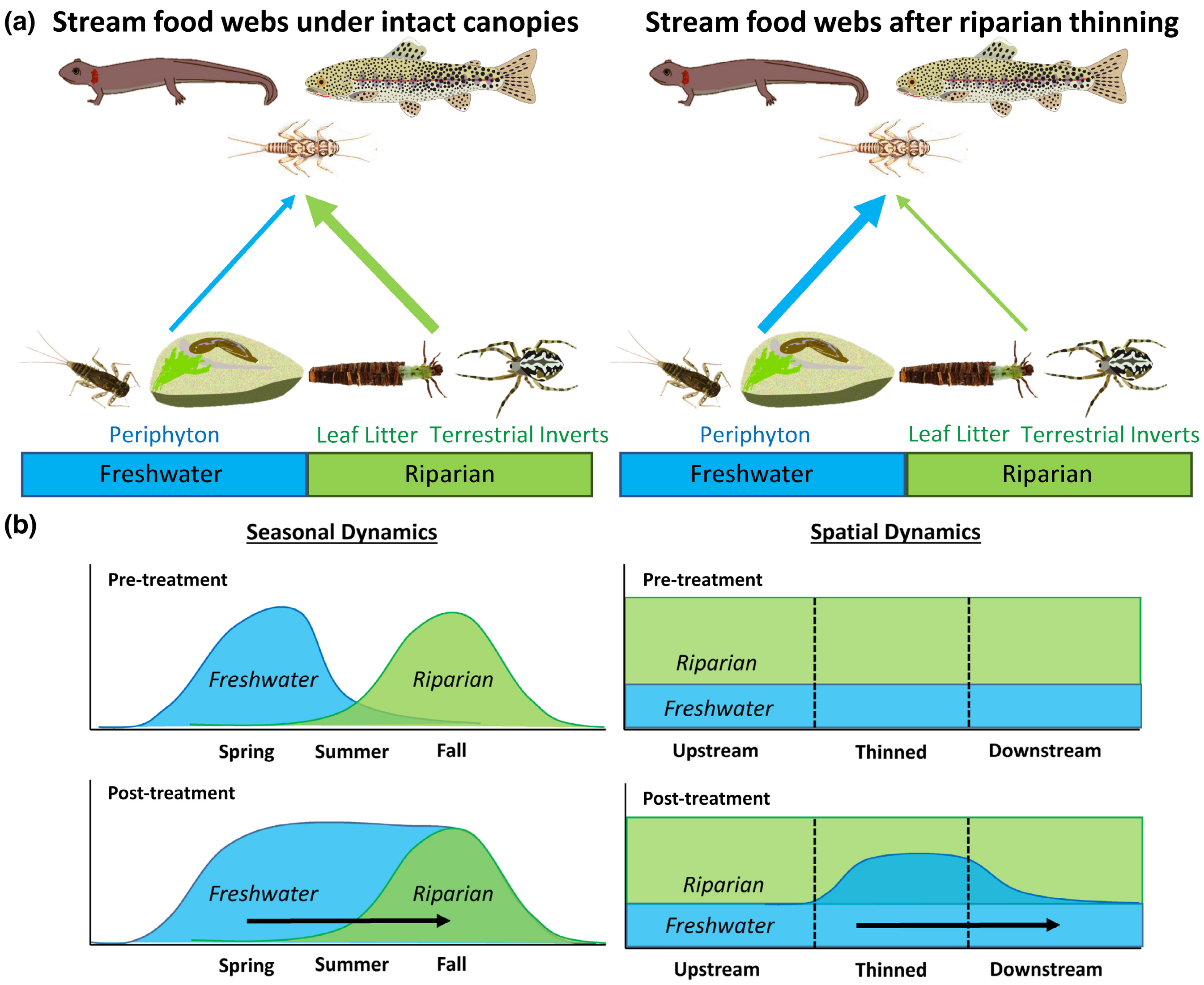

FIGURE 1 Conceptual models of (a) how riparian thinning could shift trophic pathways in stream food webs and (b) how thinning could shift seasonal and spatial dynamics of stream food webs in forested watersheds.

and therefore, local responses to thinning would be reflected in downstream reaches albeit to a lesser extent (Gregory et al., 1987).

METHODS

Study systems

This study took place in three watersheds in coast redwood forests of northern California (Figure 2). The west and east forks of Tectah Creek are on private timber land owned by the Green Diamond Resource Company and flow into the lower Klamath River. The middle fork of Lost Man Creek is in Redwood National Park and flows into Prairie Creek, a tributary of Redwood Creek. All study systems consisted of small forested watersheds (<10 km^2) within 15 km of the Pacific Ocean, which experience a temperate, maritime climate heavily influenced by coastal fog (Welsh et al., 2000).

Riparian forests at the study sites are composed of 30- to 60-year-old stands of second-growth forests that provide ~95% canopy closure (Roon et al., 2021). Riparian forest canopies in the Tectah watersheds were primarily composed of red alder but also included coast redwood, Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), tanoak (*Notholithocarpus densiflorus*), and western red cedar (*Thuja plicata*). Riparian forests in the Lost Man watershed were composed primarily of second-growth coast redwood and red alder, with less abundant Douglas-fir, western hemlock, and western red cedar. Riparian understories were composed of salmonberry (*Rubus spectabilis*), skunk currant (*Ribes glandulosum*), evergreen and red huckleberry (*Vaccinium ovatum* and *Vaccinium parvilfolium*), vine maple (*Acer circinatum*), and sword fern (*Polystichum munitum*).

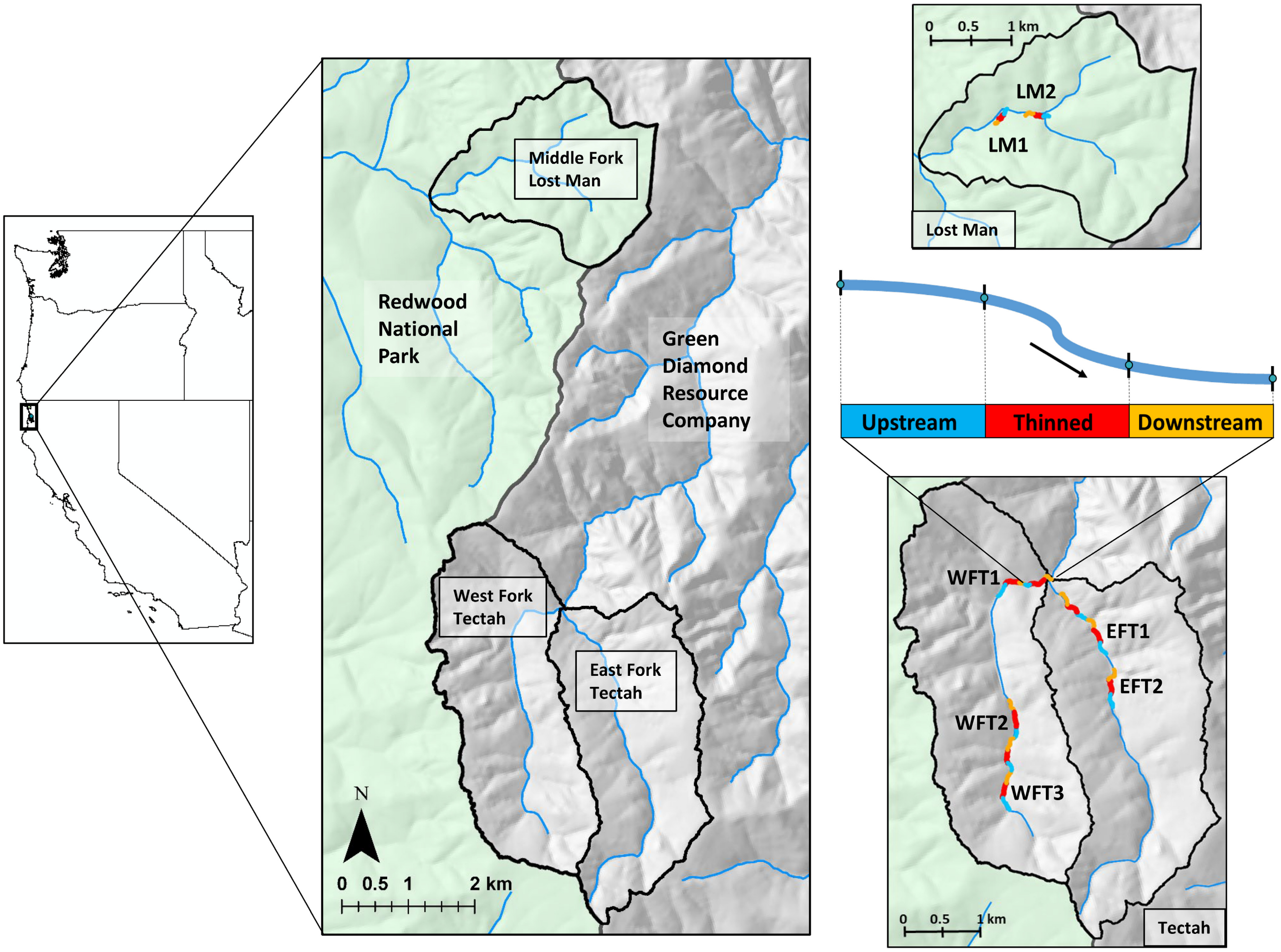

FIGURE 2 Study sites and watersheds in northern California, USA, where we examined stream food web responses to riparian thinning. The inset line represents the experimental design where each study site consisted of an upstream reference, thinned, and downstream reach. This three-reach sequence was repeated across seven total sites in three watersheds. Site names indicate watershed abbreviations: EFT, East Fork Tectah; LM, Lost Man; WFT, West Fork Tectah.

All three watersheds supported resident populations of stream fish and amphibians, but their relative abundance varied among watersheds. Sites in the Tectah watersheds supported coastal cutthroat trout, as well as coastal giant salamanders and coastal tailed frogs, whereas sites in the Lost Man watershed occurred above a natural barrier to fish and supported only stream amphibians. In addition to coastal giant salamanders and coastal tailed frogs, the study sites supported low densities of southern torrent salamanders (*Rhyacotriton variegatus*), northern red-legged frogs (*Rana aurora*), and foothill yellow-legged frogs (*Rana boylii*).

Experimental design

We followed a replicated BACI design (Underwood, 1994), in which we experimentally manipulated riparian forest canopy conditions and monitored conditions before and after in reference and treatment locations. We collected data in adjacent upstream reference, thinned, and downstream reaches that were 100–200 m in length and repeated this three-reach design at seven sites distributed across the three watersheds (Figure 2, Table 1). We collected data during 1 year pre-treatment (2016) and 1 year post-treatment (2018). We did not analyze data collected during the treatment year (2017) due to the staggered timing of treatments and the influx of logging slash that likely confounded our ability to test the hypothesis that increases in light associated with thinning would influence autotrophic processes (Erdozain et al., 2019). To capture seasonal variability in stream food webs, we sampled in spring (late April to mid-May), summer (July), and fall (mid-September to early October).

Although the experimental design and implementation of experimental treatments followed a similar structure, thinning treatment prescriptions varied between

TABLE 1 Characteristics of experimental thinning reaches in the Tectah and Lost Man watersheds in northern California, USA.

Watershed	Site	Watershed position (m)	Reach length (m)	Bankfull width (m)	Change in riparian shade (%)	Change in light (%)	Change in stream temperature (°C)
East Fork Tectah	EFT1	990	210	6.1	−19.2	19.9	1.8
	EFT2	1850	170	4.6	−30.5	29.3	3.8
West Fork Tectah	WFT1	535	175	6.0	−24.0	35.1	2.1
	WFT2	2750	205	4.7	−26.2	28.8	3.5
	WFT3	3840	220	3.2	−23.6	14.4	2.7
Lost Man	LM1	1450	125	4.5	−4.1	3.4	0.3
	LM2	2300	130	4.1	−4.2	3.8	0.4

Note: Change in shade, light, and stream temperature are summarized as before–after control–impact differences (see: *Experimental design* in *Methods* for details). Watershed position was measured as distance upstream from confluence (in meters). Change in stream temperature is the summer maximum weekly average of the maximum temperature.

landowners. In the Tectah watersheds, thinning treatments were part of a larger riparian canopy experiment and targeted a reduction of up to 50% canopy closure within the riparian zone on both sides of the stream channel to the stream edge along 200-m reaches. Thinning treatments targeted red alder and left large conifers that would contribute to an eventual source of large wood. Thinning treatments bordered upslope harvest units, and trees were removed via cable yarding. Non-thinned reaches adjacent to upslope harvests were lined by a one-sided 45-m-wide riparian buffer (the other side bordered by intact forest) following Green Diamond's standard Aquatic Habitat Conservation Plan (Green Diamond Resource Company, 2016). In the Lost Man watershed, thinning treatments corresponded to a larger restoration thinning effort to promote the recovery of old-growth redwood forest (Soland et al., 2021), and targeted a reduction of up to 50% of the basal area on both sides of the channel along 100–150 m reaches on slopes less than 20%. Thinning treatments targeted Douglas-fir and red alder, and felled trees following a lop-and-scatter protocol, which left trees on streambanks but out of the stream channel. Roon et al. (2021) provide more details on treatment prescriptions.

Light

To quantify changes in light associated with riparian thinning treatments, we measured solar radiation before and after thinning using silicon pyranometers, a broad-spectrum light sensor, deployed both above and below the riparian canopy to estimate the amount of light that filters into the stream. We characterized light conditions during midsummer in upstream reference, thinned, and downstream reaches during pre- and post-treatment years. See Roon et al. (2021) for more details on light methods.

Nutrients

To characterize nutrient concentrations, which can co-limit primary production (Warren et al., 2017), we collected water samples seasonally from the downstream ends of thinned reaches during the pre-treatment year and from the downstream ends of upstream reference and thinned reaches in the post-treatment year. Samples were filtered and frozen until analysis. Nutrient samples were analyzed for nitrate (NO_3-N) and phosphate (PO_4-P) by the Cooperative Chemical Analytical Laboratory at Oregon State University (Corvallis, OR, USA).

Stream periphyton

We measured periphyton ash-free dry mass (AFDM) on natural substrates to determine whether changes in light associated with thinning affected stream periphyton abundance (Ambrose et al., 2004). Following Steinman et al. (2017), we scrubbed periphyton from natural substrates collected from riffle or glide habitats at three systematically spaced transects within each reach. We collected a composite sample from three cobbles per transect. We scrubbed a 31.2-cm^2 area delineated by a PVC ring from each cobble with a wire brush. All material scrubbed from the rock surface was collected in a 50-ml vial and mixed with ~45 ml of stream water. Samples were kept frozen before analysis. We sampled periphyton abundance on natural substrates seasonally in upstream reference, thinned, and downstream reaches before and after experimental thinning treatments.

To determine whether top-down effects from invertebrate scrapers mediate periphyton responses to thinning (Feminella et al., 1989), we conducted a post hoc analysis during the post-treatment year. Following the methods described in Lamberti and Resh (1985), we deployed unglazed ceramic tiles (225 cm^2) to measure periphyton accrual and invertebrate colonization. To see whether invertebrate scrapers affected periphyton accrual, we manipulated tile elevation, placing half of the tiles on the streambed (more accessible to invertebrate scrapers) and the other half on platforms elevated 10–20 cm above the streambed (less accessible to invertebrate scrapers). We deployed five streambed and five elevated tiles per reach and placed tiles side by side in pools every ~20–30 m through upstream reference, thinned, and downstream reaches for ~5 weeks in late summer (late July to end of August). At the end of the experiment, we rinsed invertebrates from tiles onto a 500-μm sieve and stored invertebrates in 90% ethanol for later analysis. We then scrubbed periphyton from the tile surface with a wire brush and split the sample for analysis of AFDM and chlorophyll *a*. AFDM samples were frozen in 50-ml vials, while chlorophyll *a* samples were filtered onto a 47-mm Whatman glass microfiber filter folded in quarters, and wrapped in foil. All samples were kept frozen before analysis.

In the laboratory, we processed samples for AFDM following Steinman et al. (2017). We filtered thawed samples onto pre-weighed 47-mm glass microfiber filters. We dried samples for 24 h at 60°C, ashed samples in a combustion oven for 2 h at 550°C, allowed samples to cool in a desiccator, and then measured the difference in mass before and after ashing to estimate AFDM. We processed chlorophyll *a* samples using an acetone extraction and fluorometric analysis following the methods described in Arar and Collins (1997) and Kaylor and Warren (2017). We extracted chlorophyll *a* by placing thawed filters in 20-ml glass scintillation vials filled with 15 ml of 90% acetone in a dark space at room temperature for 2 h. We then further diluted the extract solution with acetone and measured fluorescence using an AquaFluor handheld fluorometer (Turner Designs, San Jose, CA, USA) before and after the addition of 0.1 N HCl to estimate chlorophyll *a* (Arar & Collins, 1997). To estimate the biomass of invertebrate communities that colonized tiles, we identified, enumerated, and measured the length of invertebrates, and converted length measurements to biomass using published length–weight regression models (Roon, 2021).

Diets and biomass of top predators

To evaluate how thinning affected top predators and their prey resources, we collected diet samples from coastal giant salamanders and coastal cutthroat trout and estimated predator biomass. We collected salamanders and trout using backpack electrofishing, which we repeated seasonally at upstream, thinned, and downstream reaches during pre- and post-treatment years. We subsampled each reach in 2–3 systematically spaced 40-m sections isolated at the downstream and upstream extents using fine-mesh block nets. Using a Smith-Root LR 24 electrofisher (Smith-Root Inc., Vancouver, WA, USA), we collected amphibians and fish with a single upstream pass. We kept captured amphibians and fish for short periods before processing, either in 20-L buckets filled with well-oxygenated stream water with an aerator if densities were low, or in mesh enclosures placed in the stream channel when densities were higher. We held species and life stages in separate locations to prevent artificial predation. We anesthetized trout using AQUI-S 20E (Aqua Tactics Fish Health, Kirkland, WA, USA) and salamanders using MS-222. Once sufficiently anesthetized, we measured length (to the nearest millimeter) and weight (to the nearest 0.1 g) of all individuals captured.

To estimate top predator biomass, we summed the biomass of all individuals collected from single-pass surveys and standardized biomass estimates per reach area. Although single-pass surveys did not capture all individuals present, the sampling effort was consistent across reach types and years. Accordingly, we focused on relative changes in predator biomass being mindful of the caveats associated with single-pass electrofishing (Bateman et al., 2005).

We collected diet samples from a random subsample of each species via nonlethal gastric lavage using a 10-ml MiniPET Aqueous Pipettor (SP Bel-Art, Wayne, NJ, USA) by gently flushing water down the throat until all stomach contents were collected and stored in 90% ethanol. To account for individual variation in diets (Falke et al., 2020; Li et al., 2016), we collected 10–15 replicate samples for each species per reach at all sites for all three seasons during pre- and post-treatment years, which yielded a total sample size of 2498 (salamander: $n = 1436$; trout: $n = 1062$). We allowed salamanders and trout to recover before returning them to the sites of capture.

In the laboratory, we identified, enumerated, and measured the length of all prey in diet samples to estimate biomass using published length–weight regression models (Roon, 2021). We generally identified aquatic invertebrates to family, but genus-level identification was needed to distinguish between scraper versus shredder functional feeding groups for certain families of Coleoptera, Diptera, and Trichoptera (Merritt & Cummins, 2002). However, we did not distinguish Chironomid genera due to difficulties in identification (Hawkins & Sedell, 1981). We identified terrestrial invertebrates to order. We categorized prey according to their functional feeding groups following Merritt and Cummins (2002): scrapers, shredders, collector-gatherers, collector-filterers, predators, emerged adult aquatic invertebrates, terrestrial invertebrates, aquatic vertebrates, or unclassified taxa. However, given that some invertebrate taxa exhibit omnivory (Mihuc & Minshall, 1995; Rosi-Marshall et al., 2016), functional groups were considered as generalized indications of feeding preferences rather than strict categories. Digested prey items were identified to be the lowest possible taxonomic resolution (e.g., order) or labeled as unknown, and length was approximated to estimate biomass. No reliable sources were found to estimate the biomass of aquatic vertebrates in diets from their lengths, so we generated length–dry mass relationships for trout fry ($n = 26$), larval salamanders ($n = 24$), and tailed frog tadpoles ($n = 14$). Following the methods in Utz and Hartman (2006), we dried vertebrates at 60°C for 48 h (see derived values in Roon, 2021).

Stable isotopes

To complement diet sampling, which provides snapshots of prey consumption during specific times of year, we used stable isotopes of carbon ($\delta^{13}C$) to infer how thinning affected energy flow over longer timescales (Finlay, 2001; Hershey et al., 2017; Middleburg, 2014). From the study sites in the Tectah watersheds, we collected stream periphyton from the streambed by scraping material off rock surfaces with a wire brush. We collected multiple taxa of invertebrates as taxa varied seasonally and between sampling sites: scrapers (Heptageniidae mayflies, *Juga* snails, Uenoidae caddisflies), and predators (Perlidae stoneflies). For stream amphibians and fish, we collected small nonlethal fin or tail clips (0.5–1.0 cm^2) from a subset of individuals that were collected for diet sampling. We collected three replicate composite samples for basal resources and invertebrates, but collected 10 replicate samples from individual fish and amphibians to account for expected variation in carbon signatures of top predators. We collected samples seasonally at the same time as diet sampling, before and after thinning treatments for a total sample size of 2825. All samples were frozen until later analysis. In the laboratory, we freeze-dried sample materials, ground the material into a fine powder with mortar and pestle, and packaged the material in tin capsules. Samples were then analyzed for natural abundance of carbon ($\delta^{13}C$) at the UC Davis Stable Isotope Facility (Davis, CA, USA).

DATA ANALYSES

All analyses were plotted in the ggplot2 package (Wickham, 2016) and conducted in R (R Core Team, 2020) unless noted otherwise.

Linear mixed-effects models

To evaluate the effects of thinning on stream food webs, we applied linear mixed-effects models using the nlme package (Pinheiro et al., 2020). First, we conducted a categorical BACI analysis (Underwood, 1994) to evaluate the effects of riparian thinning on various food web responses including stream periphyton biomass, biomass of prey in diets, and biomass of top predators. To do this, we used mean estimates of response variables for upstream reference, thinned, and downstream reaches from our pre- and post-treatment years using the model:

$$\text{BACI model: Response Variable} \sim \text{Reach Type} + \text{Year} \\ + \text{Reach Type} \times \text{Year} + \mathcal{E}.$$

To account for spatial variation among sites ($n = 7$), we included a random effect of Site. We determined an effect of thinning as a significant BACI effect of Reach Type × Year ($\alpha = 0.05$). We then estimated BACI differences and 95% confidence intervals (CIs) for thinned and downstream reaches using the following equations:

$$\begin{aligned} &\text{BACI difference in thinned reaches} \\ &= (\text{Thinned}_{\text{Post}} - \text{Thinned}_{\text{Pre}}) \\ &\quad - (\text{Upstream}_{\text{Post}} - \text{Upstream}_{\text{Pre}}), \end{aligned}$$

$$\begin{aligned} &\text{BACI difference in downstream reaches} \\ &= (\text{Downstream}_{\text{Post}} - \text{Downstream}_{\text{Pre}}) \\ &\quad - (\text{Upstream}_{\text{Post}} - \text{Upstream}_{\text{Pre}}). \end{aligned}$$

If 95% CIs did not overlap 0, we considered the effect to be significant. We ran separate BACI models for each season and response variable. Although treatment intensities varied among sites (riparian shade loss: Tectah = 20%–30%, Lost Man = 4%–5%; Roon et al., 2021), we grouped responses across all sites and watersheds to characterize mean treatment effects from thinning. Second, to determine how stream periphyton accrual and invertebrate colonization on experimental tiles varied with thinning and to evaluate the top-down effects from invertebrate scrapers, we applied models that included the fixed effects of Reach Type (upstream reference, thinned, and downstream), Tile Elevation (streambed vs. elevated), and a Reach Type × Tile Elevation interaction and random effect of Site. We checked the residuals of all models to make sure we met assumptions of constant variance and normality. Some models did not initially meet assumptions, so we log-transformed values when necessary.

Community analyses

We evaluated how thinning affected the composition and structure of macroinvertebrate communities in the diets of top predators by conducting multivariate community analyses. First, to determine seasonal patterns in freshwater and riparian energy sources, we plotted the percent composition of prey biomass by functional groups for coastal giant salamanders and coastal cutthroat trout using these groups: invertebrate scrapers, collector-gatherers, invertebrate predators, other benthic invertebrates (including collector-filterers and taxa of unknown functional groups), aquatic vertebrates (trout fry and larval amphibians), emerged adult life stages of aquatic invertebrates, invertebrate shredders, terrestrial invertebrates, and invertebrates of unknown origins. Second, we used nonmetric multidimensional scaling (NMS) ordination to visualize how the structure of prey communities varied between watersheds, seasons, predator species, and the BACI effect of Reach Type × Year. To do this, we constructed a similarity matrix of the mean relative abundance of invertebrate taxa in the diets based on the percent composition by biomass for all prey taxa identified at family or order level depending on aquatic or terrestrial origin as indicated above. We repeated this for all reaches across all sites, seasons, species, and years to build a matrix of 186 observations. Third, we applied permutational multivariate analysis of variance (PERMANOVA) to test for differences according to these factors. Fourth, we conducted an indicator species analysis to determine which taxa were responsible for driving any variation in community structure according to the factors of watershed, season, species, and the BACI effect of Reach Type × Year. We conducted the NMS ordination and PERMANOVA tests in the vegan package (Oksanen et al., 2013) and the indicator species analysis in the indicspecies package (De Caceres et al., 2020).

Stable isotopes

We evaluated the extent to which changes in carbon ($\delta^{13}C$) signatures of stream periphyton associated with thinning were reflected by higher trophic levels. Overlapping $\delta^{13}C$ signatures between basal resources and functional feeding groups precluded the use of mixing models to estimate relative contributions of autochthonous carbon to the food web (Finlay, 2001; Middleburg, 2014). We therefore compared BACI responses in $\delta^{13}C$ in stream periphyton to primary consumers, including tailed frog tadpoles and invertebrate scrapers (Heptageniidae mayflies, *Juga* snails, and Uenoidae caddisflies), and top predators including Perlidae stoneflies, coastal giant salamander, and coastal cutthroat trout.

Food web correlations

We used correlation matrices following Kaylor and Warren (2017) to examine how changes in shade and light associated with thinning correlated with food web responses, as well as how different food web responses correlated with each other. We used the corrplot package (Wei & Simko, 2021) to plot correlation matrices of different food web responses including shade, light, stream temperature, periphyton biomass on natural substrates, periphyton biomass on tiles, invertebrate biomass on tiles, scraper and total biomass of prey in diets, and predator biomass. We used before–after differences in each food web response variable for upstream reference, thinned, and downstream reaches and focused on summer months when most data were available.

RESULTS

Light

Only a small amount (~5%) of solar radiation reached the stream channel during midsummer under pre-treatment conditions. Thinning increased light levels post-treatment (BACI effect: $p < 0.001$), but responses ranged widely among watersheds (Table 1). In the Tectah watersheds, thinning increased light levels by a mean of 25% (95% CIs: 18, 33), but in the Lost Man watershed, thinning increased light by a mean of 4% (95% CI: 0, 6) (Table 1).

Nutrients

Nutrient concentrations varied seasonally and among watersheds but did not vary consistently pre- and post-thinning (Appendix S1: Figure S1). Pre-treatment data indicated that concentrations of nitrate (NO_3-N) showed more seasonal variation in the Tectah watersheds versus the Lost Man watershed (Appendix S1: Figure S1). Post-treatment data indicated that nitrate concentrations tended to increase in the Tectah watersheds relative to pre-treatment conditions but did not vary in a consistent direction between upstream and thinned reaches (Appendix S1: Figure S1). Concentrations of phosphate (PO_4-P) were slightly lower in Lost Man than in Tectah but otherwise did not vary seasonally or between upstream and thinned reaches during the post-treatment year (Appendix S1: Figure S1).

Stream periphyton

Periphyton biomass on natural substrates varied seasonally during both the pre- and post-treatment years but did not differ in thinned or downstream reaches relative to upstream reference reaches during the post-treatment year in either the Tectah or the Lost Man watershed for

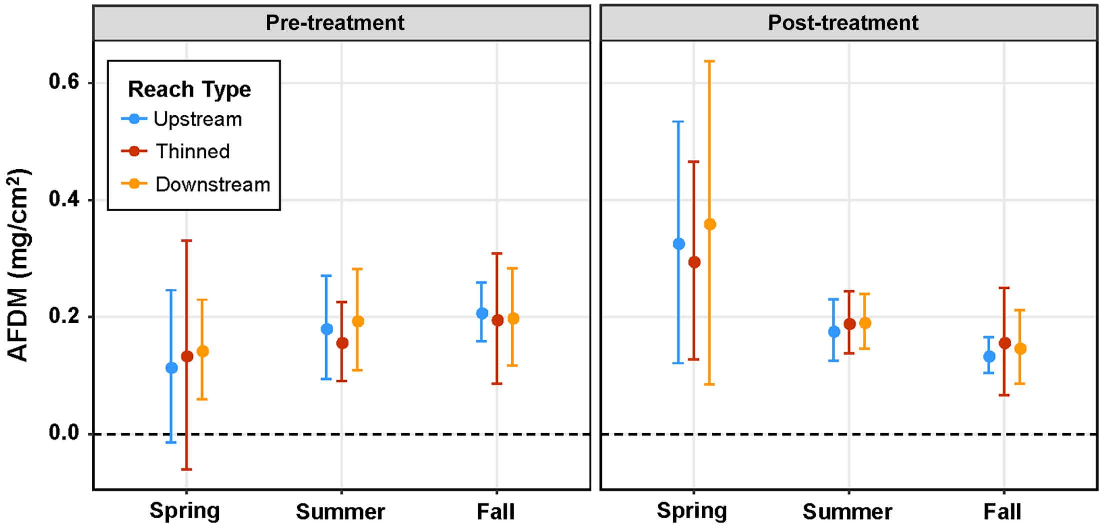

FIGURE 3 Seasonal patterns of stream periphyton standing stocks as ash-free dry mass (AFDM) on natural substrates in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah and Lost Man watersheds in northern California, USA. Points represent mean estimates of all sites ($n = 7$), and error bars represent 95% CIs.

any season (spring, summer, or fall) (BACI effect: $p > 0.05$) (Figure 3).

Periphyton accrual on experimental tiles increased by ~2–3× in thinned reaches relative to upstream and downstream reaches in both the Tectah and the Lost Man watersheds, as measured by AFDM ($p < 0.001$) and chlorophyll *a* ($p < 0.001$) (Figure 4a,b). Elevated tiles less accessible to invertebrate scrapers supported ~20% more periphyton accrual than streambed tiles, which were more accessible to scrapers (AFDM: $p = 0.002$) (Figure 4a,b). Accordingly, tiles in the thinned reaches supported more invertebrate biomass relative to upstream and downstream reaches (Figure 4c,d). Invertebrate biomass increased by ~2.5× on the more accessible streambed tiles ($p < 0.001$) and by ~50% on elevated tiles (Figure 4c). Thinning shifted the composition of invertebrate communities on streambed tiles, supporting a greater percentage of invertebrate scrapers (~75% of biomass) in thinned reaches relative to upstream and downstream reaches (~60% of biomass) (Figure 4d).

Diets of top predators

Prey biomass in the diets of coastal giant salamanders and coastal cutthroat trout varied seasonally and between predator species but did not differ due to thinning in either the Tectah or the Lost Man watershed (BACI effect: $p > 0.05$) (Figure 5). Scraper biomass in diets peaked in spring relative to summer and fall for both predators. Scraper biomass in salamander diets in thinned reaches decreased by ~50% in spring and increased by ~30% in fall, but these responses did not differ among reach types (BACI effect: $p > 0.05$) (Figure 5). Scraper biomass did not differ in the diets of cutthroat trout in any season (BACI effect: $p > 0.05$) (Figure 5). Total biomass in the diets did not change due to thinning for either predator during any season (BACI effect: $p > 0.05$) (Figure 5). We also observed no change in prey biomass in downstream reaches relative to upstream reference reaches for either predator during any season (BACI effect: $p > 0.05$) (Figure 5).

The diets of salamanders and trout, when summarized by functional feeding groups, varied more among seasons, and between predators and watersheds than due to thinning treatments, so results were pooled across reach types within watersheds (Figure 6). In the Tectah watersheds, both salamanders and trout relied primarily on freshwater invertebrates (scrapers, collector-gatherers, predators, and other aquatic taxa) in spring (percent composition of total biomass in diets for salamanders: 72.7%; for trout: 63.3%). Their diets diverged in later seasons; salamanders continued to rely on freshwater energy sources for over half of the biomass in their diet (summer: 57.4%; fall: 58.1%), whereas trout increasingly relied on terrestrial invertebrates in summer (50.9%) and fall (64.3%) (Figure 6). Salamanders in the Lost Man watershed largely reflected the seasonal patterns of salamanders in Tectah but relied more on terrestrial invertebrates during summer and fall (Figure 6). Invertebrate scrapers accounted for a substantial proportion of biomass in the diets for salamanders and trout primarily in spring (11.8%–32.5%) and continued to be important prey items for salamanders during later seasons, while becoming less important for trout (Figure 6). These seasonal patterns remained intact between pre- and post-treatment years (Figure 6).

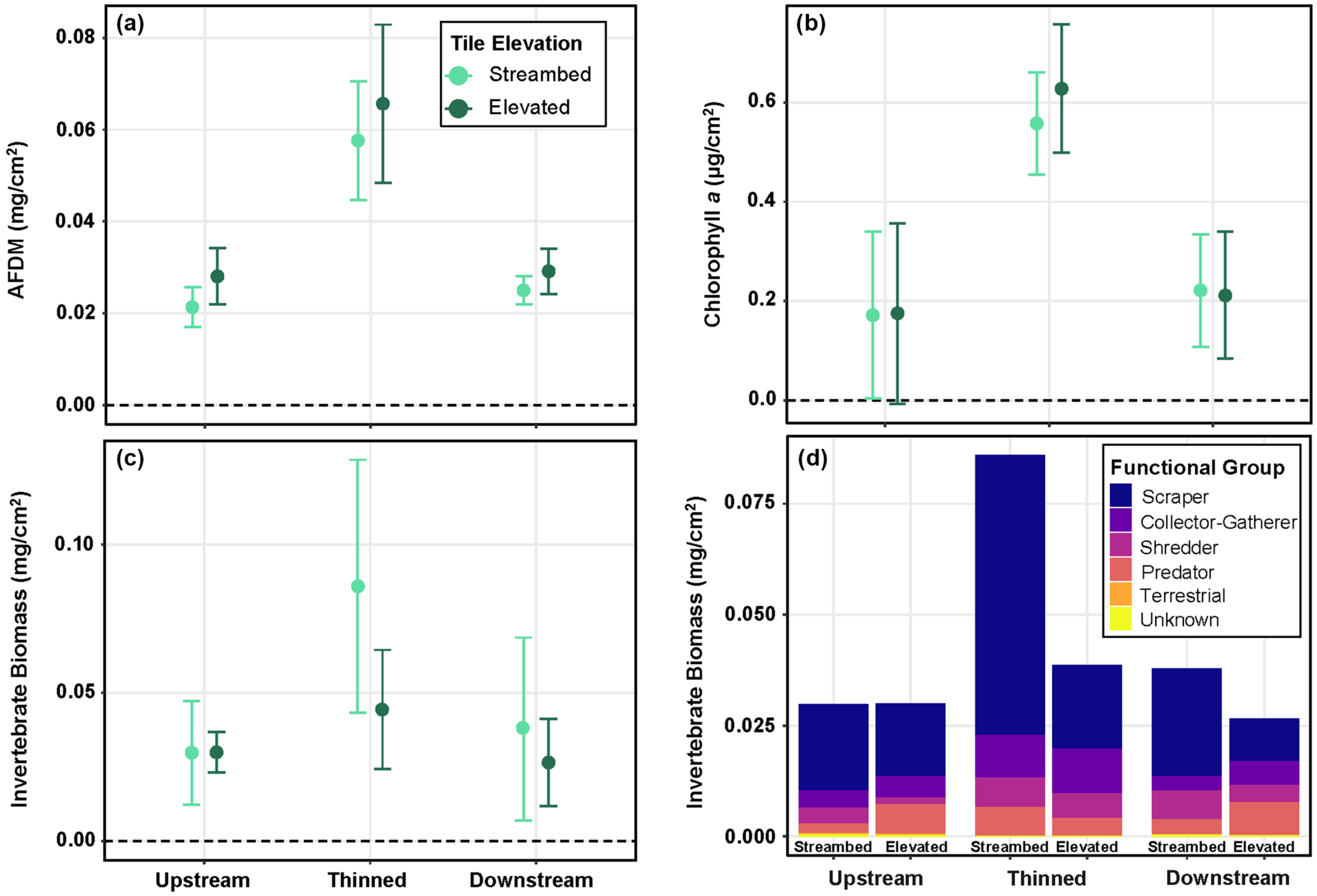

FIGURE 4 Post-treatment patterns of stream periphyton accrual and invertebrate colonization on streambed and elevated ceramic tiles during summer low flows in upstream reference, thinned, and downstream reaches in the Tectah and Lost Man watersheds in northern California, USA. Stream periphyton accrual as (a) ash-free dry mass and (b) chlorophyll *a*. Invertebrate colonization on experimental tiles as (c) invertebrate biomass and (d) community composition. Points represent mean estimates of all sites ($n = 7$), and error bars represent 95% CIs. Bar chart shows relative composition of invertebrate functional groups.

Finer-scale community analyses supported patterns from functional feeding groups, in that the structure of prey communities varied among seasons and between predators, but not due to thinning (Figure 7). Both NMS ordinations and PERMANOVA tests indicated prey communities differed due to season (PERMANOVA: $p < 0.001$) and predator species (PERMANOVA: $p < 0.001$) but not due to thinning indicated by the BACI model of Reach Type × Year (PERMANOVA: $p = 0.375$) (Figure 7). Indicator species analyses determined that variation in community structure among seasons was primarily due to the prevalence of aquatic invertebrates in spring (e.g., Baetidae, Ameletidae, Ephemerellidae, and Heptageniidae mayflies, and Elmidae beetles), the influx of terrestrial invertebrates, the emergence of adult aquatic invertebrates, and aquatic vertebrates (trout fry and larval amphibians) in summer and fall. Variation between predators was largely due to the increased reliance by salamanders on benthic prey items such as *Juga* snails, Perlidae stoneflies, Leptophlebiidae and Heptageniidae mayflies, Pteronarcyidae stoneflies, and a combination of cased and free-living caddisflies (e.g., Glossosomatidae, Limnephilidae, Rhyacophilidae, and Uenoidae), whereas trout relied more on terrestrial invertebrates, emerged adult aquatic invertebrates, and trout fry. Only a few taxa corresponded to thinning treatments and included terrestrial flies, Perlidae stoneflies, and *Ecclisomyia*—a scraping Limnephilidae caddisfly.

Stable isotopes

Thinning enriched stream periphyton carbon δ^{13}C stable isotope ratios relative to pre-treatment in the Tectah watersheds, although the magnitude of this response varied between seasons (Figure 8). Post-thinning carbon signatures increased by 4.1‰ (95% CIs: 2.2, 5.9) in spring, by 1.6‰ (0.6, 2.5) in summer, and by 0.6‰ (−0.2, 1.4) in fall (Figure 8). These shifts in

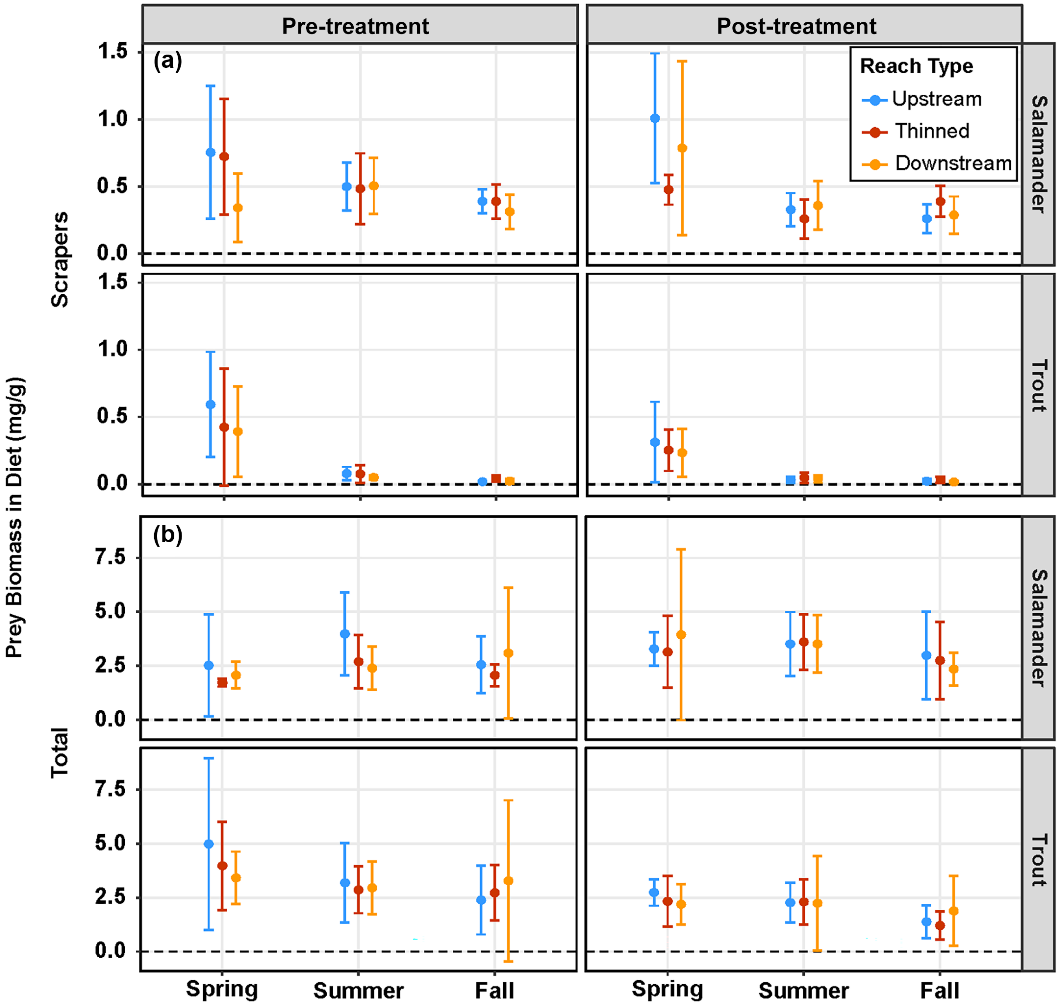

FIGURE 5 Seasonal patterns of prey biomass in the diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah and Lost Man watersheds in northern California, USA. Prey biomass (in milligrams) in diets is standardized per gram of predator biomass and characterized as (a) scraper biomass and (b) total biomass. Points represent mean estimates of all sites ($n = 7$), and error bars represent 95% CIs.

carbon signatures were partially reflected by primary consumers, although responses varied among taxa and among seasons. Tailed frog tadpoles showed consistent increases in carbon signatures in response to thinning in spring and summer across all sites, while Heptageniidae mayflies had variable responses in spring and summer, but displayed increased carbon signatures across all sites in fall. In contrast, Uenoidae caddisflies showed mixed responses where some sites responded strongly in spring and summer, but not in fall. *Juga* snails also showed minimal changes. Changes in carbon signatures in periphyton were not reflected by top predators during any of the three seasons we sampled (Figure 8). Some of the periphyton and primary consumer responses in carbon signatures in thinned reaches were reflected in downstream reaches, but the magnitude of these responses was often more muted than in thinned reaches (Figure 8).

Predator biomass

Whereas both salamander and trout biomass exhibited substantial variation between years and among seasons (Figure 9), neither yielded statistically detectable responses to thinning (BACI effect; salamander—spring: $p = 0.65$, summer: $p = 0.58$, fall: $p = 0.33$; trout—spring: $p = 0.10$, summer: $p = 0.14$, fall: $p = 0.09$) (Figure 9). However, in contrast to salamanders, thinned reaches during the post-treatment year supported on average 35%–60% more cutthroat trout biomass than upstream reference and downstream reaches (Figure 9).

Food web correlations

Correlation matrices of food web responses indicated that changes in shade and light associated with thinning

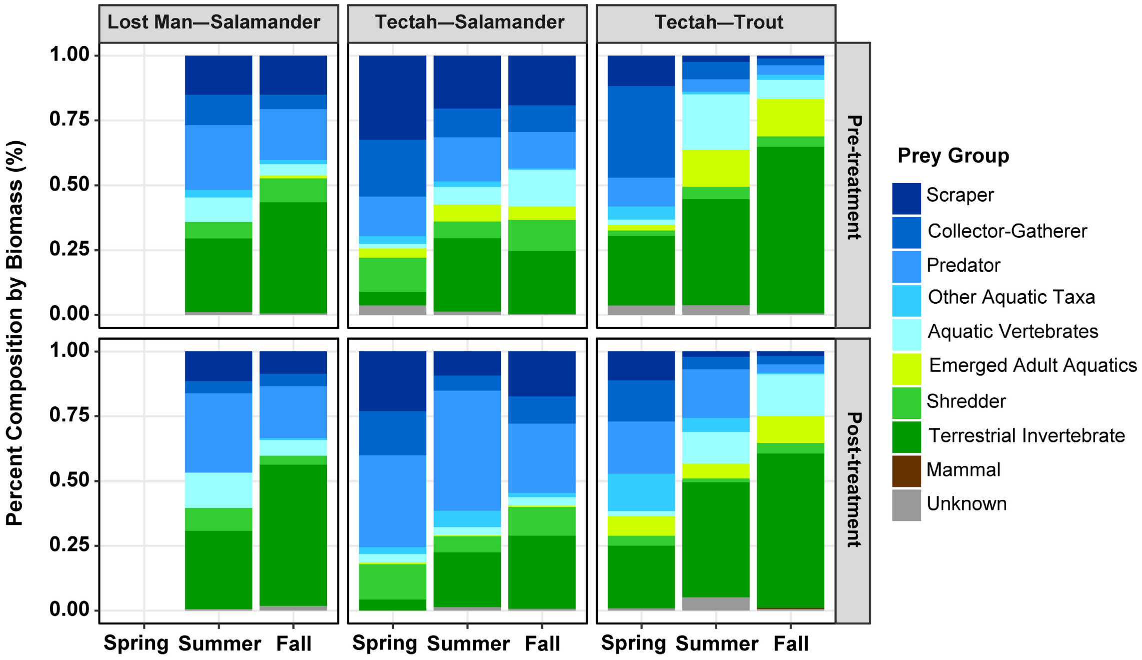

FIGURE 6 Seasonal patterns of percent composition of prey broken down by functional groups in the diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) during pre- and post-treatment years across sites in the Tectah and Lost Man watersheds in northern California, USA. No differences were observed between upstream, thinned, and downstream reaches, so results are pooled across reach types. Prey groups included the following: invertebrate scraper, collector-gatherer, invertebrate predator, other aquatic taxa (taxa that we could not identify to functional group or groups that did not account for much biomass such as collector-filterer or parasitic taxa), aquatic vertebrates (trout fry and larval amphibians), emerged adult aquatic invertebrates, shredders, terrestrial invertebrates, terrestrial mammal, and taxa that we could not identify.

correlated more strongly with lower trophic levels than with top predators (Figure 10). Changes in light correlated the most with stream periphyton on tiles (AFDM_tile: $r = 0.92$, Chla_tile: $r = 0.82$), followed by invertebrate biomass on tiles (InvertBio_tile: $r = 0.72$) and stream temperature (Temperature: $r = 0.68$). Salamander biomass did not correlate with light or any other food web variables ($r < 0.3$) (Figure 10). Cutthroat trout biomass correlated weakly with light (Light: $r = 0.37$) but correlated more strongly with stream temperature (Temperature: $r = 0.51$), shade ($r = -0.48$), chlorophyll a on tiles ($r = 0.45$), and invertebrate biomass on tiles ($r = 0.45$) (Figure 10).

DISCUSSION

In this study, we explored how relatively subtle increases in light associated with riparian forest thinning influenced stream food webs across multiple taxa and trophic levels in a large replicated field experiment. In contrast to our predictions that increases in light associated with experimental thinning treatments would enhance aquatic productivity and shift trophic pathways as documented in previous riparian canopy experiments (Bilby & Bisson, 1992; Kaylor & Warren, 2017; Kiffney et al., 2004; Wilzbach et al., 2005; Wootton, 2012), results from our experiment showed that thinning had limited influence on stream food webs with responses being largely constrained to lower trophic levels. Moreover, we observed that these muted responses by stream food webs to riparian thinning were consistent across a range of treatment intensities (Appendix S2). These results suggest that either: (1) increases in light did not generate sufficient energy to propagate up to upper trophic levels; (2) top predators were resistant to changes in stream–riparian food webs; (3) other factors may be driving food web dynamics in these small forested watersheds; or (4) we only monitored responses 1 year post-treatment and responses may have needed more time to manifest.

Stream periphyton

Riparian thinning increased light to the stream channel, alleviating light limitation in these densely forested streams (Gregory et al., 1987; Hill et al., 1995; Kiffney et al., 2004), yet we observed mixed stream periphyton responses. We documented no change in stream periphyton standing stocks on natural substrates in either the

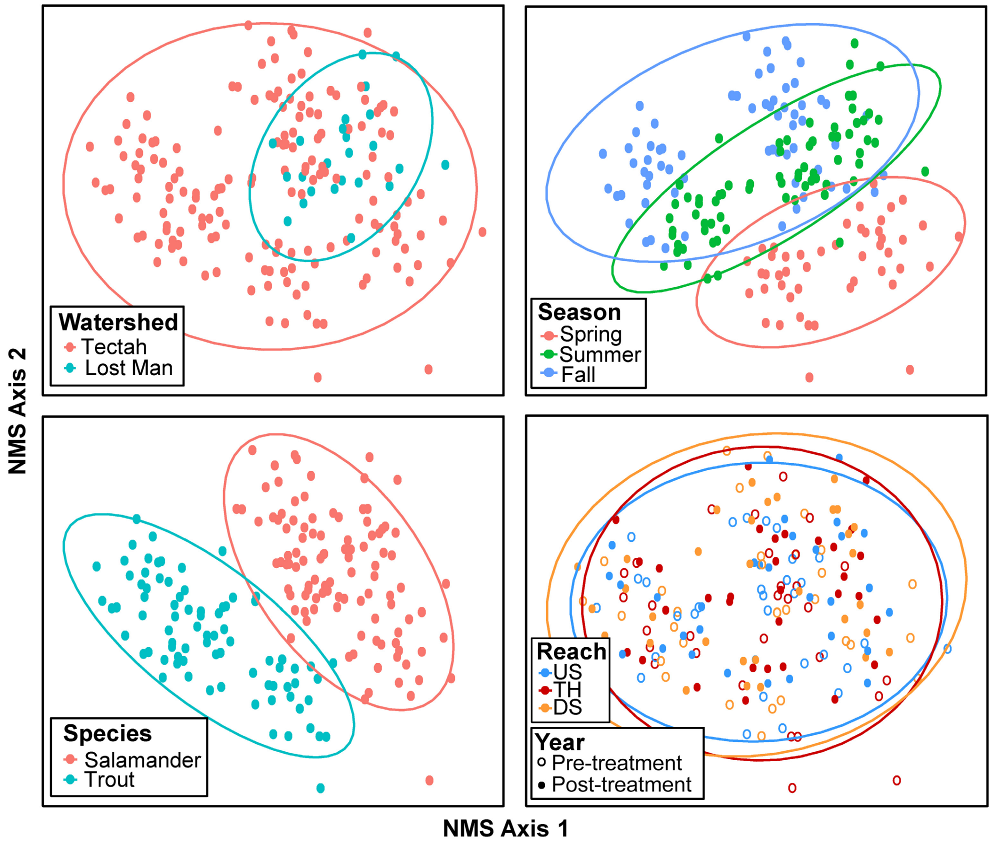

FIGURE 7 Nonmetric multidimensional scaling (NMS) ordinations indicating the structure of prey communities in diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) across all study sites ($n = 7$) in northern California, USA. NMS ordinations are repeated to indicate how the structure of prey communities varied by (a) watershed, (b) season, (c) species, and (d) following the design of the before–after control–impact experiment (Reach × Year). All points represent individual communities ($n = 186$), and the proximity of points indicates the similarity between communities. Stress = 0.19. Ellipses indicate the 95% CIs surrounding each grouping variable.

Tectah or the Lost Man watershed but observed strong evidence that thinning increased stream periphyton accrual on experimental tiles, especially under the more intensive thinning treatments in the Tectah watersheds. As a result, we only found partial support for our hypothesis that thinning would increase stream periphyton abundance. These differential responses are consistent with previous riparian canopy experiments where changes in stream periphyton occurred less frequently as standing stocks on natural substrates (Ambrose et al., 2004), and more frequently as accrual on experimental tiles (Feminella et al., 1989; Kiffney et al., 2003; Wootton, 2012). Although stream periphyton conditions on experimental tiles should approximate those on natural substrates (Lamberti & Resh, 1985), discrepancies could be due to differences in assemblages where natural substrates are most likely composed of more persistent taxa, while tiles are more likely colonized by early-successional taxa adapted to faster growth and turnover (Cattaneo & Amireault, 1992; Danehy et al., 2007). As a result, although tiles could be more likely to detect changes in riparian canopies than natural substrates, they may not fully represent stream periphyton dynamics and their responses to disturbance (Cattaneo & Amireault, 1992).

Given that periphyton is a complex of autotrophic algae and heterotrophic bacteria, fungi, and microorganisms (Steinman et al., 2017), the mixed periphyton responses observed in this study could be due to the fact that the coarse-level AFDM estimates were insufficient to isolate algal responses within periphyton assemblages. In contrast to bulk AFDM, which led to inconsistent responses between the tiles and natural substrates, chlorophyll *a* and carbon δ^{13}C isotopes were more effective in detecting algal responses and provided consistent evidence that autotrophic energy sources increased post-thinning regardless of the method even across a gradient of thinning intensities. These results suggest that approaches that more directly quantify algal responses may be useful for detecting subtle changes in autotrophic pathways in response to modern forestry practices such as thinning (Ambrose et al., 2004; Wootton, 2012). Furthermore, the addition of other methods quantifying

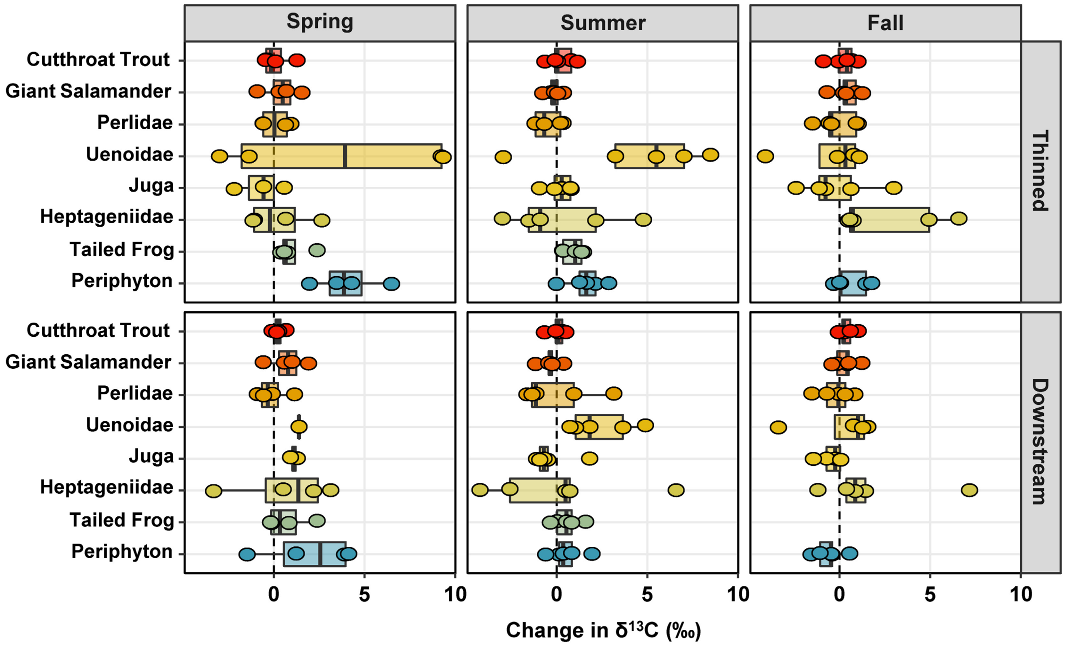

FIGURE 8 Seasonal before–after control–impact responses of carbon (δ^{13}C) stable isotopes for multiple components of the food web in thinned and downstream reaches for sites in the Tectah watersheds in northern California, USA. Food web components include the following: stream periphyton, scrapers (tailed frog tadpoles, Heptageniidae mayflies, Juga snails, Uenoidae caddisflies), and predators (Perlidae stoneflies, coastal giant salamander, and coastal cutthroat trout). Points represent the mean values of individual sites, while boxplots show the distribution of data.

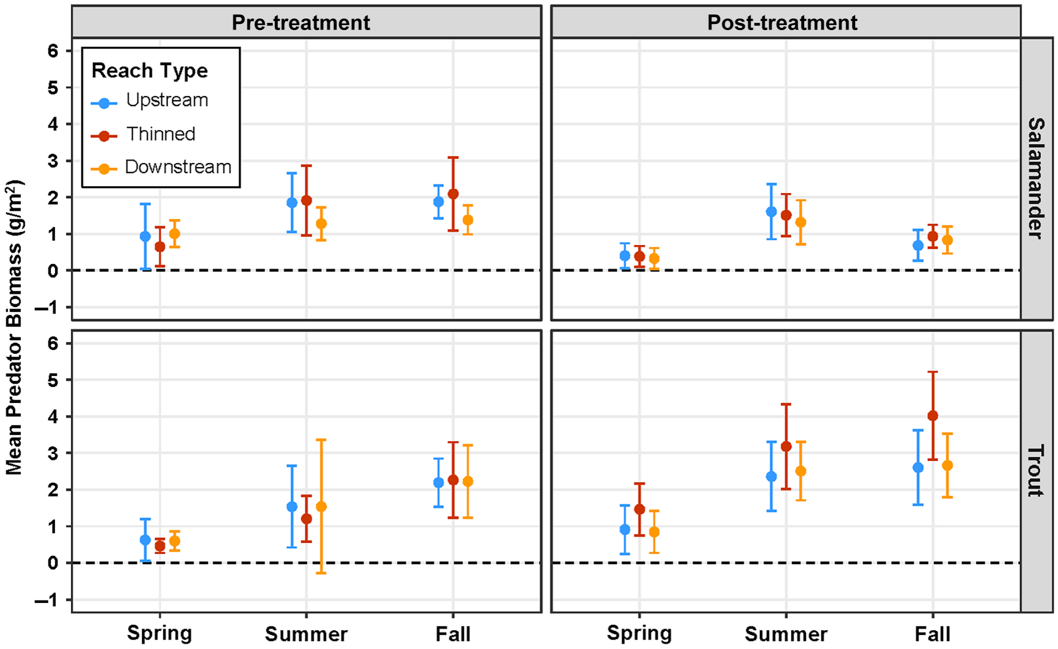

FIGURE 9 Seasonal patterns of predator biomass of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah and Lost Man watersheds in northern California, USA. Points represent mean estimates of all sites ($n = 7$), and error bars represent 95% CIs.

primary production (e.g., whole-stream metabolism) or the composition of periphyton communities may lend further insights not possible from coarser-level biomass estimates alone (Steinman et al., 2017).

Stream periphyton responses indicated that other factors beyond light likely mediated responses to thinning. Nutrients can co-limit aquatic primary production in streams, and once light limitation is alleviated, nutrient

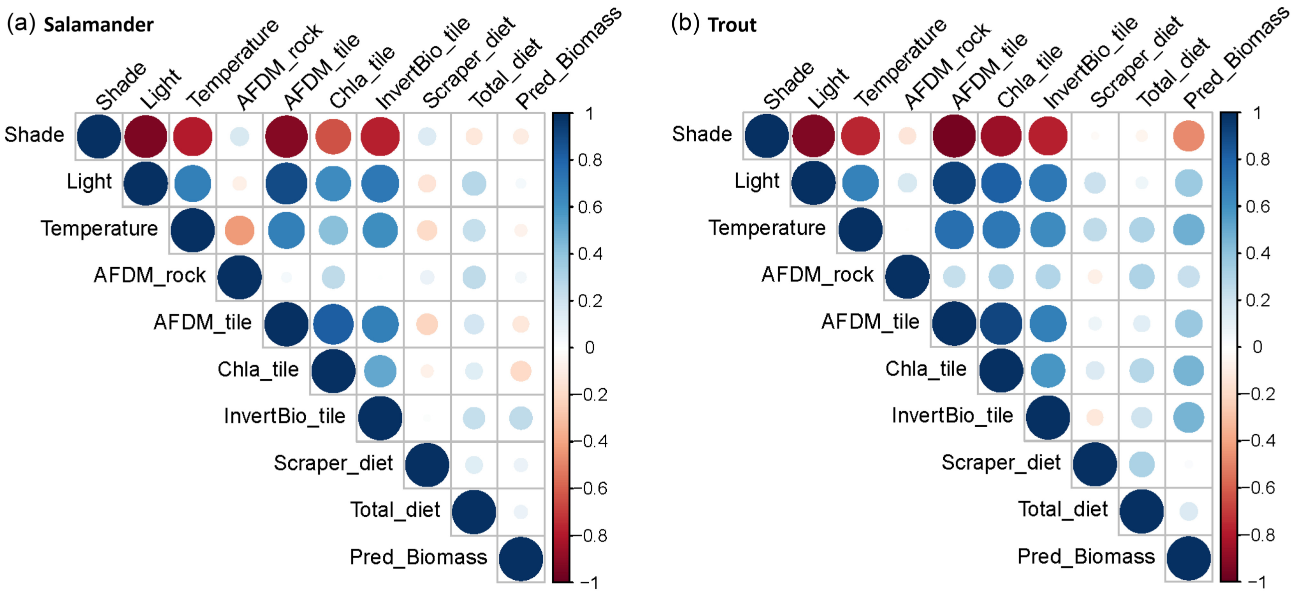

FIGURE 10 Correlation matrices of stream food web responses to riparian thinning in northern California, USA. Data represent before–after differences in summer responses in upstream reference, thinned, and downstream reaches for different components of the food web, including shade, light, stream temperature, periphyton (AFDM_rock, AFDM_tile, and Chla_tile), benthic invertebrates (InvertBio_tile), prey biomass in diets (Scraper_diet, Total_diet), and predator biomass (Pred_Biomass). (a) Correlation matrix for coastal giant salamanders (*Dicamptodon tenebrosus*) in the Lost Man and Tectah watersheds. (b) Correlation matrix for coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in the Tectah watersheds. The diameter and width of the circle correspond to the strength of the correlation.

limitation can develop (Gregory et al., 1987; Hill & Knight, 1988; Warren et al., 2017). Concentrations of nitrate and phosphate were low overall and did not change with thinning. N:P ratios (all <16, mean: 6.4, range: 1.9–15.5) combined with a previous nutrient limitation experiment conducted in the same watersheds (Ambrose et al., 2004) suggest evidence of potential nitrogen limitation. McIntyre et al. (2018) also documented minimal responses by stream periphyton to canopy treatments in western Washington streams and hypothesized the result was likely driven by low nutrient concentrations. In contrast, an experiment involving canopy reductions similar in magnitude to our study but with much higher nutrient concentrations yielded much larger responses in primary production that propagated up to higher trophic levels (Wootton, 2012). These results suggest that low nutrient concentrations were likely a key constraint on aquatic primary production, which could have led to insufficient autotrophic energy available to propagate up to higher trophic levels in these small, forested streams positioned high in the network (Binkley et al., 2004; Power & Dietrich, 2002).

Top-down effects by invertebrate scrapers can mediate periphyton responses to changes in riparian canopies (Feminella et al., 1989; Hill et al., 1995; Rosemond et al., 2000). Our tile experiment provided evidence that periphyton accrual was partially muted by invertebrate scrapers in that elevated tiles supported more periphyton accrual and fewer invertebrate scrapers than streambed tiles, consistent with observations by Feminella et al. (1989). In contrast to Hill et al. (1995), however, results from our tile experiment indicated stronger canopy effects than scraper effects. Furthermore, invertebrate communities that colonized tiles in thinned reaches were composed of a greater percentage of scraping taxa, suggesting that thinned reaches supported more scrapers, consistent with hypotheses predicting strengthened autotrophic processes (Bilby & Bisson, 1992; Kaylor & Warren, 2017). Altogether, these results suggest that the lack of periphyton response observed on natural substrates in thinned reaches could be due in part to top-down effects by scrapers.

Diets of top predators

Diet sampling revealed no evidence that thinning increased the abundance of prey resources supporting top predators. Given that previous research has documented increased macroinvertebrate biomass in response to opening riparian canopies (Bilby & Bisson, 1992; Kaylor & Warren, 2017), we predicted that this would be reflected by increased prey biomass in the diets of top predators. A key mechanism for this hypothesis was that increased scraper biomass associated with thinning would lead to increased biomass in predator diets.

Although we detected increased colonization of scraping invertebrates on tiles in thinned reaches, we observed no evidence that this increase in autotrophic resources tracked up to top predators. Instead, scraper biomass composed a small portion of predator diets and did not change with thinning, leading to no change in total prey biomass for either predator. These observations were not supported by previous diet studies that found that opening riparian canopies can lead to increased prey biomass in diets of juvenile coho salmon (*Oncorhynchus kisutch*) in western Washington (Bilby & Bisson, 1992) and brook trout (*Salvelinus fontinalis*) in West Virginia (Niles & Hartman, 2021). Our results suggest that potential changes in prey availability are not always reflected by top predators (Li et al., 2016; Romero et al., 2005). This could be due to the reliance of predators on multiple sources of prey—not just scrapers (Li et al., 2016; Nakano & Murakami, 2001), prey selection preferences (Utz & Hartman, 2007), increased predator biomass leading to heightened competition for prey resources (Hughes & Grand, 2000), or that predators did not feed at maximum rates to avoid terrestrial predators (Harvey & White, 2017; Penaluna et al., 2021). Alternatively, increases in water temperature (Roon et al., 2021) could have led to faster predator digestion rates potentially masking any increase in prey consumption associated with thinning (Beauchamp, 2009).

Community analyses indicated no evidence that thinning shifted the composition and structure of prey communities toward the increased influence of autotrophic pathways. Again, we hypothesized that scrapers would act as important trophic links connecting potential changes in aquatic primary production to top predators, leading to shifts in composition and structure of prey communities in diets toward increased reliance on aquatic energy sources (Bilby & Bisson, 1992). However, we saw no increased influence of scrapers leading to shifts in composition or structure of diets of either predator after thinning. Instead, we found that prey composition and structure in diets varied more seasonally (Li et al., 2016; Morley et al., 2016; Rundio & Lindley, 2008) and between predators (Falke et al., 2020) than due to thinning treatments. We predicted that, as benthic predators (Falke et al., 2020; Parker, 1994), salamanders would be more likely to benefit from any increase in scraper abundance than cutthroat trout. Diet results partially supported this prediction, where salamanders generally preyed more on scrapers than cutthroat trout (Falke et al., 2020), even relying extensively on *Juga* snails and stone-cased caddisflies that are otherwise known as "invulnerable grazers" (Atlas et al., 2013; Esseltyn & Wildman, 1997; Power & Dietrich, 2002). However, we saw no evidence that salamander consumption of scrapers and other freshwater energy sources changed with thinning. Whereas salamanders preyed on scrapers across all three seasons we sampled, cutthroat trout preyed primarily on scrapers and other aquatic invertebrates in spring when flows were higher (Falke et al., 2020; Li et al., 2016; Raggon, 2010). As flows receded and aquatic invertebrate availability likely decreased (Li et al., 2016), cutthroat trout increasingly preyed on terrestrial invertebrates in summer and fall—composing 50%–65% of their diets (Li et al., 2016; Romero et al., 2005). However, this reliance on terrestrial invertebrates did not decline as predicted or as documented elsewhere (Benjamin et al., 2022; Niles & Hartman, 2021). Together, these patterns suggest that top predators relied on distinct trophic pathways that remained intact even after thinning.

Stable isotopes

Stable isotopes complemented results from other methods supporting the finding that thinning primarily influenced lower trophic levels and that those effects did not propagate up to top predators. Thinning shifted stream periphyton isotopic signatures as previously documented with changes in canopy cover (Ishikawa et al., 2012; Wootton, 2012), and they were reflected by increases in stream periphyton biomass on tiles both as AFDM and as chlorophyll *a*. However, the magnitude of these shifts indicated seasonal variation in primary production and the composition of periphyton assemblages (Finlay, 2001; Hill & Middleton, 2006; McCutchan & Lewis, 2001). Primary consumers sometimes reflected these shifts in carbon, but responses varied across taxa and seasons. The timing of responses of some primary consumers (e.g., Uenoidae caddisflies and Heptageniidae mayflies) varied among seasons, suggesting that differences in growth and metabolism among primary consumers could be due to the rate of carbon assimilation (McNeely et al., 2007). However, in contrast to lower trophic levels, we observed minimal responses by all top predators. Wootton (2012) documented similar shifts in stream periphyton carbon signatures in response to canopy treatments of similar magnitude on the Olympic Peninsula in Washington, but this shift in carbon propagated up to the top consumer in the system—juvenile coho salmon. Kiffney et al. (2018) observed responses similar to ours, where the experimental addition of salmon carcasses in western Washington streams shifted carbon and nitrogen isotope signatures of lower trophic levels, but not top predators. In contrast, McIntyre et al. (2018) observed no change in stream periphyton stable isotope signatures or biomass in response to a range of riparian buffer treatments in Washington streams. As a result, there was no apparent shift toward autotrophic energy sources supporting higher trophic levels, leading McIntyre et al. (2018) to conclude that terrestrial resources were likely the dominant energy source. While we could not run a mixing model to partition aquatic and terrestrial energy sources (Finlay, 2001; Middleburg, 2014), tracking shifts in $\delta^{13}C$ signatures of stream periphyton paired with our BACI study design provided a useful approach for detecting changes in response to thinning. This approach was particularly effective when combined with predator diets for detecting shifts in trophic pathways supporting energy flow in these systems across short- and long-term temporal scales (Naman et al., 2022).

Top predators

We observed differential responses of top predators to riparian thinning and associated changes in light availability. Salamander biomass did not change with thinning and correlated poorly to light and food web responses, which does not support our hypothesis that as benthic predators, salamanders would be more likely to respond to thinning treatments. This pattern occurred in both the Tectah and the Lost Man watersheds, suggesting it was consistent across thinning intensities. Previous research has indicated that salamander biomass often exceeds that of cutthroat trout in watersheds of the Pacific Northwest (Hawkins et al., 1983; Murphy & Hall, 1981; Roni, 2002), so the relatively low biomass documented in this study could be a function of low capture probabilities via electrofishing that potentially underestimated population sizes (Kaylor & Warren, 2017; Olson et al., 2014). Nevertheless, our results support previous observations that salamander biomass responses to riparian canopy experiments are frequently context-dependent (Murphy & Hall, 1981) in this case, indicating that salamanders were largely resistant to riparian thinning treatments regardless of treatment intensity (Hawkins et al., 1983; Heaston et al., 2018).

In contrast to salamanders, cutthroat trout biomass potentially increased with thinning by 35%–60%, but biomass estimates ranged widely among sites in the Tectah watersheds, so responses were not statistically significant. Trout biomass responses were not reflected by diets or isotopes, and the correlations with light were much weaker than those reported by Kaylor and Warren (2017), suggesting minimal evidence that responses could be directly attributed to changes in autotrophic pathways. However, potential increases in trout biomass could be driven by other processes associated with thinning. For example, previous research by Wilzbach et al. (2005) indicated that increased cutthroat trout density in response to riparian canopy treatments coincided with faster growth rates, suggesting that changes in biomass could be due to increased local fish production. Along those lines, cutthroat trout biomass correlated more strongly with increases in stream temperature than with light, suggesting trout responses could be due to physiological (bioenergetic) processes. Stream temperatures increased post-thinning in the Tectah watersheds by 2–4°C (Roon et al., 2021). Assuming sufficient prey resources were available, thermally driven increases in fish metabolism could then lead to increased biomass (Hughes & Grand, 2000; Railsback, 2022). Because changes in light and temperature co-occur (Moore et al., 2005), it is challenging to discern the driver of changes in trout biomass. As a result, further research is needed to elucidate the thermal and trophic processes associated with thinning and their effects on cutthroat trout growth and energetics (Beauchamp, 2009) to further explore what may be driving potential responses in fish biomass and production (Wipfli & Baxter, 2010).

Seasonal and longitudinal shifts in food web dynamics

Given that stream food webs can vary seasonally and spatially (Li et al., 2016; Power & Dietrich, 2002), a second objective of this study was to understand how thinning affected their seasonal and longitudinal dynamics (Hawkins & Sedell, 1981). We predicted that increases in light associated with thinning could strengthen the influence of autotrophic pathways—both seasonally and spatially in these watersheds. Most food web studies focus on summer months (e.g., Bilby & Bisson, 1992), and so few have explored seasonal dynamics (but see Falke et al., 2020; Li et al., 2016; Rundio & Lindley, 2008). Some of our observations in thinned reaches supported the prediction of extended seasonal influences: increased periphyton accrual on tiles during late summer, increased scraper consumption by salamanders in fall, shifted carbon signatures by primary consumers during summer and fall months, and increased trout biomass in summer and fall. However, most of the food web responses we observed indicate that inherent seasonal variation exceeded the treatment effects from riparian thinning (Morley et al., 2016). In contrast to seasonal responses and our a priori predictions, we saw little evidence of downstream propagation of local responses to thinning (Hawkins & Sedell, 1981), even though increases in stream temperature propagated into downstream reaches (Roon et al., 2021). This could be because local responses were minor, resulting in little energy to propagate downstream (Danehy et al., 2011). In contrast, a study by Erdozain et al. (2021) documented local increases in allochthony from forest harvest propagated to downstream reaches. Similarly, the influx of slash from thinning treatments could have propagated terrestrial organic matter into downstream reaches, potentially buffering the influence of any strengthened autotrophic signals from drifting invertebrates. Alternatively, key food web responses tended to occur in summer, a period of low streamflows and therefore reduced longitudinal connectivity that limited the propagation between thinned and downstream reaches (Feijo-Lima et al., 2018; Humphries et al., 2014).

Management implications

Resource managers are interested in whether riparian thinning may serve as a viable strategy to address multiple management objectives including a way to accelerate the recovery of second-growth riparian forests recovering from the legacy of historical timber harvests. Whereas it may take centuries to meet many riparian forest restoration objectives (e.g., old-growth structure and large wood recruitment), more immediate questions have emerged regarding whether thinning can strike a balance between opening riparian canopies to enhance aquatic productivity while simultaneously minimizing changes to stream temperatures (Wilzbach et al., 2005). Although we found little consistent evidence that riparian thinning treatments shifted trophic pathways leading to increased aquatic productivity across multiple trophic levels, observations from this study have direct implications for managers interested in the application of riparian thinning as a restoration strategy.

First, although some assume that opening riparian forest canopies may lead to enhanced aquatic productivity (Griffith & Kiffney, 2022; Kiffney et al., 2003; Newton & Ice, 2015), we found mixed evidence that riparian thinning influenced autotrophic pathways supporting the food webs in the small, forested streams in our northwestern California study watersheds. Our results did not align with previous riparian canopy experiments that explored the effects of more intensive historical forestry practices such as clear-cutting (Bilby & Bisson, 1992; Hawkins et al., 1983; Murphy & Hall, 1981; Wilzbach et al., 2005) or the effects of less intensive recent practices such as riparian buffers or selective logging (England & Rosemond, 2004; Griffith & Kiffney, 2022; Heaston et al., 2018; Niles & Hartman, 2021; Wootton, 2012). Instead, the mixed responses documented in our study suggest that riparian thinning is not a guaranteed means for increasing aquatic productivity in forested streams (see McIntyre et al., 2018) and that outcomes do not always meet expectations due to a host of contingencies that could drive variable outcomes (e.g., Nash et al., 2021). Part of this variation in responses could be due to conditions unique to the context of the study watersheds such as low nutrient concentrations that potentially limited primary production (Ambrose et al., 2004; McIntyre et al., 2018; Warren et al., 2017) or the importance of terrestrial invertebrate subsidies supporting top predators (Li et al., 2016; Nakano & Murakami, 2001; Romero et al., 2005). Given that stream networks exhibit extensive spatial heterogeneity within and among systems, it is not surprising to see different responses among locations (Whitney et al., 2020). Future research could synthesize findings of recent studies to further explore the environmental drivers leading to context dependency and variation in food web responses. Identification of key drivers in different contexts could help managers identify the likelihood of alternative riparian management designs leading to desired food web responses.

Second, while we did not observe strong food web responses in this study, we also observed no adverse effects on the aquatic communities we measured. Food web responses indicated widespread resistance to thinning treatments across multiple taxa and trophic levels (Lewis et al., 2014; Nelson et al., 2021). This resistance by stream ecosystems could be due to the complexity of stream–riparian food webs (Nakano & Murakami, 2001; Nelson et al., 2021), which could have helped buffer responses to thinning treatments (Benjamin et al., 2022). Alternatively, resistance could be due to the relatively small scale of thinning treatments (100–200 m in reach length) that were much less intensive than historical timber harvest practices that completely removed riparian canopies over broader spatial extents (Bilby & Bisson, 1992; Murphy & Hall, 1981; Wilzbach et al., 2005). Thus, the less intensive treatments could have led to minor treatment responses that were smaller in magnitude than inherent seasonal and spatial variation in the system (Morley et al., 2016).

Third, our observations on thinning effects are short-term in nature, as we only monitored responses 1 year post-treatment. Although reductions in riparian canopies can have immediate physical effects on shade, light, and stream temperatures (Roon et al., 2021), and previous research has documented immediate biological responses to canopy reductions (Kiffney et al., 2003; Wilzbach et al., 2005; Wootton, 2012), those responses can be short-lived as the canopy fills in via epicormic branching or understory expansion (Moore et al., 2005). Therefore, it is important to keep in mind that food web responses to thinning (e.g., potential increases in trout biomass) may also be short-lived. On the contrary, treatment effects in food webs that depend on the interaction between multiple species and trophic levels may take more time to generate (Yodzis, 1988) and other studies have documented such delayed responses (Olson et al., 2014; Olson & Ares, 2022). As a result, future studies should monitor responses over longer periods of time to fully capture their temporal dynamics, especially as forests recover (Kaylor & Warren, 2018; Warren et al., 2016).

Fourth, although we focused on whether thinning can enhance aquatic productivity via autotrophic processes, stream–riparian systems are complex, so thinning may still have implications for other ecological processes that were beyond the scope of this study (Baxter et al., 2005; Benjamin et al., 2022). For example, changes in riparian canopy composition can influence the terrestrial inputs of leaf litter and invertebrates to aquatic consumers (Baxter et al., 2005). Alternatively, increased light associated with thinning could have led to more efficient foraging conditions for stream predators (Wilzbach & Hall, 1985). Short-term benefits from riparian thinning treatments may also come at the expense of negative effects on ecological processes such as increases in stream temperature (Roon et al., 2021) or reductions in large wood inputs (Pollock & Beechie, 2014). As a result, new approaches are needed to integrate the multiple pathways by which thinning can influence aquatic systems, as well as explicitly consider the interactions and feedbacks between species within food webs. Application of food web simulation models, such as the Aquatic Trophic Productivity model (Bellmore et al., 2017; Benjamin et al., 2022), may provide comprehensive insights not possible from empirical observations alone. Such insights provided by modeling may complement empirical studies to more fully understand the effects of riparian forest restoration on aquatic systems and can be used to guide future management (Benjamin et al., 2022).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Roon, 2022) are available from the Open Science Framework: https://doi.org/10.17605/OSF.IO/JQPKF.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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