AN ABSTRACT OF THE DISSERTATION OF

David Alexander Roon for the degree of Doctor of Philosophy in Fisheries Science presented on June 24, 2021.

Title: Evaluating the Ecological Trade-Offs of Riparian Thinning for Stream Ecosystems in Second-Growth Redwood Forests of Northern California

Abstract approved: ____

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Riparian forests provide a myriad of ecosystem functions for adjacent streams and rivers, and due to these linkages, changes in riparian forest conditions can have direct implications for stream ecosystems. Resource managers in the coast redwood forests (*Sequoia sempervirens*) of northern California (USA) are actively thinning second-growth stands to accelerate the recovery of old-growth redwood forest conditions. These restoration thinning treatments have focused on upland forests to date due to contemporary riparian protections, but now attention is shifting towards second-growth forests in riparian zones recovering from previous timber harvests. As a result, resource managers across the Pacific Northwest are interested in exploring whether thinning second-growth riparian forests may have benefits to address multiple management objectives for riparian and stream ecosystems. However, complex ecological trade-offs may emerge to riparian thinning between potential increases in stream temperature that can exceed the thermal tolerance of cold-water adapted species and possible increases in aquatic productivity.

In this dissertation I evaluated the influences of riparian thinning on stream ecosystems by examining the effects of thinning on: 1) riparian shade, light, and reach-scale stream temperature responses; 2) how local responses in stream temperature propagated downstream at a watershed extent; 3) light-mediated trophic pathways supporting the food webs of top predators - coastal giant salamander (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*); and 4) how these potential changes in thermal and trophic resources interacted to influence the growth and energetics of coastal cutthroat trout that occupied the study watersheds. Using a unique watershed-scale field experiment following a before-after-control-impact design, I evaluated the effects of riparian thinning by experimentally manipulating riparian canopy conditions and tracking stream responses before and after treatment. Key findings that emerged from this work include: 1) thinning treatments decreased shade and light to the stream, but the magnitude of these changes ranged widely depending on the intensity of treatments; 2) stream temperatures increased locally with thinning under more-intensive treatments, but did not change under less-intensive treatments; 3) local responses in stream temperature often propagated downstream, but the spatial extent of those responses depended on the local magnitude of increase; 4) increases in light associated with thinning had limited influence on trophic pathways supporting stream food webs and food web responses were largely confined to lower trophic levels; 5) growth and energetics of coastal cutthroat trout often varied more seasonally and due to body size than due to thinning treatments. Bioenergetics models estimated that cutthroat trout growth potential could increase with thinning primarily due to increases in consumption highlighting the importance of trophic processes supporting these stream fish. However, the effects of thinning on thermal and trophic processes supporting growth potential for cutthroat trout varied seasonally, where trophic processes were more influential both in spring and overwinter whereas thermal processes had greater influence in summer.

Collectively, results from this series of studies highlight that managers need to consider both thermal and food web processes when thinking about the implications of riparian forest management like thinning on stream ecosystems. Moreover, these results illustrate the value of process-based approaches that tease apart underlying mechanisms. An understanding of processes is especially powerful when analyses are combined with year-round studies that capture seasonal variation and watershed-scale analyses that capture spatial patterns across broader spatial extents. Combined, as in this dissertation, such results contribute a more holistic understanding of aquatic responses to riparian thinning that have direct implications for resource managers considering restoration strategies for riparian forests in the redwoods of northern California, but may also apply to other forested watersheds under similar conditions.

Evaluating the Ecological Trade-Offs of Riparian Thinning for Stream Ecosystems in Second-Growth Redwood Forests of Northern California

by

David Alexander Roon

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented June 24, 2021
Commencement June 2022

Doctor of Philosophy dissertation of David Alexander Roon presented on June 24, 2021.

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David Alexander Roon, Author

ACKNOWLEDGEMENTS

I am so incredibly fortunate to have the opportunity to return to graduate school and work on this dissertation. I have learned so much through this experience and I could not have completed this on my own and so have many to thank. First and foremost, major thanks to my advisor Jason Dunham who has been an unparalleled mentor during my time at OSU. He pushed my thinking in so many directions (and scales) and inspired me to always ask *why?* He was incredibly generous with his time despite the many competing interests, making large amounts available for weekly chats and spur of the moment epiphanies. Thanks to my graduate committee Dede Olson, Ryan Bellmore, and Bret Harvey who challenged me to make sure I did great science while also making sure it was relevant to managers. Thanks to all the stream ecologists that make Corvallis such a wonderful and collaborative research environment. Dana Warren and his lab provided a welcoming surrogate lab space to discuss all things streams and light. Thanks to everyone in the Forest Service Pacific Northwest Research Station and USGS Forest and Rangeland Ecosystem Science Center who provided a supportive network of scientists to discuss ideas, ask questions, and were generous in allowing me to borrow critical laboratory space in order to complete my lab work. Thanks goes to Gordie Reeves, Sherri Johnson, Brooke Penaluna, Steve Perakis, and Collin Eagles-Smith.

I was lucky enough to spend the larger part of four years in the redwood forests of Humboldt County, California to collect data for this project. Working amongst the towering trees and lush riparian forests while hiking streams in search of fish and amphibians helped me appreciate how dynamic headwater systems can be in this part of the world. This surprisingly wild region of California also offered more adventure than I ever expected. From the Humboldt hippies, Arcata anarchists, guerrilla growers, and rugged loggers, field research was never boring in this remote corner of California.

This research was supported by Green Diamond Resource Company who acted as a supportive stakeholder in this research. Green Diamond was instrumental in guiding initial questions, designed and carried out the experimental treatments, provided access to study watersheds, and provided financial and logistical support for this research. The late Lowell Diller was instrumental in guiding the questions asked, shared his knowledge and enthusiasm for the unique assemblages of amphibians that inhabit the watersheds in this part of the world, and inspired the watershed-scale evaluation of thinning applied in this dissertation. He was an excellent scientist and always willing to put data to questions that many deemed too controversial to touch. Thanks for everything Lowell.

Matt House and Keith Hamm helped make sure things stayed on track and provided constructive feedback throughout the study process. Pat Righter bent over backwards to help pull off the on-the-ground logistics of getting the study up and running, made sure we had everything we needed in the field while simultaneously coordinating his own teams busy field season, and made sure we made it home safely from the field each night. I appreciated the support by all the aquatic biologists at Green Diamond Resource Company who helped get the study off the ground, helped with a wide array of field tasks from marching up watersheds in search of temperature sensors to hiking in unreasonable amounts of sampling gear to collect fish and amphibians, and taught me so much about the amphibians and fish that inhabit these watersheds. Thanks to Matt Kluber, Will Devenport, Matt Nannizzi, Jon Pini, Mike Zontos, Jonathan O'Connell, Sean Studer, Dave Dimitre, and Teal Richards-Dimitre for all their time and hard work; I couldn't have completed this without your help.

Along those lines thanks also goes to all the technicians who put in countless hours in the field and in the lab making this research happen. Thanks so much to Kyle Smith, Jerika Wallace, Thomas Starkey-Owens, Mary Carlquist, Ashley Sanders, Morgan Turner, Alex Scharfstein, Cedar Mackaness, and Laura Nepstad as well as the Humboldt State University student volunteers that helped collect data in the Lost Man watershed.

Jason Teraoka, Vicki Ozaki, and Dave Anderson at Redwood National Park helped us extend the study over the ridge into the national park. Not only did this physically expand the study, it also helped broaden its impact making it more applicable to a greater range of managers. Thanks especially goes to Jason for spending those initial days of reconnaissance in Lost Man, his willingness to work with us to schedule the treatments in Lost Man to match our experimental design, and coordinating much-needed freezer space during our pre-treatment year when we were camping down the road. Save the Redwoods League and their research grant program helped make expanding our research into RNP a reality.

Other funding and support for this research came from the Forest Service Pacific Northwest and Southwest Research Stations and from the Department of Fisheries and Wildlife at Oregon State University and their scholarship program which helped support my graduate research assistantship during this research.

Last but not least, thanks goes to my family. Thanks for your support through all of this. I appreciated the nonstop cheerleading and willingness to listen while I likely sounded like a one-track record talking about my dissertation research. Thanks especially goes to my dad who seemed to know that returning for a PhD would be my eventual path even before I did. Thanks to Leila (and Lovett) for being perfect partners to get through the pandemic and for their endless love and support.

CONTRIBUTION OF AUTHORS

Jason Dunham was an advisor and editor on all manuscripts included in this dissertation. Jeremy Groom helped with the analysis, interpretation, and writing for Chapter 2. Christian Torgersen helped develop the riverscape analysis we applied and the associated manuscript in Chapter 3. Ryan Bellmore, Dede Olson, and Bret Harvey helped guide the food web analysis and the writing in Chapter 4. Joe Benjamin, Ryan Bellmore, and Bret Harvey helped with the bioenergetics analysis and interpretation in Chapter 5.

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CHAPTER 1: GENERAL INTRODUCTION

Riparian forests provide a wide array of ecological functions and processes for adjacent stream ecosystems (Gregory et al. 1991, Naiman et al. 2010). Riparian shade limits solar radiation to the stream channel which controls in-stream photosynthesis and keeps stream temperatures cool for cold-water adapted species (Moore et al. 2005). Inputs of large wood physically structure aquatic habitats (Gregory et al. 1987). Roots of riparian vegetation modulate fluxes of nutrients and fine sediments (Murphy et al. 1981, Greathouse et al. 2014). Riparian contributions of allochthonous resource subsidies (e.g. leaf litter and terrestrial invertebrates) support aquatic species at multiple trophic levels (Vannote et al. 1980, Wipfli and Baxter 2010). As a result, terrestrial disturbances that alter riparian forests can have direct implications for a broad spectrum of processes in stream ecosystems and warrant investigation whenever riparian forest conditions change.

In the Pacific Northwest (USA), timber harvest is the most common terrestrial disturbance affecting riparian forests (Moore and Richardson 2012). Historical timber harvest practices frequently removed riparian forests from the landscape, resulting in a myriad of effects to stream and river systems (Gregory et al. 1987, Richardson and Beraud 2014). For example, opening riparian canopies increased solar radiation to the stream channel raising stream temperatures (Brown and Krygier 1970, Moore et al. 2005). Additionally, extraction of riparian vegetation from the streambanks caused influxes of fine sediments negatively affecting spawning habitats for salmonid fishes (Murphy et al. 1981). However, despite these adverse effects, initial studies also documented increased aquatic productivity across multiple trophic levels (Murphy and Hall 1981, Bilby and Bisson 1992). These increases in productivity were most likely due to increases in autotrophic (light-mediated) processes (Bilby and Bisson 1992, Kiffney et al. 2004, Kaylor and Warren 2017). Together these results suggest that timber harvest often resulted in ecological trade-offs for stream ecosystems where increases in aquatic productivity coincided with increases in stream temperature which sometimes exceeded the thermal tolerance of these cold-water adapted species (Gregory et al. 1987, Bilby and Bisson 1992).

To mitigate the deleterious effects of timber harvest on stream temperatures and fine sediments, contemporary forest management practices now require riparian buffer protections (Berg 1995, Moore et al. 2005). Recent studies have found riparian buffers to be largely effective in restoring many key ecological functions such as reducing stream temperatures (Moore et al. 2005, Groom et al. 2011). However, others have pointed out that a new set of issues arise with riparian buffer protections (Marczak et al. 2010, Richardson et al. 2012). For example, the effectiveness of riparian buffers often depends on their width (Moore et al. 2005, Sweeney and Newbold 2014), which varies widely depending on land ownership (Boijolie et al. 2019). Riparian buffer policies often require uniform buffer widths which are easy to administer but ignore inherent variability in landscape conditions (Richardson et al. 2012). Furthermore, buffer protections focus on protecting fish-bearing watersheds and non-fish-bearing headwater streams are often left unprotected although they act as key refugia for many stream amphibian species (Olson et al. 2007). Finally, the forests that these buffers protect are a legacy of previous clearcutting and therefore differ substantially in structure and composition than the old-growth forest conditions that preceded them (Warren et al. 2016). As a result, forests that compose riparian buffers tend to be dense even-aged stands of early-seral species and contribute high levels of shade over the stream channel (Warren et al. 2016). Given that it can take a long time for old-growth forest features to recover naturally (Martens et al. 2019), some natural resource managers and scientists are raising the question of whether more active management within riparian buffers may be necessary (Swanson and Franklin 1992, Berg 1995, Carey 2003).

In the Pacific Northwest, resource managers are increasingly interested in whether applying silvicultural approaches such as selective logging and variable-density thinning may be a viable restoration strategy for second-growth forests in riparian zones (Berg 1995, Russell 2009). This interest in thinning seeks to address multiple management objectives for riparian forest and stream restoration (Berg 1995). First, managers are interested in whether thinning can accelerate the recovery of old-growth forest structure and composition (O’Hara et al. 2010, Teraoka and Keyes 2011). Second, managers are interested in whether thinning can shift the successional trajectory of second-growth forests from early-seral deciduous species towards conifer to provide an eventual source of large wood (Pollock et al. 2014, Benda et al. 2016, Reeves et al. 2016). Both of these objectives address long-term ecological processes and in the meantime there is also interest in whether thinning may be able to strike a balance between the potential adverse effects of smaller increases in stream temperature and benefits of allowing light to filter through canopy to increase aquatic productivity (Wilzbach et al. 2005). Some have gone so far to suggest that riparian forests should be managed in this way to explicitly increase aquatic productivity for salmonid fishes (Newton and Ice 2015).

A prime example of interest in riparian thinning is represented by the coast redwood (*Sequoia sempervirens*) forests of northern California. In this region only 3 to 5% of old-growth forests remain with former old-growth redwood stands largely replaced by dense second-growth (Russell 2009). In attempting to restore old-growth forest structure and composition, foresters are actively thinning second-growth forests (O'Hara et al. 2010, Teraoka and Keyes 2011). Thinning treatments have largely been applied to upland forests to date, but as second-growth riparian forests appear similarly impacted (Russell 2009, Keyes and Teraoka 2014), managers are now increasingly interested in expanding restoration thinning efforts into riparian zones. Given that riparian thinning involves multiple influences and potential trade-offs (e.g., the potential benefits of increased in-stream productivity versus the possibility of temperatures warming beyond levels tolerated by cold-water biota), however, additional study is warranted as treatments are implemented.

Previous research provides a foundational understanding of the linkages that connect riparian forests and streams, but major knowledge gaps remain. Previous research has only examined how dramatic changes in forest cover (i.e. complete canopy removal) influence stream ecosystems. We know far less about the effects of more subtle changes in forest cover such as riparian thinning (England and Rosemond 2004, Lecerf et al. 2012). Can we necessarily assume that smaller changes in riparian conditions via thinning will translate into smaller effects? More specifically, how will thinning influence exposure of cold-water biota to unsuitably warm stream temperatures versus the potential benefits of increased aquatic productivity? This question is often posed at a single location and localized scales, but the question of how local changes in riparian forest cover influence stream ecosystems at larger spatial extents such as across entire watersheds also remains to be addressed (Reid 1998, Fausch et al. 2002, Wiens 2002). This is essential as this is the scale that mobile species such as stream fishes interact with their environment (Schlosser 1991) and that disturbance and changes in land-use can impact freshwater systems (Allan 2004). Finally, while studies have documented that opening riparian canopies resulted in increased growth and abundance of resident fishes (Wilzbach et al. 2005), the underlying mechanisms driving those responses were not clearly elucidated. Although many assume this is most likely due to increases in aquatic productivity (Kiffney et al. 2004, Kaylor and Warren 2017), increases in stream temperature as long as they do not exceed a species' thermal tolerance can also lead to increases in growth (Rosenberger et al. 2015). Teasing apart interacting thermal and trophic processes would provide a more mechanistic understanding of the sensitivity of cold-water species to changes associated with riparian thinning. Such insights are more relevant when they are addressed across landscapes or riverscapes to more fully describe the potential cumulative watershed effects associated with riparian forest thinning on aquatic organisms linked through stream-riparian food webs (Polis et al. 1997, Power and Dietrich 2002, Baxter et al. 2005, Bellmore et al. 2017).

In this dissertation, I attempt to provide a holistic, whole-system perspective of how riparian thinning influences aquatic ecosystems at watershed scales. To do so, I explored the effects of thinning in several different ways. First, I quantified how thinning treatments affected shade and light conditions over the stream channel and how those changes in shade and light affected reach-scale stream temperatures seasonally and across multiple descriptors of the thermal regime. Second, I applied a riverscape approach to explore how local responses in stream temperature propagated downstream at a watershed extent across multiple spatiotemporal scales. Third, I tracked the extent to which changes in light associated with thinning influenced trophic pathways supporting stream food webs of stream fish and amphibians in these watersheds. Last, I combined empirical observations of stream temperature, prey composition and energy density in diets, and growth rates of coastal cutthroat trout in a bioenergetics model to understand how thinning affected energetics and growth processes for these stream fish. In this analysis I combined reach-scale estimates of relative consumption and my network of temperature sensors to estimate growth potential at the watershed-scale. Collectively, in this dissertation I provide a watershed-scale evaluation of riparian thinning in forested watersheds where managers are interested in evaluating whether thinning may serve as a restoration strategy for second-growth riparian forests recovering from previous harvest and implications for aquatic systems and the species they support. Results from this research can help guide managers and other decision makers concerned with the potential costs and benefits of riparian thinning for stream ecosystems and the aquatic organisms that inhabit them.

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CHAPTER 2: CITATION INFORMATION

SHADE, LIGHT, AND STREAM TEMPERATURE RESPONSES TO RIPARIAN THINNING IN SECOND-GROWTH REDWOOD FORESTS OF NORTHERN CALIFORNIA

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This chapter is published in PLoS ONE

Published: February 21, 2021

https://doi.org/10.1371/journal.pone.0246822

Abstract

Resource managers in the Pacific Northwest (USA) actively thin second-growth forests to accelerate the development of late-successional conditions and seek to expand these restoration thinning treatments into riparian zones. Riparian forest thinning, however, may impact stream temperatures – a key water quality parameter often regulated to protect stream habitat and aquatic organisms. To better understand the effects of riparian thinning on shade, light, and stream temperature, we employed a manipulative field experiment following a replicated Before-After-Control-Impact (BACI) design in three watersheds in the redwood forests of northern California, USA. Thinning treatments were intended to reduce canopy closure or basal area within the riparian zone by up to 50% on both sides of the stream channel along a 100-200 m stream reach. We found that responses to thinning ranged widely depending on the intensity of thinning treatments. In the watersheds with more intensive treatments, thinning reduced shade, increased light, and altered stream thermal regimes in thinned and downstream reaches. Thinning shifted thermal regimes by increasing maximum temperatures, thermal variability, and the frequency and duration of elevated temperatures. These thermal responses occurred primarily during summer but also extended into spring and fall. Longitudinal profiles indicated that increases in temperature associated with thinning frequently persisted downstream, but downstream effects depended on the magnitude of upstream temperature increases. Model selection analyses indicated that local changes in shade as well as upstream thermal conditions and proximity to upstream treatments explained variation in stream temperature responses to thinning. In contrast, in the study watershed with less intensive thinning, smaller changes in shade and light resulted in minimal stream temperature responses. Collectively, our data shed new light on the stream thermal responses to riparian thinning. These results provide relevant information for managers considering thinning as a viable restoration strategy for second-growth riparian forests.

Introduction

Riparian forests provide numerous ecosystem functions for their associated stream and river systems (Gregory et al. 1991, Naiman et al. 2010). Due to these linkages, changes in riparian forest conditions can directly affect adjacent stream ecosystems (Warren et al. 2016).

After decades of unregulated timber harvest practices that removed riparian forests from forested landscapes in the Pacific Northwest (USA), riparian buffers now largely protect riparian forests (Broadmeadow and Nisbet 2004, Moore et al. 2005). As a result, buffer protections that limit forest harvest in riparian zones have successfully restored some key ecological functions (Broadmeadow and Nisbet 2004, Moore et al. 2005, Naiman et al. 2010). However, riparian management policies continue to vary by state, species presence (fish-bearing or not), and landownership, and their implementation tends to reflect the goal of administrative simplicity (i.e., uniform buffer widths) rather than taking into account local ecological context, all of which may limit their effectiveness (Olson et al. 2007, Richardson et al. 2012, Boijolie et al. 2019).

Riparian forests protected by buffers often reflect the legacy of past land-use (Foster et al. 2003). Dense, even-aged stands of early-seral species tend to dominate regenerating forests within riparian buffers and therefore these forests differ in structure and composition from the old-growth forests that preceded them (Pan et al. 2011, McIntyre et al. 2015). To address this, resource managers have expressed interest in more active management within riparian zones (Berg 1995, Carey 2003). For example, federal land managers in the Pacific Northwest are exploring the application of silvicultural methods such as selective logging and variable density thinning as restoration strategies to accelerate the development of late-successional forest structure and composition (Anderson et al. 2007). Moreover, managers are interested in understanding whether thinning accelerates the recovery of large conifers in riparian forests to provide an eventual source of large woody debris, promote riparian zone heterogeneity, and enhance aquatic and riparian biodiversity and productivity (Pollock et al. 2014, Benda et al. 2016, Reeves et al. 2016). As a result, there is a growing interest in thinning as a restoration strategy to address multiple objectives for second-growth riparian forests impacted by previous land-use.

Forest restoration is a key concern in the coast redwood forests (*Sequoia sempervirens*) of northern California. Only 3-5% of old-growth redwood forests remain in this region and have been largely replaced by dense second-growth stands often dominated by commercially-planted species such as Douglas-fir (*Pseudotsuga menziesii*) or early-successional species such as red alder (*Alnus rubra*) (Russell 2009, Keyes and Teraoka 2014). Resource managers actively thin these forests in an attempt to promote the recovery of old-growth redwood forests and increase heterogeneity of dense-second growth stands (O’Hara et al. 2010, Teraoka and Keyes 2011). To date, restoration thinning treatments have targeted upland forests, but as the composition and structure of second-growth riparian forests appear similarly affected by previous harvest (Russell 2009, Keyes and Teraoka 2014), there is interest in expanding thinning activities into riparian zones. However, given that changes in riparian forest conditions can affect adjacent stream ecosystems (Warren et al. 2016), it is important to understand the effects of riparian thinning on streams.

Changes in riparian forests can influence stream conditions in many ways, but the most immediate responses to canopy removal include changes in shading, solar radiation, and stream temperature (Moore et al. 2005). Stream thermal conditions are primary drivers of ecological processes in aquatic ecosystems (Magnuson et al. 1979, Caissie 2006). Large-scale reductions in riparian shade associated with historical timber harvest practices such as clearcutting frequently led to warming stream temperatures that exceeded the thermal tolerance of Pacific Northwest cold-water adapted stream fishes and amphibians (Brown and Krygier 1970, Johnson and Jones 2000, Moore et al. 2005). As a result, state and federal policies now limit the magnitude of change in stream temperature caused by land-use activity like timber harvest (Moore et al. 2005). Recent research suggests that contemporary forest management practices that include riparian buffers often effectively prevent temperature increases, although substantial variability and context dependence have been documented (Moore et al. 2005, Gomi et al. 2006, Groom et al. 2011, Janisch et al. 2012, Bladon et al. 2016).

Recent studies of stream temperature responses to contemporary forestry provide critical insights, yet many knowledge gaps remain surrounding the effects of forest thinning in riparian zones. First, in comparison to the information available on the effects of historical forestry practices (Moore et al. 2005), we know little about the effects of more subtle changes in shade and light associated with thinning second-growth riparian forests. Most studies to date have evaluated the effects of clearcutting with no buffer or riparian harvests outside of an untouched buffer (Moore et al. 2005, Anderson et al. 2007). In contrast, few studies have quantified the effects of thinning within riparian buffers near streams. Second, regulatory requirements focus on single descriptors of stream temperature (e.g., summer maxima), which may inadequately describe thermal influences on ecological processes (Steel et al. 2012). Recent studies that characterize stream temperature as a *thermal regime* including the magnitude, variability, duration, frequency, and timing have been effective in developing a more comprehensive understanding of stream thermal conditions (Poole et al. 2004, Arismendi et al. 2013a, Isaak et al. 2020). However, few studies have applied this approach to understand how stream thermal regimes respond to disturbance such as forest management (Steel et al. 2017).

In this study we evaluated the effects of riparian thinning on shade, light, and stream temperature in a manipulative field experiment following a Before-After-Control-Impact (BACI) study design (Underwood 1994) in three watersheds located in the second-growth redwood forests of northern California. The objectives of this study were to evaluate: 1) the effects of experimental riparian thinning treatments on shade and light conditions; 2) how changes in shade and light associated with thinning affected stream temperatures at a reach-scale both locally and downstream; 3) how thermal responses varied seasonally; and 4) how these thermal responses were expressed across the broader thermal regime to gain a more complete understanding of thinning on stream temperatures in these watersheds.

BACI designs are effective in detecting changes and have been applied in many similar experiments (e.g., Groom et al. 2011, Bladon et al. 2016). However, further investigation is needed to disentangle the environmental factors responsible for driving observed responses. Therefore, we also employed additional analyses to evaluate the underlying relationships hypothesized to influence stream heat budgets (Moore et al. 2005, Caissie 2006). For this series of analyses, we used correlation and model selection approaches (Burnham and Anderson 2002) to evaluate a suite of models to determine which best explained the variability in different descriptors of stream thermal regimes and their responses to thinning.

Methods

Study systems

We conducted this study in three watersheds located in the coast redwood forests of northern California (Figure 2.1). The West Fork Tectah and East Fork Tectah watersheds were located on private timber land owned by Green Diamond Resource Company and flow into the lower Klamath River. The Lost Man watershed was located in Redwood National Park and flowed into Prairie Creek, a major tributary to Redwood Creek. All three watersheds were drained by low-order streams (watershed areas 5.8 – 8.4 km^2) located within 15 km of the Pacific Ocean and experienced a temperate, maritime climate heavily influenced by coastal fog (Dawson 1998). Riparian forests bordering these streams were primarily composed of dense second-growth forests regenerating from timber harvest 40-60 years ago. Riparian canopies consisted of a mix of red alder, coast redwood, Douglas-fir, western hemlock (*Tsuga heterophylla*), tanoak (*Notholithocarpus densiflorus*), and western red cedar (*Thuja plicata*). Flow regimes in these systems are highly seasonal, driven by frequent coastal rainstorms that result in high flows during winter months followed by descending summer low flows supplemented by coastal fog, upwelling groundwater, and hyporheic flow (Welsh 2000). Resident populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), coastal giant salamander (*Dicamptodon tenebrosus*), and coastal tailed frog (*Ascaphus truei*) occupy these watersheds and are sensitive to increases in stream temperature (Huff et al. 2005, Bury 2008).

Experimental design

We collected data for this study as part of a manipulative field experiment following a replicated BACI design. We collected pre-treatment data in 2016, experimental thinning treatments occurred in 2017, and we collected post-treatment data in 2017 and 2018. We collected post-treatment riparian shade and light data in 2017 and 2018, but we limited the analysis of post-treatment stream temperature data to 2018 due to the staggered timing of the thinning treatments. Rather than establishing a control watershed as in many stream temperature studies (e.g., Groom et al. 2011, Bladon et al. 2016), to account for inherent spatial heterogeneity within and between watersheds all experimental thinning reaches (130-225 m in length) immediately bordered an upstream reference reach, similar to the design described in Groom et al. (2011). To determine the longitudinal persistence of local thermal responses associated with thinning we also monitored conditions in downstream reaches ~150-200 m in length. We replicated this three-reach design at 10 total sites distributed across these three watersheds (Table 2.1). We did not randomly select the study sites, so the results have limited inference to the Tectah and Lost Man watersheds, but may also apply to similar locations in the northern California redwood forests. Our sites sometimes occurred sequentially along the three stream channels and therefore not all sites were statistically independent. However, we included variables in our analysis to account for spatial non-independence.

The landowners included in this study followed distinct riparian thinning treatment prescriptions tailored to their management objectives.

In the Tectah watersheds on Green Diamond Resource Company property, thinning prescriptions intended to reduce overstory canopy closure within the riparian zone to 50% on both sides of the channel along a ~200 m stream reach. Thinning treatments targeted red alder and some conifers depending on the composition and density of the stand, but left all large conifers that would contribute as an eventual source of large woody debris. Thinning treatments occurred next to upslope timber harvest units and trees were removed from the riparian zone via cable yarding. Upstream reference and downstream reaches were bordered by either intact forest on both sides of the stream channel or, when within harvest units, by intact forest on one side and a riparian buffer following Green Diamond's standard buffer prescription on the harvest side of the stream. The one-sided buffer prescription consisted of 45 m wide buffer with a 22.5 m inner zone of 85% canopy retention and a 22.5 m outer zone of 70% canopy retention as prescribed by Green Diamond's Aquatic Habitat Conservation Plan with the National Marine Fisheries Service and United States Fish and Wildlife Service (Green Diamond Resource Company 2006). Although upstream and downstream reaches occurred both inside and outside harvest units, we documented no difference in shade, light, and stream temperature conditions in an analysis of reference reach types, allowing us to group them together (File A2.1).

In the Lost Man watershed in Redwood National Park (RNP) riparian thinning treatments coincided with a larger upland forest restoration thinning effort in the Middle Fork of the Lost Man Creek watershed (Redwood National Park 2014). Riparian thinning treatments sought to remove up to 40% of the basal area within the riparian zone on slopes less than 20% on both sides of the channel along a ~100-150 m reach. Riparian thinning treatments primarily targeted Douglas-fir and red alder to achieve RNP's objective of promoting the recovery of late-successional coast redwood forests (Teraoka and Keyes 2011). While thinning treatments removed trees from upland forests, trees within the riparian zone were felled following a lop-and-scatter protocol which left trees in the riparian zone but out of the stream channel.

Riparian shade

We measured riparian shade over the stream channel using hemispherical photography following the methods described in Ringold et al. (2003). We took hemispherical photographs with a Canon EOS 70D digital camera (Canon Inc., Tokyo, Japan) equipped with a circular fisheye lens attached to a leveled tripod and oriented to north. To characterize shade within upstream reference, thinned, and downstream reaches during leaf-out conditions, we took photographs mid-summer each year 1 m above the stream channel every 10 m at mid-bankfull width (n = 10-22 photographs/reach). We took photographs early in the morning and under a range of exposures to ensure that direct sunlight would not interfere with shade characterization. We analyzed photographs in HemiView Canopy Analysis Software version 2.1 (Delta-T Devices 1998), which classifies light and dark pixels to quantify shade. In HemiView, we selected two output metrics to characterize riparian shade: 1) canopy closure – which considers the total amount of shade in the entire photograph using the formula: Canopy Closure (%) = (1-VisSky)*100, where VisSky represents the total number of "open" pixels visible to the sky; and 2) effective shade – which considers the amount of shade that covers the solar pathway over that location using the formula: Effective Shade (%) = (1-GSF)*100, where GSF (Global Site Factor) is the number of "open" pixels within the path of the sun.

Light

We measured solar radiation reaching the stream channel using silicon pyranometers (Onset Solar Radiation Smart Sensor, Onset Computer Corporation, Bourne, MA USA), which detect a broad spectrum of light (300 – 1100 nm). To measure the amount of solar radiation available above the forest canopy, we deployed a weather station equipped with a pyranometer attached to an Onset Micro Station (Onset Computer Corporation, Bourne, MA USA) on a ridge nearby each watershed. To measure the amount of solar radiation that filters through the canopy to the stream in upstream reference, thinned, and downstream reaches mid-summer, we deployed four pyranometers within each reach at 25 m intervals 1 m above the stream attached to a central Onset Micro Station for 24 hours during the same time of year that we took hemispherical photographs. Pyranometers recorded solar radiation hourly during this 24-hour window. We expressed the amount of light that filtered through the canopy to the stream as a percentage of the amount of above-canopy light available.

Stream temperature

We measured stream temperatures using digital temperature sensors (a combination of Onset Hobo Water Temperature Pro v2 and TidbiT Water Temperature Data Loggers, Onset Computer Corporation, Bourne, MA USA). Before deployment we checked that all sensors were properly calibrated following Heck et al. (2018). We protected sensors from solar radiation using solar shields constructed from 5 cm diameter polyvinyl chloride (PVC) pipe ~13cm in length. We anchored sensors to the streambed using Duckbill Earth Anchors (MacLean Civil Products, Fort Mill, SC, USA) modified with 5mm diameter vinyl-coated galvanized steel cables in gravel and cobble dominant habitats or with waterproof epoxy (Pettit Splash Zone Marine Epoxy, Pettit

Paint, Rockaway, NJ, USA) in habitats where bedrock or large boulders predominated. We deployed temperature sensors at the upstream and downstream extent of upstream reference, thinned, and downstream reaches. We deployed sensors in the Tectah watersheds in fall of 2015 and in the Lost Man watershed in spring of 2016. We then monitored stream temperature hourly through the end of the 2018 water year.

To develop a more comprehensive understanding of how thinning influenced stream thermal regimes, we characterized stream temperature responses using a suite of descriptors described in Arismendi et al. (2013a) and Benjamin et al. (2016). To determine the extent to which temperature increased, we used the following descriptors of magnitude: average daily maximum, the maximum weekly average of the maximum (MWMT), average daily mean, the maximum weekly average of the mean (MWAT), cumulative seasonal degree days, and average daily minimum. To determine how the distribution and spread of stream temperature changed, we used the following descriptors of variability: average daily range, maximum daily range, average variance, and maximum variance. To determine the temporal frequency and duration of these temperature changes above common regulatory cold-water thresholds (Benjamin et al. 2016, Groom et al. 2017), we used the following frequency and duration descriptors: number of days where daily temperature > 16°C, the number of consecutive days > 16°C, the number of days > 20°C, and the number of consecutive days > 20°C. To determine the timing of temperature responses, we noted the seasonal occurrence during the water year (Fall, Winter, Spring, Summer). In order to calculate these descriptors, hourly temperature data were summarized as daily values. Daily values were then summarized seasonally for all responses described above. We defined seasonal windows by the start of the water year (Oct 1 – Sep 30) and by the inherent seasonal patterns of thermal conditions in these streams: Fall (Oct 1 – Dec 31), Winter (Jan 1 – Mar 31), Spring (Apr 1 – Jun 30), and Summer (Jul 1 – Sep 30).

Data analyses

Due to the differences in thinning treatment prescriptions we evaluated Tectah and Lost Man separately for each analysis. Because temperature sensors were deployed in the spring of 2016 in the Lost Man watershed, we limited before-after analyses for Lost Man to spring and summer unless specified. All analyses were conducted in R (R Core Team 2020).

BACI analysis

We conducted a classic BACI analysis (Underwood 1994) to evaluate the effects of thinning on riparian shade, light, and stream temperature using linear mixed-effects models (Zuur et al. 2009) in the nlme package in R (Pinheiro et al. 2020). To do this, we used mean estimates of response variables for upstream reference, thinned, and downstream reaches from our pre-treatment and post-treatment years using the fixed-effects model:

BACI model: Response Variable ~ Reach + Year + Reach*Year + ε

This BACI model tests whether the response variable is explained by Reach (upstream reference vs. thinned vs. downstream), Year (pre-treatment vs post-treatment), and the interaction of Reach*Year (BACI effect). Under this design, a significant BACI effect of Reach*Year effect indicates an effect of thinning ($\alpha = 0.05$). To account for the variation between sites, we included a random intercept by Site and a weights argument to relax the assumption of constant variance among Reaches and Years (Zuur et al. 2009). Remaining unexplained error is represented by ε. We then estimated BACI differences for thinned and downstream reaches following the formulas:

BACI difference for thinned reaches: $(\text{Thinned}_{Post} - \text{Thinned}_{Pre}) - (\text{Upstream}_{Post} - \text{Upstream}_{Pre})$

BACI difference for downstream reaches: $(\text{Downstream}_{Post} - \text{Downstream}_{Pre}) - (\text{Upstream}_{Post} - \text{Upstream}_{Pre})$

We estimated the BACI differences and 95% confidence intervals. If 95% confidence intervals did not overlap 0, we considered the effect to be statistically significant. We checked the residuals for all BACI models to make sure we met assumptions of constant variance and normality (Zuur et al. 2009).

Longitudinal profiles

We plotted reach-scale longitudinal profiles of MWMT following the methods described in Arismendi and Groom (2019) to visualize how local temperature increases associated with thinning propagated downstream. To do this, we set the pre-post difference in temperature (MWMT) for the sensor at the upstream end of the upstream reference reach to 0 to standardize comparisons of temperature responses between sites for upstream, thinned, and downstream reaches. We then repeated longitudinal profiles of each site for each season to visualize seasonal variability of temperature responses in thinned and downstream reaches.

Multivariate analyses of thermal regimes

We applied multivariate analyses to evaluate how the structure of stream thermal regimes responded to thinning. We used non-metric multidimensional scaling (NMS) ordination to visualize how the structure of the entire thermal regime (including multiple descriptors for magnitude, variability, duration, and frequency) varied. To do this, we created a matrix for selected descriptors (n = 16) of our stream thermal regimes for all reaches and sites for our pre-treatment and post-treatment years for each season (n = 220 total combinations). We then ran NMS ordinations using a Euclidean distance measure that followed an iterative optimization procedure (n = 999 times) (Arismendi et al. 2013a). We checked the final solution against goodness of fit tests and for overall stress and displayed the results in two dimensions. We added ellipses indicating the 95% confidence intervals for each reach (upstream reference vs. thinned vs. downstream) to indicate how the structure of thermal regimes varied between reaches during each season. We then applied permutational multivariate analysis of variance (PerMANOVA) to test whether the structure of stream thermal regimes differed due to thinning indicated by a significant BACI effect of Reach*Year ($\alpha = 0.05$). All multivariate analyses were conducted in the vegan package in R (Oksanen et al. 2019).

Environmental factors

We further explored the environmental factors driving the variation in thermal responses associated with thinning by evaluating the role of shade, light, and other environmental covariates. First, we related BACI responses in summer MWMT to the responses in shade and light associated with thinning for all sites. Second, we evaluated the correlations between summer MWMT and environmental covariates frequently considered in stream temperature studies (Moore et al. 2005, Caissie 2006, Groom et al. 2011, Janisch et al. 2012). Environmental covariates included: shade, light, upstream temperatures, air temperature, proximity to upstream treatments, as well as physical site characteristics such as distance upstream, reach length, bankfull width, gradient, aspect, and elevation. See Table A2.2 for more detailed descriptions of the environmental covariates we considered. Correlations were assembled in a correlation matrix using the corrplot package in R (Wei and Simko 2017).

Model selection

To better understand the factors driving the variability in different descriptors of stream thermal regimes and their responses to thinning, we applied a model selection approach following the methods provided by Burnham and Anderson (2002) and Zuur et al. (2009). Model selection focused on summer conditions when most covariates were available. We used a correlation matrix to guide the fixed effects we included in our candidate models and avoided covariates that were highly correlated ($r > 0.6$) or represented similar ecological processes (Figure A2.1). We also checked variance inflation factor scores of the variables within candidate models to ensure that multicollinearity did not occur between variables. Starting with a "beyond optimal" fully overparameterized model we selected a random effects structure. Random effects were fit using Restricted Maximum Likelihood. We then ranked candidate sets of *a priori* models exploring different fixed effects using AIC_c values in the AICcmodavg package in R (Mazerolle 2020). Fixed effects models were fit using Maximum Likelihood. The best supported model determined by the lowest AIC_c value was then refit with Restricted Maximum Likelihood to obtain unbiased parameter estimates. We checked the residuals for all best supported models to make sure we met assumptions of constant variance and normality for fixed and random effects (Zuur et al. 2009). See Table A2.2 for the full list of models considered in candidate model sets. Best supported models for each response variable are listed in Table A2.3.

Results

BACI analysis - riparian shade

Pre-treatment estimates of riparian shade in 2016 indicated uniformly high levels of canopy closure and effective shade across all three reach types (upstream reference, thinned, and downstream) and did not differ among reaches in the Tectah or Lost Man watersheds (Figure 2.2). Post-treatment estimates in 2017 and 2018 indicated that riparian thinning treatments decreased riparian shade, but the extent of reductions varied between watersheds (Figure 2.2, Table A2.1). In the Tectah watersheds, BACI models indicated that riparian shade decreased significantly in thinned reaches as canopy closure by a mean of 18.7% (95% confidence intervals: -21.0, -16.3) in 2017 and 16.9% (-19.2, -14.6) in 2018 and as effective shade by a mean of 25.4% (-28.6, -22.3) in 2017 and 23.0% (-25.8, -20.1) in 2018 (Figure 2.2, Table A2.1). In the Lost Man watershed, effective shade decreased in thinned reaches by a mean of 4.8% (95% confidence intervals: -8.0, -0.5) in 2017 and 4.1% (-8.3, -0.3) in 2018, but BACI models determined that reductions in canopy closure (-2.1% in 2017 and -1.9% in 2018) were not significant in either year (Figure 2.2, Table A2.1).

BACI analysis - light

Pre-treatment estimates of below-canopy light in 2016 documented that only a small portion of the overall solar radiation available (~6%) filtered through the canopy to the stream channel and did not differ among reaches in the Tectah or Lost Man watersheds (Figure 2.2). Post-treatment estimates in 2017 and 2018 indicated that riparian thinning increased below-canopy light, but the intensity of responses varied between watersheds (Figure 2.2, Table A2.1). In the Tectah watersheds, BACI models indicated that below-canopy light increased significantly in thinned reaches by a mean of 33.0% (95% confidence intervals: 27.3, 38.5) in 2017 and 27.1% (20.4, 33.8) in 2018 (Figure 2.2, Table A2.1). In the Lost Man watershed, we observed below-canopy light increase slightly in thinned reaches by a mean of 2.9% (-0.7, 6.5) in 2017 and 2.5% (-1.6, 5.6) in 2018, but BACI models determined that these increases were not statistically significant (Figure 2.2, Table A2.1).

BACI analysis - stream temperature

Stream temperatures varied seasonally for each descriptor of the thermal regime we considered (magnitude, variability, frequency, and duration) during the pre-treatment water year, but did not differ between reaches for any descriptor (Figure 2.3).

Riparian thinning increased the magnitude of stream thermal regimes in thinned and downstream reaches, but responses varied seasonally and between watersheds (Figure 2.3, Tables 2.2 and 2.3). In the Tectah watersheds, BACI models indicated that responses in magnitude were most pronounced as changes in maximum temperatures, which increased MWMT in thinned reaches during spring by a mean of 1.7°C (95% confidence intervals: 0.9, 2.5), summer by a mean of 2.8°C (1.8, 3.8), and fall by a mean of 1.0°C (0.5, 1.5) and increased in downstream reaches during spring by a mean of 1.0°C (0.0, 2.0) and summer by a mean of 1.4°C (0.3, 2.6) (Tables 2 and 3, Table A2.1). BACI models indicated that thinning increased mean temperatures as MWAT and cumulative seasonal degree days in thinned reaches during spring (MWAT: 0.5°C; degree days 18.6°C) and summer (MWAT: 0.9°C; degree days: 77.7°C) and in downstream reaches during summer (MWAT: 0.6°C; degree days: 48.1°C) (Tables 2.2 and 2.3, Table A2.1). We observed no change in minimum temperatures (Figure 2.3, Tables 2.2 and 2.3). In the Lost Man watershed, BACI models indicated no effect of thinning on stream temperatures in thinned or downstream reaches for any descriptor of magnitude during any season (Tables 2.2 and 2.3, Table A2.1).

Thinning increased thermal variability in thinned and downstream reaches, but responses varied between seasons and watersheds (Figure 2.3, Tables 2.2 and 2.3). In the Tectah watersheds, BACI models indicated that increases in thermal variability in thinned reaches were most pronounced during summer increasing the daily range by a mean of 2.5°C (95% confidence intervals: 1.6, 3.4) and variance by a mean of 1.6°C (0.7, 2.5), but also increased during spring (daily range: 0.5°C; variance: 0.3°C) and fall (daily range: 0.4°C; variance: 0.1°C) (Table A2.1). Increases in thermal variability in downstream reaches were limited to summer (daily range: 0.7°C; variance: 0.5°C) (Table A2.1). In the Lost Man watershed, BACI models indicated no effect of thinning on thermal variability in thinned or downstream reaches (Table A2.1).

Thinning increased the frequency and duration of warm water events in thinned and downstream reaches, but responses occurred exclusively in the Tectah watersheds (Figure 2.3, Tables 2.2 and 2.3). The frequency of days with temperatures greater than 16°C increased in summer by a mean of 42.9 more days (95% confidence intervals: 31.5, 53.8) in thinned reaches and a mean of 16.3 more days (6.1, 27.4) in downstream reaches (Tables 2.2 and 2.3). Temperatures greater than 16°C persisted for a mean duration of 31.1 more consecutive days (21.0, 41.1) in thinned reaches and 11.6 more consecutive days (3.9, 20.0) in downstream reaches (Tables 2.2 and 2.3). Responses in frequency and duration occurred earlier in the year, starting in spring in both thinned and downstream reaches (Tables 2.2 and 2.3). Temperatures exceeded 20°C in two of the eight sites in the Tectah watersheds. Within these locations, the WFT1_low site temperatures exceeded 20°C for a period of 30 days and 14 consecutive days, while the WFT2_up site exceeded 20°C for a period of 3 days.

Longitudinal profiles

Reach-scale longitudinal profiles indicated that local temperature responses associated with thinning frequently persisted into downstream reaches, but the extent of downstream responses reflected the magnitude and timing of local increases (Figure 2.4). In the Tectah watersheds, local increases in temperature were highest in the summer in all sites, followed by spring and fall, and lowest in the winter (Figure 2.4). Downstream trajectories varied in direction where in some sites temperatures remained elevated at the downstream extent of the downstream reach (e.g., EFT1_up, EFT2, WFT1_low, WFT1_up, WFT2_up, and WFT3), whereas in other sites local increases recovered to its initial state at the downstream extent of the downstream reach (e.g., EFT1_low, WFT2_low). In contrast, Lost Man sites showed no to minor responses in temperature in thinned or downstream reaches during any of the four seasons (Figure 2.4).

Multivariate analyses of thermal regimes

NMS ordinations indicated that thinning shifted the structure of stream thermal regimes in thinned and downstream reaches, but the extent of these shifts varied seasonally and between watersheds (Figure 2.5). Shifts in the structure of thermal regimes were observed in the Tectah watershed during the post-treatment year in thinned and downstream reaches, but did not change in the Lost Man watershed (Figure 2.5). Shifts occurred primarily during summer, but were also visible to a lesser extent during fall and spring. No change in the structure of stream thermal regimes was evident during winter. PerMANOVA tests partially supported the patterns in NMS ordinations and documented that the structure of stream thermal regimes differed in the Tectah watersheds in summer, but not in Lost Man during any season (BACI effect: $p < 0.05$) (Figure 2.5).

Environmental factors

Across all watersheds, the magnitude of stream temperature responses to thinning were associated with the extent of changes in shade and light (Figure 2.6). However, the strength of these relationships varied between watersheds. In the Tectah watersheds, summer MWMT correlated strongly with shade (r = -0.75) and light (r = 0.76) as well as upstream temperatures (r = 0.51) and proximity to upstream treatments (r = 0.56) (Figure A2.1). In the Lost Man watershed, summer MWMT did not correlate with shade or light, but did correlate with air temperature (r = 0.91), upstream temperatures (r = 0.73) as well as physical site characteristics such distance upstream (r = -0.91), bankfull width (r = 0.80), gradient (r = 0.81), aspect (r = -0.77), and elevation (r = -0.89), although many of these variables correlated with one another (Figure A2.1).

Model selection

The AIC_c model selection process indicated that distinct models explained the variation in thermal conditions in each watershed. In the Tectah watersheds, models that included continuous estimates of riparian shade and upstream thermal conditions consistently ranked at the top of candidate sets for all temperature descriptors considered (Table A2.2). In addition to riparian shade and upstream temperatures, proximity to upstream treatments appeared as an important variable for MWAT, degree days, and variance (Table A2.2). Gradient appeared in the top models for degree days, daily range, and variance (Table A2.2), but otherwise physical variables contributed little toward explaining model variance. In the Lost Man watershed, no single variable consistently ranked at the top of candidate model sets and the null (intercept) model often parsimoniously outperformed other variables in explaining model variation for many descriptors (Table A2.2). Exceptions to this were for MWAT and degree days which indicated that gradient and upstream temperatures provided slightly better explanations than the null model (Table A2.2). For all watersheds, best supported models ranked substantially higher than the BACI model of Reach*Year, which frequently ranked towards the bottom of the candidate sets of the models we considered (Table A2.2).

Discussion

In this study we found that responses to the experimental riparian thinning treatments we evaluated differed greatly depending on treatment intensity. In the Tectah watersheds where thinning treatments were more intensive the reductions in shade and increases in light were sufficient to shift stream thermal regimes in thinned and downstream reaches. Thinning treatments were less intensive in the Lost Man watershed, resulting in small changes in shade and light that had minimal influence on stream temperatures. These results suggest that riparian thinning can influence thermal conditions of small streams both locally and further downstream, but the extent of the thermal responses depend on the amount of shade lost and light gained.

Riparian shade and light responses to thinning varied strongly between watersheds. Reductions in riparian shade were five to six times more intensive in the Tectah watersheds versus Lost Man and increases in light were nine to ten times more intensive. BACI models supported these patterns indicating significant reductions in shade and increases in light in the Tectah watersheds, yet the less intensive treatments in the Lost Man watershed were only significant as effective shade. Although all thinning treatment prescriptions targeted a 40-50% reduction in canopy closure or basal area, estimates of riparian shade and light indicated much smaller overall, yet more variable changes over the stream channel. This discrepancy could be due to the fact that thinning prescriptions were made from within the riparian forest and not over the stream. Alternatively it could be due to differences in prescription methods where targets based on canopy closure resulted in larger changes in shade and light whereas targets based on basal area resulted in smaller changes. Slope restrictions in the steep Lost Man watershed (no thinning on slopes greater than 20%) likely provided additional constraints to the implementation of thinning treatments. Although the thinning treatments included in this study were not consistent across the study watersheds, this range in treatment intensity provided a broad range of conditions for us to evaluate.

Stream temperature responses to thinning reflected the magnitude of changes in shade and light, ranging widely between watersheds. In the Tectah watersheds where treatment intensity was higher, BACI models indicated that thinning treatments altered stream temperatures in thinned and downstream reaches across multiple descriptors of the thermal regime and these responses extended over multiple seasons. In contrast, BACI models indicated that stream temperatures did not change in the Lost Man watershed in thinned or downstream reaches for any descriptor or any season.

Overall, the temperature responses to thinning observed in this study were lower than previously documented responses to historical timber harvest practices which often clearcut forests to the stream edge (Brown and Krygier 1970, Johnson and Jones 2000, Moore et al. 2005). Instead our results coincided more closely to stream temperature responses observed with contemporary forest management practices that include riparian buffers which have often resulted in smaller, yet more variable temperature increases (Gomi et al. 2006, Groom et al. 2011, Janisch et al. 2012, Bladon et al. 2016). Variation in temperature responses in these contemporary studies tends to be associated with riparian buffer width where undetectable to small changes in temperature coincided with wider buffers (Gomi et al. 2006, Groom et al. 2011) or riparian buffers of various widths adjacent to upland thinning (Anderson et al. 2007, Leach et al. 2017), whereas larger increases in stream temperatures were more likely to occur with narrower buffers adjacent to upland clearcutting (Gomi et al. 2006, Groom et al. 2011).

Few comparable analyses of forest thinning within riparian buffers exist in the literature. However, a study by Rex et al. (2012) found that variable-retention treatments within riparian buffers in British Columbia that reduced riparian shade between 30 and 50% increased MWAT by 3°C and MWMT by 5-6°C, both higher than documented in our study. Studinski et al. (2012) found that thinning treatments that targeted a 50% reduction in basal area in some West Virginia streams resulted in a similar reduction in canopy closure to the treatments in the Tectah watersheds, yet resulted in much smaller increases (0.2-0.5°C/100m) than what we observed and were more in line with the responses documented in Lost Man. Another study in Minnesotan boreal streams found that their most intensive thinning treatment resulted in a 10% reduction in canopy closure but increased summer maximum temperatures by ~4°C (Kreutzweiser et al. 2009). These studies highlight that the magnitude of responses to thinning are often system dependent, making broader-scale generalizations challenging.

Local temperature responses to thinning were not limited to thinned reaches and effects frequently extended into downstream reaches. Downstream effects reflected the magnitude and timing of upstream temperature increases and were typically ~50% of the response observed in respective thinned reaches, similar to results observed by Davis et al. (2016) ~300 m downstream of harvest. Longitudinal profiles revealed three distinct downstream trajectories at the reach scale, with temperature remaining elevated 150 to 200 m downstream, dissipating either partially or completely, or remaining undetectable where minimal change occurred upstream (e.g., Lost Man). Downstream effects sometimes propagated beyond the extent of the downstream reach and into adjacent sites where sequentially located. Subsequent temperature responses were more likely to be elevated, which suggests the potential for cumulative heating in cases where harvests are spaced closer together. These patterns suggest that local temperature within our sites were not independent from upstream sites and that there was a high degree of longitudinal connectivity in these streams (Ward 1989, Moore et al. 2005). Although we limited our analysis to immediate reach-scale responses in downstream effects ~150-200 m downstream from thinning treatments, we recognize that in some reaches the spatial extent of downstream effects likely extended further (Davis et al. 2016, Arismendi and Groom 2019). For example, Wilzbach et al. (2005) documented that local increases in temperature associated with complete canopy removal along a 100 m reach persisted up to 430 m downstream.

Thermal responses to thinning exhibited strong seasonal variation, although the extent of seasonal dependence varied between watersheds. For all watersheds, temperature responses were greatest in summer, which coincided with the period of low flows in these watersheds (Arismendi et al. 2013b). However, in the Tectah watersheds where thinning treatments were more intensive, thermal responses extended beyond summer into spring and fall, consistent with findings from Washington State (McIntyre et al. 2018). In the Tectah watersheds, multi-seasonal responses were most evident for MWMT, daily range and variance, whereas responses of other descriptors and downstream reaches were limited to summer months. Temperature exceedances over common cold-water thresholds were primarily limited to summer months similar to patterns observed in McIntyre et al. (2018) although a few sites also exceeded 16°C in the spring. We did not observe treatment effects in the winter. Winters in these coastal systems are characterized by high flows and weak solar radiation filtered by dense clouds and coastal fog, which would likely limit the influence of any differences in canopy conditions associated with thinning (Caissie 2006). Most temperature studies focus their analyses on summer conditions and so few attempt to quantify the seasonality of thermal responses. By collecting year-round data we successfully tracked not just the magnitude of thermal responses to thinning, but also the timing and temporal duration of those changes. Given that thermal regimes naturally fluctuate seasonally in the Pacific Northwest (Leach et al. 2017), a better understanding of the timing and temporal duration of these changes provide important information for managers when considering the effects on sensitive aquatic species.

Our multivariate analyses effectively captured the multidimensional local and downstream shifts in the structure of stream thermal regimes due to thinning. Similar to other analyses, multivariate responses varied between watersheds. In the Lost Man watershed, we detected no structural changes in stream thermal regimes. However, in the Tectah watersheds we observed that shifts in thermal regimes within thinned and downstream reaches that peaked in summer, but also were observed to a lesser extent during spring and fall, whereas all sites were similar in winter. Our results align with recent efforts to better characterize thermal regimes (Poole et al. 2004, Isaak et al. 2020) and how they may shift to disturbances such as wildfire (Koontz et al. 2018). These studies highlight that thermal responses to disturbance are not limited to single descriptors (e.g., summer maxima) but can shift in multiple directions. Although specific descriptors of magnitude such MWMT and MWAT are important for regulatory purposes (Bladon et al. 2016, Steel et al. 2017), other descriptors such as changes in thermal variability and the frequency and duration of those changes may have more relevance for affecting ecological processes and aquatic species in streams (Steel et al. 2012, Benjamin et al. 2016). A thermal regime approach as applied here provided additional value as a more holistic evaluation of overall thermal changes not possible by relying on individual descriptors alone (Arismendi et al. 2013a, Isaak et al. 2020).

Analyses that further explored the environmental factors driving the variation in stream thermal regimes and their responses to thinning observed distinct sets of drivers in each watershed. In the Tectah watersheds, variation in thermal responses appear to be largely driven by reductions in riparian shade and increases in light. Correlation analyses revealed that the intensity of temperature responses in thinned reaches was strongly associated with the amount of shade lost and light gained following the thinning treatments. Model selection analyses supported this pattern finding that including continuous estimates of shade more effectively captured the variation in thermal responses that the categorical variables in the BACI model could not. These results align with the findings of Johnson (2004) and Cassie (2006) that solar radiation is a primary driver of energy budgets in small streams. In contrast neither shade nor light were primary drivers of temperature responses in the Lost Man watershed. This is likely because thinning treatments did not increase solar radiation enough to affect stream temperatures. Alternatively, the pervasive groundwater and hyporheic flow in this watershed could have mediated the influence of any increased solar radiation from thinning treatments on stream temperatures.

In addition to local changes in shade and light, our model selection results indicated that upstream thermal conditions and proximity to upstream treatments explained additional variation in thermal responses in the Tectah watersheds. These results suggest that thermal responses depended on both longitudinal advective processes as well as local radiative processes of heat transfer (Moore et al. 2005). Groom et al. (2011) also documented that upstream thermal conditions act as an important driver of thermal responses to contemporary forest management practices in western Oregon. Our correlation analyses corroborated these results, finding that local temperature response in thinned reaches strongly correlated with upstream temperatures and proximity to upstream treatments. Best supported models sometimes included physical site characteristics such as gradient and reach length, but this was not consistent for all descriptors. Inclusion of these variables suggests that the physical dimensions of study sites only sometimes helped explain thermal responses to thinning, a finding not supported by other stream temperature studies (Janisch et al. 2012).

Although the correlation analysis for the Lost Man watershed indicated that stream temperature correlated with multiple covariates including upstream temperatures and physical site characteristics, the results from the model selection suggests that these covariates poorly explained the variation in stream thermal conditions in this watershed. Our model selection analysis found the null (intercept) model to be the best explanation for multiple temperature descriptors. Although other covariates such upstream temperatures and gradient ranked as the best supported model for two descriptors, they barely outperformed the null model. These results suggest that either the covariates we considered poorly represented the thermal conditions in the Lost Man watershed or that thermal conditions in this watershed did not vary much on their own and so there was little variation to model.

Management implications

Riparian forests in the Pacific Northwest have been extensively altered by past timber harvest practices and managers now face the challenge of restoring the desirable ecological functions that riparian forests provide as they continue to recover (Sibley et al. 2012). Managers have leaned towards passive strategies in the past, but these strategies can take centuries to work (Martens et al. 2019). As a result, there is growing interest in the application of active management approaches like thinning to help accelerate the recovery of these forests (Berg 1995, Carey 2003). However, trade-offs can emerge between the long-term benefits of restoring riparian forests and the potential short-term impacts to streams. From an adaptive management perspective, experimental data provide unique information for resource managers to address existing knowledge gaps surrounding the effects of partial canopy removal associated with thinning (Stankey et al. 2003). We believe our study offers useful insight to managers interested in thinning as a riparian restoration tool. However, a more comprehensive understanding of riparian thinning's effectiveness will also require additional research.

First, we observed that changes in shade of 5% or less caused minimal changes in temperature while reductions in shade of 20-30% resulted in much larger increases in temperature. Therefore, managers could set thinning prescriptions to strike a balance between minimizing increases in temperature while also achieving riparian restoration objectives. Future studies could examine thinning treatments at a more comprehensive range of intensities, including more intermediate intensities, to help determine how much forests can be thinned without impacting stream temperatures.

Second, we observed that thinning increased downstream temperatures and that incoming thermal conditions and proximity to upstream treatments helped explain the variation of the temperature responses. Therefore, it is important to consider the longitudinal spacing between treatments to control absolute stream temperatures. Further research needs to establish how far downstream temperature responses can travel (Davis et al. 2016). This information would be useful for developing treatment spacing guidelines for avoiding potential cumulative effects (Reid 1998).

Third, we only evaluated immediate responses one year post-treatment and questions remain about the duration of these responses as forests recover over time. Other studies have found that post-treatment increases in temperature often peak one to two years post-treatment (Groom et al. 2017, Arismendi and Groom 2019). Future research needs to monitor the length of time necessary for the riparian canopy to fill in and for stream temperatures to recover.

Fourth, this study was conducted in three small coastal streams (watershed areas <10 km^2 all within 15 km of the Pacific Ocean), and as a result our scope of inference is limited to the study watersheds, but may also apply to systems with comparable characteristics. More examples of riparian thinning are needed from a wider range of stream sizes, underlying lithologies, flow regimes, geomorphologies, climates, and other factors that can lead to the context dependency so frequently observed in stream temperature studies. Observations from more locations under a broader range of conditions would improve our understanding of the intensity and spatial frequency of riparian thinning for achieving restoration goals for second-growth riparian forests.

Finally, the changes in stream temperature documented here have broad, complex ecological implications for the aquatic species that occupy these watersheds (Magnuson et al. 1979). Future studies could establish the lethal and sublethal effects that the thermal responses observed here may have on cold-water adapted species such as stream fish or amphibians (Huff et al. 2005, Bury 2008).

Conclusions

From the experimental riparian thinning treatments evaluated in this study, we found that the responses to thinning ranged widely depending on the intensity of treatment. In the Tectah watersheds where thinning treatments were more intensive, reductions in shade and increases in light were sufficient to shift stream thermal regimes locally and in downstream reaches across multiple seasons. However, in the Lost Man watershed where thinning treatments were less intensive, small changes in shade and light resulted in minimal changes to stream temperatures. These results suggest that thinning within riparian zones in second-growth redwood forests may be a feasible restoration strategy without impacting stream temperatures when conducted less intensively. Collectively, this study provides new insights into the effects of riparian thinning on reach-scale responses of shade, light, and stream thermal regimes. The results from this study provide relevant information for managers to help guide decisions about whether and how much thinning may be applied to restore second-growth riparian forests recovering from previous harvest.

Acknowledgements

We thank the project stakeholders and landowners Green Diamond Resource Company and Redwood National Park for guiding the questions addressed in this research, implementing the experimental treatments, and providing access to the study watersheds. We appreciate the funding support provided by Green Diamond Resource Company, Save the Redwoods League, and the Department of Fisheries and Wildlife at Oregon State University. The project depended upon the help of OSU field technicians and aquatic biologists at Green Diamond Resource Company for assistance with field work. Thanks to Bret Harvey, Dede Olson, Matt Kaylor, and two anonymous reviewers for providing constructive feedback that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 2.1. Study site characteristics.

Watershed	Site ID	Distance Upstream (m)	Reach Length (m)	Bankfull Width (m)	Aspect (°)	Gradient (%)	Elevation (m)
West Fork Tectah	WFT1_lower	140	225	6.6	75	1.4	351.3
	WFT1_upper	535	175	6.0	90	2.2	359.2
	WFT2_lower	2750	205	4.7	350	2.9	409.0
	WFT2_upper	3320	195	3.7	15	3.2	429.2
	WFT3	3840	220	3.2	25	6.4	456.5
East Fork Tectah	EFT1_lower	450	195	5.3	310	3.9	363.5
	EFT1_upper	990	170	6.1	325	5.3	385.5
	EFT2	1850	225	4.6	345	3.8	421.3
Lost Man	LM1	1450	130	4.5	220	2.8	357.8
	LM2	2300	140	4.1	275	3.1	368.8

Physical site characteristics of experimental thinning reaches (n=10) distributed across three study watersheds – West Fork Tectah, East Fork Tectah, and Lost Man in northern California second-growth redwood forests. Distance Upstream indicates watershed position as distance upstream (in meters) from the confluence.

Table 2.2. Stream thermal regime responses in thinned reaches.

Temperature Response (Δ°C)	Watershed	Fall	Winter	Spring	Summer
Magnitude					
Daily Maximum	Tectah:	1.4 (1.0, 1.8)	0.1 (-0.1, 0.2)	1.7 (1.1, 2.3)	2.9 (2.1, 3.6)
	Lost Man:	0.1 (0.1, 0.2)	0.1 (0.0, 0.1)	0.4 (0.1, 0.6)	0.3 (0.1, 0.5)
MWMT	Tectah:	1.0 (0.6, 1.4)	-0.1 (-0.1, 0.1)	1.6 (1.0, 2.2)	2.7 (2.0, 3.4)
	Lost Man:	0.1 (-0.1, 0.1)	0.1 (0.0, 0.1)	0.1 (-0.2, 0.5)	0.2 (-0.1, 0.4)
Daily Mean	Tectah:	0.0 (-0.1, 0.1)	0.0 (-0.1, 0.1)	0.2 (0.1, 0.3)	0.8 (0.6, 1.0)
	Lost Man:	0.1 (0.0, 0.1)	0.1 (0.0, 0.1)	-0.2 (-0.6, 0.1)	0.2 (0.1, 0.2)
MWAT	Tectah:	0.1 (0.0, 0.2)	0.0 (-0.1, 0.1)	0.5 (0.3, 0.6)	0.9 (0.6, 1.1)
	Lost Man:	0.1 (0.0, 0.1)	0.1 (0.0, 0.1)	0.0 (-0.2, 0.1)	0.2 (0.1, 0.3)
Degree Days	Tectah:	3.3 (-3.0, 9.6)	0.7 (-2.2, 3.5)	17.1 (8.7, 23.4)	73.4 (56.5, 90.3)
	Lost Man:	5.6 (-0.7, 11.9)	5.8 (2.7, 8.9)	6.8 (6.1, 7.5)	13.8 (9.5, 18.1)
Daily Minimum	Tectah:	-0.1 (-0.2, 0.0)	0.0 (-0.1, 0.0)	0.0 (0.0, 0.1)	0.1 (-0.1, 0.3)
	Lost Man:	0.0 (-0.1, 0.1)	0.1 (0.0, 0.1)	-0.1 (-0.2, 0.1)	0.1 (0.0, 0.1)
Variability					
Average Daily Range	Tectah:	0.4 (0.2, 0.5)	0.0 (-0.1, 0.1)	0.5 (0.3, 0.8)	2.4 (1.8, 3.0)
	Lost Man:	0.0 (0.0, 0.1)	0.0 (0.0, 0.1)	0.2 (0.0, 0.4)	0.1 (0.0, 0.1)
Maximum Daily Range	Tectah:	1.2 (0.7, 1.8)	-0.1 (-0.4, 0.2)	1.5 (0.7, 2.2)	2.9 (2.0, 3.8)
	Lost Man:	0.0 (0.0, 0.0)	0.1 (0.0, 0.3)	0.2 (0.1, 0.2)	0.1 (0.1, 0.2)
Average Variance	Tectah:	0.1 (0.1, 0.2)	0.0 (-0.1, 0.1)	0.3 (0.1, 0.5)	1.5 (0.9, 2.3)
	Lost Man:	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.1)
Maximum Variance	Tectah:	0.7 (0.3, 1.2)	-0.1 (-0.1, 0.1)	1.2 (0.5, 2.0)	2.4 (1.4, 3.7)
	Lost Man:	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.0 (0.0, 0.1)	0.1 (0.0, 0.2)
Frequency and Duration (Number of Days)					
Days > 16°C	Tectah:	0	0	0.9 (0.0, 2.1)	42.9 (31.5, 53.8)
	Lost Man:	0	0	0	0
Consecutive Days > 16°C	Tectah:	0	0	0.5 (0.0, 1.3)	31.1 (21.0, 41.1)
	Lost Man:	0	0	0	0

Summary of temperature responses in thinned reaches for selected descriptors of stream thermal regimes including magnitude, variability, frequency, and duration in northern California second-growth redwood forests. Mean estimates of BACI differences for sites within the Tectah and Lost Man watersheds with lower and upper 95% confidence intervals in parentheses. We estimated non-parametric 95% confidence intervals using a bootstrapping protocol if responses did not follow a normal distribution in the boot package in R (Canty and Ripley 2020). Temperature responses were summarized according to four seasons: Fall (October-December), Winter (January-March), Spring (April-June), and Summer (July – September). No pre-treatment data were available during fall and winter seasons for Lost Man so values reflect post-treatment differences between thinned and upstream reaches. See text for explanations of response variable acronyms.

Table 2.3. Stream thermal regime responses in downstream reaches.

Temperature Response (Δ°C)	**Watershed**	**Fall**	**Winter**	**Spring**	**Summer**
Magnitude					
Daily Maximum	Tectah:	0.6 (0.3, 0.8)	0.0 (-0.2, 0.2)	1.0 (0.3, 1.8)	1.3 (0.7, 2.1)
	Lost Man:	0.1 (0.0, 0.1)	0.1 (0.0, 0.1)	0.1 (-0.1, 0.3)	0.1 (-0.1, 0.3)
MWMT	Tectah:	0.3 (0.0, 0.5)	0.0 (-0.1, 0.1)	0.9 (0.1, 1.6)	1.3 (0.7, 2.1)
	Lost Man:	0.1 (0.0, 0.1)	0.1 (0.0, 0.1)	0.1 (-0.1, 0.2)	0.1 (-0.1, 0.2)
Daily Mean	Tectah:	0.1 (-0.1, 0.1)	0.1 (-0.1, 0.1)	0.1 (-0.1, 0.3)	0.5 (0.2, 0.7)
	Lost Man:	0.0 (-0.1, 0.1)	0.1 (0.0, 0.1)	-0.1 (-0.1, 0.1)	0.0 (-0.1, 0.1)
MWAT	Tectah:	0.1 (-0.1, 0.2)	0.0 (-0.1, 0.1)	0.3 (-0.1, 0.6)	0.6 (0.3, 0.9)
	Lost Man:	0.0 (0.0, 0.1)	0.1 (0.0, 0.1)	0.0 (-0.1, 0.1)	0.0 (-0.1, 0.1)
Degree Days	Tectah:	4.6 (-2.1, 11.8)	1.3 (-1.9, 4.7)	9.6 (-9.3, 23.7)	44.9 (22.0, 68.1)
	Lost Man:	-0.9 (-3.9, 2.2)	4.7 (0.6, 8.9)	-2.3 (-11.6, 7.0)	0.4 (-8.9, 9.8)
Daily Minimum	Tectah:	0.0 (-0.1,0.1)	0.0 (0.0, 0.1)	0.0 (-0.1, 0.1)	0.3 (0.1, 0.4)
	Lost Man:	0.0 (-0.1, 0.0)	0.1 (0.0, 0.1)	-0.1 (-0.1, 0.1)	0.0 (-0.1, 0.1)
Variability					
Average Daily Range	Tectah:	0.1 (0.0, 0.2)	0.0 (-0.1, 0.1)	0.3 (-0.1, 0.6)	0.6 (0.2, 1.0)
	Lost Man:	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.0 (-0.1, 0.1)	0.1 (0.0, 0.2)
Maximum Daily Range	Tectah:	0.2 (-0.1, 0.5)	-0.2 (-0.6, 0.3)	0.8 (-0.1, 1.6)	0.7 (-0.1, 1.6)
	Lost Man:	0.1 (0.0, 0.1)	-0.1 (-0.2, 0.0)	-0.4 (-0.9, 0.1)	0.2 (0.1, 0.3)
Average Variance	Tectah:	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.2 (0.0, 0.4)	0.4 (0.1, 0.8)
	Lost Man:	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
Maximum Variance	Tectah:	0.1 (0.0, 0.3)	0.0 (-0.1, 0.1)	0.8 (0.0, 1.6)	0.9 (0.1, 1.7)
	Lost Man:	0.0 (0.0, 0.0)	0.0 (-0.1, 0.0)	0.0 (0.0, 0.0)	0.1 (0.0, 0.1)
Frequency and Duration (Number of Days)					
Days > 16°C	Tectah:	0	0	0.4 (0.0, 1.1)	16.3 (6.1, 27.4)
	Lost Man:	0	0	0	0
Consecutive Days > 16°C	Tectah:	0	0	0.3 (0.0, 0.8)	11.6 (3.9, 20.0)
	Lost Man:	0	0	0	0

Summary of temperature responses in downstream reaches for selected descriptors of stream thermal regimes including magnitude, variability, frequency, and duration in northern California second-growth redwood forests. Mean estimates of BACI differences for sites within the Tectah and Lost Man watersheds with lower and upper 95% confidence intervals in parentheses. We estimated non-parametric 95% confidence intervals using a bootstrapping protocol if responses did not follow a normal distribution in the boot package in R (Canty and Ripley 2020). Temperature responses were summarized according to four seasons: Fall (October-December), Winter (January-March), Spring (April-June), and Summer (July – September). No pre-treatment data were available during fall and winter seasons for Lost Man so values reflect post-treatment differences between downstream and upstream reaches. See text for explanations of response variable acronyms.

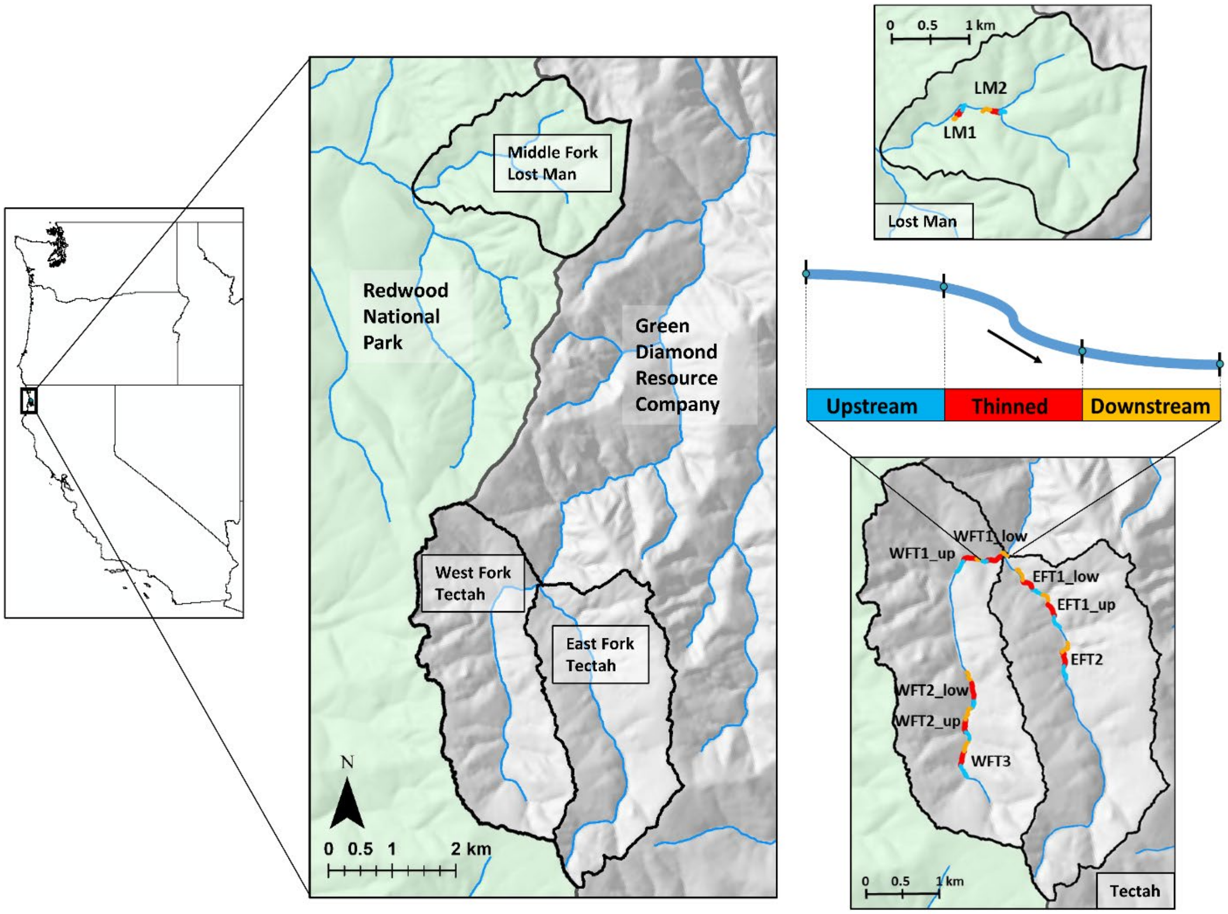

Figure 2.1. Study watersheds map. Map of study watersheds in northern California second-growth redwood forests. Data were collected in upstream reference, thinned, and downstream reaches, which were replicated at 10 total sites distributed across these three watersheds. Temperature sensors were deployed at the top and bottom of each reach indicated by blue points in illustration of study reaches. See Table 2.1 for characteristics of study sites. Map by David A. Roon in ArcGIS Pro (ESRI, Redlands, CA USA) using data collected by the authors and publicly-available GIS shapefiles from the California State Geoportal: https://gis.data.ca.gov/ (California Department of Fish and Wildlife 2020, California Department of Water Resources).

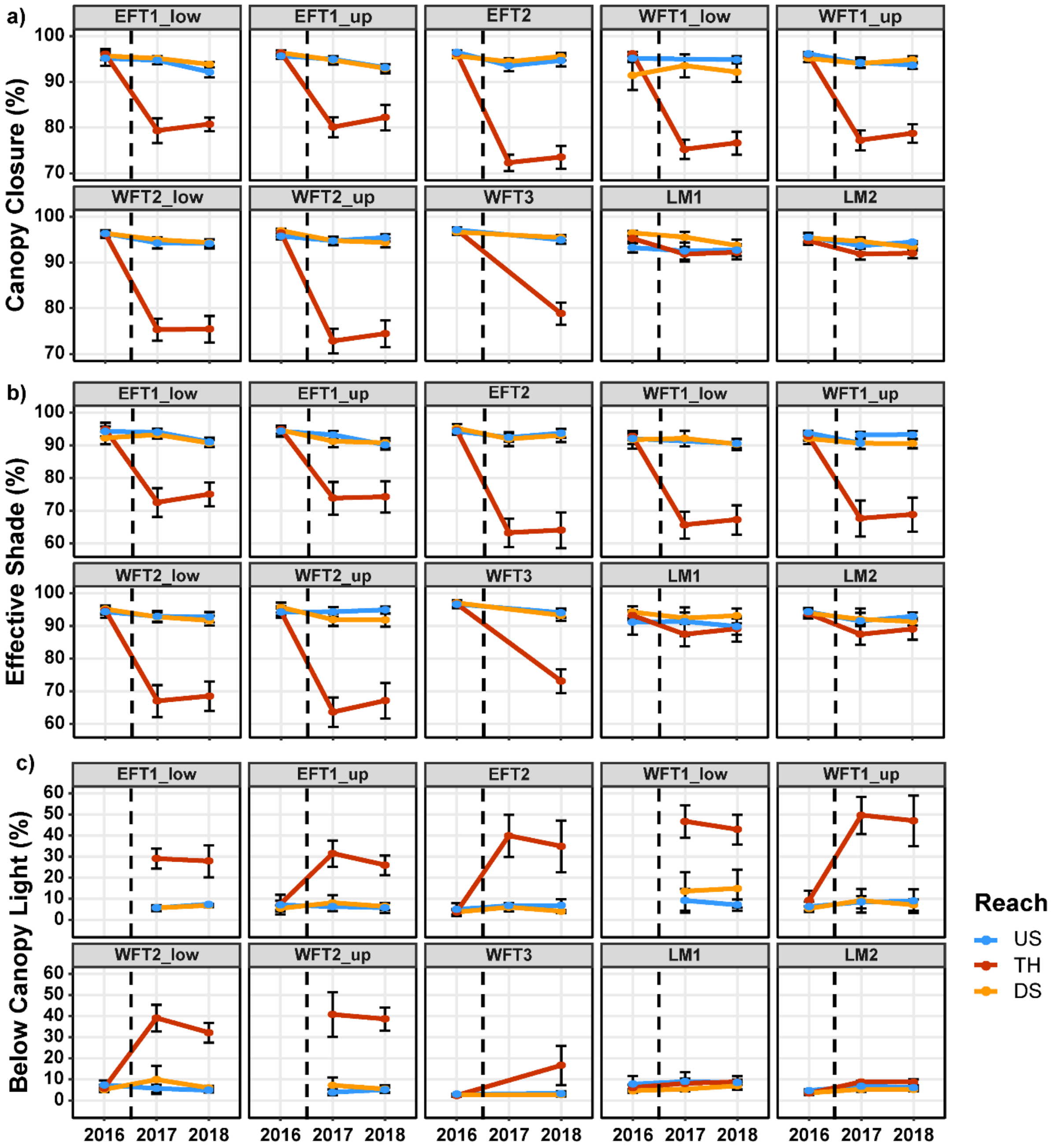

Figure 2.2. Riparian shade and light responses to riparian thinning. Riparian shade and light responses to riparian thinning in northern California second-growth redwood forests. Riparian shade summarized as a) canopy closure (%), b) effective shade (%), and solar radiation summarized as c) below canopy light (%) for Tectah and Lost Man sites. Data collected in upstream reference (US), thinned (TH), and downstream (DS) reaches during pre-treatment (2016) and post-treatment years (2017 and 2018) for each site. Points indicate mean estimates with error bars indicating 95% confidence intervals. Vertical hashed line indicates the timing of experimental thinning treatments.

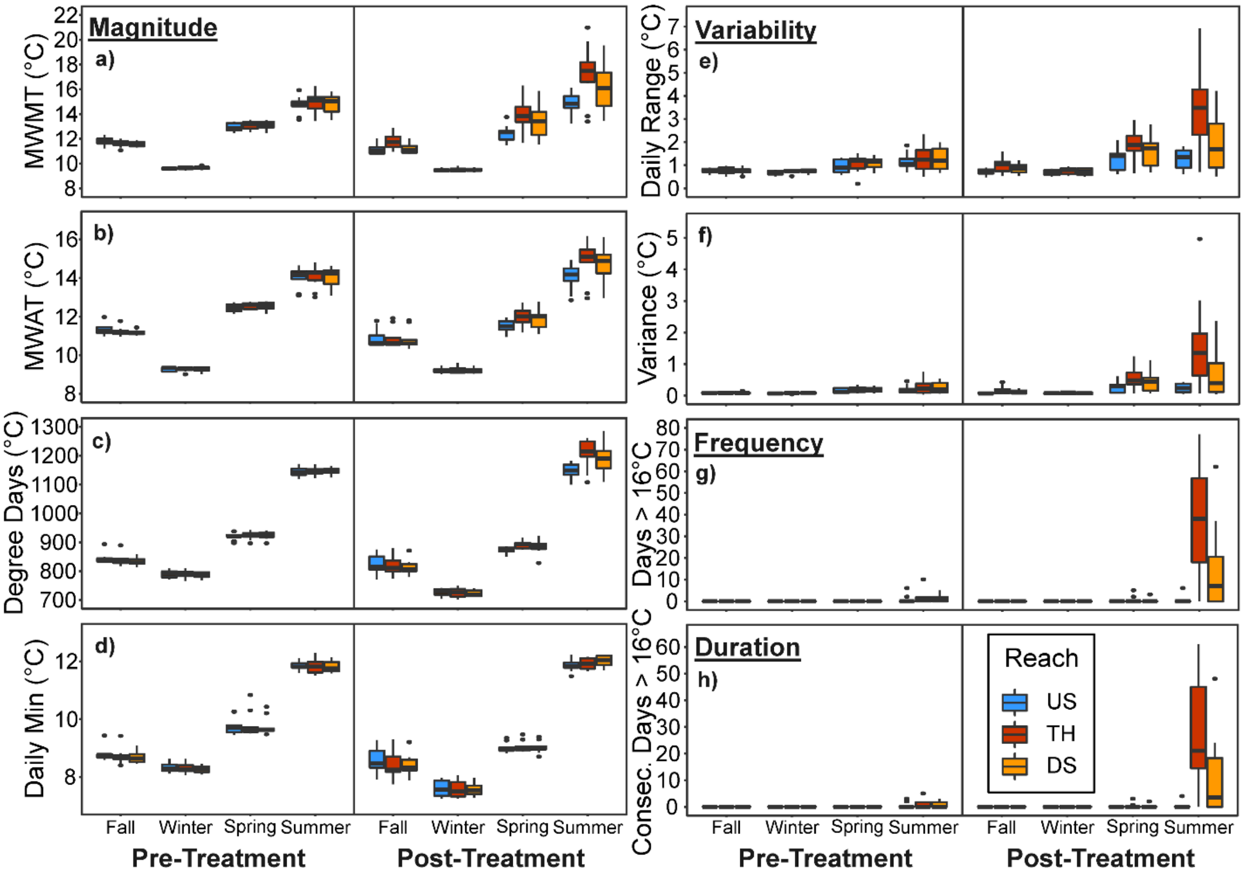

Figure 2.3. Stream thermal regime responses to riparian thinning. Seasonal patterns in stream temperature in upstream reference (US), thinned (TH), and downstream (DS) reaches during pre-treatment (2016) and post-treatment (2018) water years in northern California second-growth redwood forests. Boxplots show the distribution of responses across all sites (n=10) for selected stream thermal regime descriptors including: magnitude (a-d), variability (e-f), frequency (g), and duration (h). Stream temperature responses were summarized for each seasonal window: Fall (October-December), Winter (January-March), Spring (April-June), and Summer (July – September).

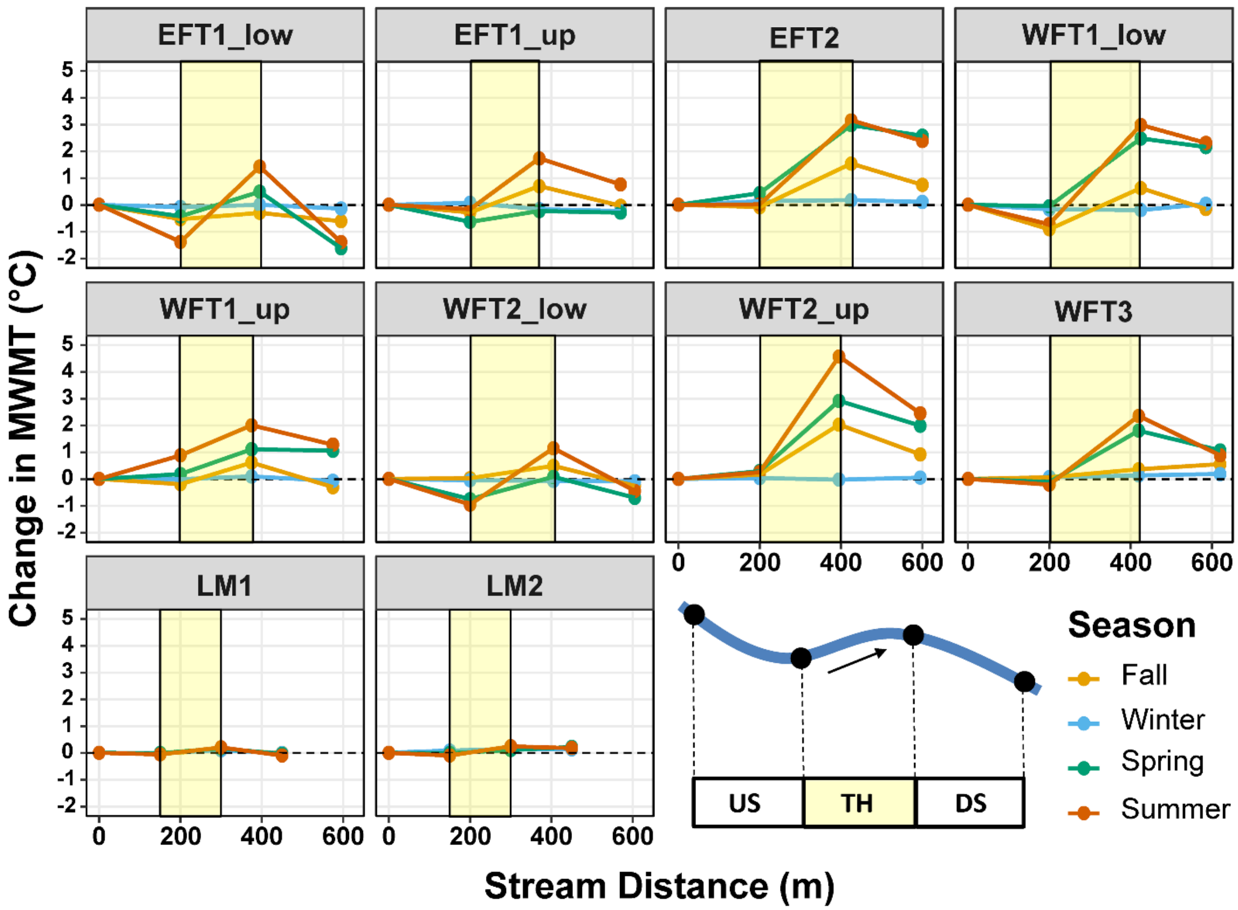

Figure 2.4. Reach-scale longitudinal profiles of stream temperature responses. Seasonal variation in reach-scale longitudinal profiles of stream temperature responses (pre-treatment - post-treatment) in upstream reference (US), thinned (TH), and downstream (DS) reaches for individual sites (n=10) in northern California second-growth redwood forests. The position of thinned reaches is indicated by the yellow polygons. Black dots on blue line depict temperature sensor locations along upstream, thinned, and downstream reaches.

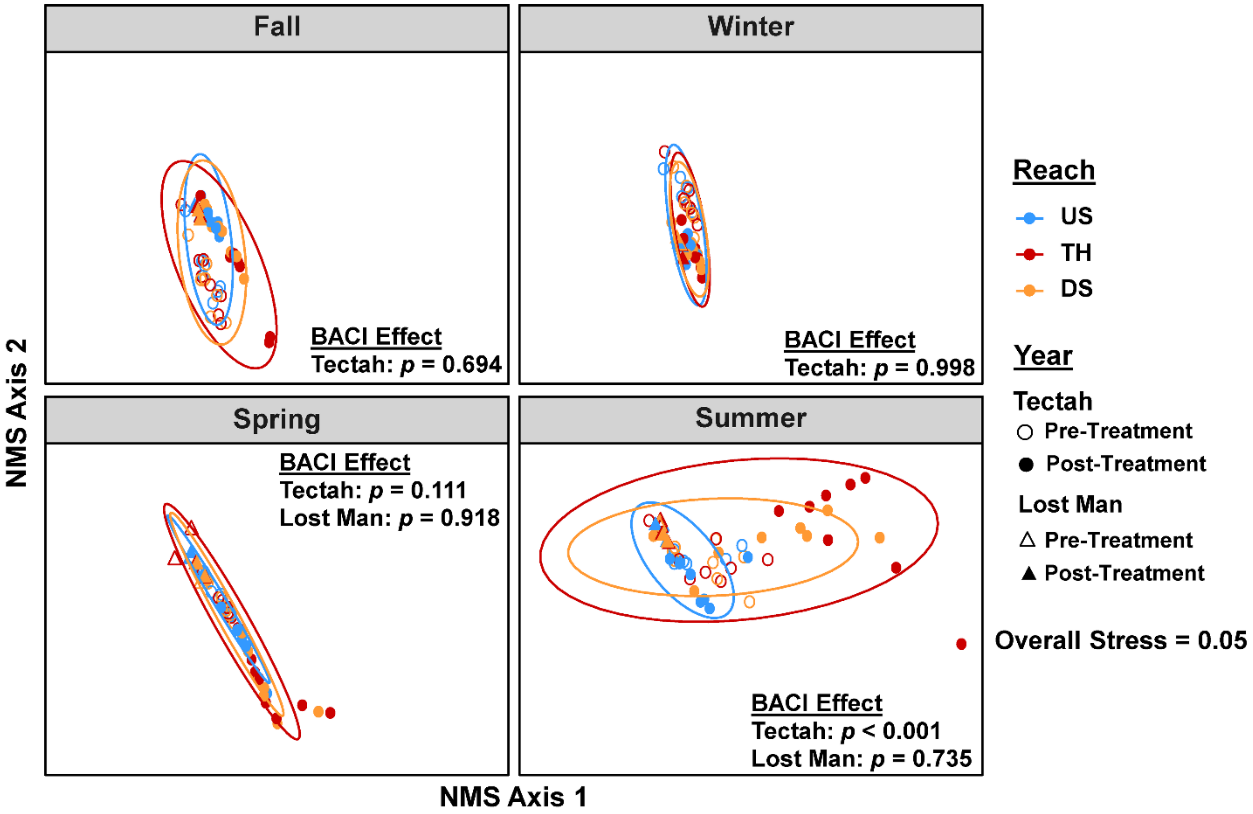

Figure 2.5. NMS ordinations of stream thermal regimes. Non-metric multidimensional scaling ordinations of the structure of stream thermal regimes in response to riparian thinning in northern California second-growth redwood forests. Each point represents the structure of a stream thermal regime at a site with colors indicating reach type and shapes indicating pre-treatment or post-treatment years for each watershed. The proximity of points provides an indication of how similar thermal regimes are between reaches (upstream reference, thinned, downstream), years (pre-treatment, post-treatment), and seasons (fall, winter, spring, summer) for the Tectah and Lost Man watersheds. Ellipses indicate 95% confidence intervals around the grouping variable of reach. PerMANOVA tests indicated whether the structure of stream thermal regimes differed significantly by the BACI effect of Reach*Year ($\alpha = 0.05$).

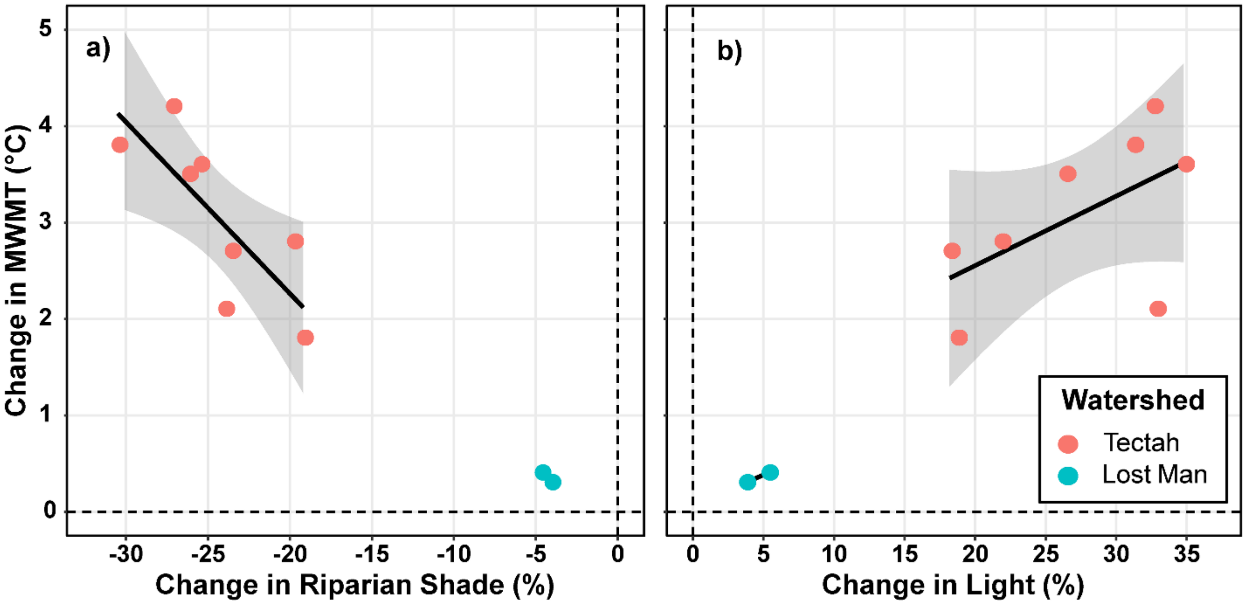

Figure 2.6. Relationships between shade, light, and stream temperature. Relationships between the responses of riparian shade (a) and light (b) and stream temperature (summer MWMT) associated with riparian thinning treatments in Tectah and Lost Man watersheds in northern California second-growth redwood forests. Responses are calculated as BACI differences. Gray shading indicates 95% confidence intervals.

CHAPTER 3: CITATION INFORMATION

A RIVERSCAPE APPROACH REVEALS DOWNSTREAM PROPAGATION OF STREAM THERMAL RESPONSES TO RIPARIAN THINNING AT MULTIPLE SCALES

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This chapter is accepted in Ecosphere 05/27/2021

Abstract

Hydrological connectivity in river networks influences their response to environmental changes as local effects may extend downstream via flowing water. For example, localized changes in riparian forest conditions can affect stream temperatures, and these effects may propagate downstream. However, studies evaluating stream temperature responses to riparian forest management have not considered cumulative effects across entire watersheds. Improved understanding at these scales is needed because land managers are increasingly required to consider broad-scale consequences of their actions. To address this question, we deployed a high-density network of sensors across watersheds to examine stream temperature responses to experimental thinning of riparian forests. A riverscape approach that combined high-resolution data throughout the study watersheds made it possible to examine local and downstream patterns of stream temperature at multiple spatial and temporal scales. We found that local responses of temperature to thinning varied widely depending on the intensity of thinning treatments. Downstream propagation of local responses extended from 100 m to over 1000 m and depended on the magnitude of the local response. We characterized these responses as a series of waveforms. In the watersheds with more intensive thinning, thermal responses occurred most often as an extended pulse where downstream increases in temperature attenuated gradually at variable distances. Although we observed no evidence of cumulative effects associated with thinning at the downstream extent of stream networks, effects emerged where thinning treatments were closely spaced (< 400 m apart) and local warming did not dissipate with downstream distance. In a watershed with less intensive thinning, there was either no response or a localized pulse with no downstream propagation. Collectively, these patterns suggest that riparian forest thinning influenced downstream thermal conditions to varying extents depending on the intensity, scale, and spatial proximity of treatments. We found that a multiscale riverscape approach and conceptual framework based on contrasting waveforms provided a foundation for understanding the cumulative watershed effects of riparian thinning. The approach developed here can be adapted more broadly when evaluating downstream propagation of local changes in river networks and has direct implications for guiding restoration in riparian ecosystems.

Introduction

Cumulative effects in watersheds emerge from the interaction of multiple land uses that affect upslope, riparian, and in-stream processes (Reid 1998, Seitz et al. 2011, Erdozain et al. 2021). Such effects differ from other systems (e.g., terrestrial, marine) because they can propagate downstream from disturbance sites via flowing water. To better understand and effectively manage for cumulative watershed effects, it is important to extend the scales of analysis beyond potentially impacted locations and consider broader spatial extents (Reid 1998, Allan 2004).

Advances in the landscape ecology of stream networks, or riverscape ecology (sensu Fausch et al. 2002, Wiens 2002), offer insights for improving our understanding of cumulative watershed effects across broader scales. Stream ecosystems have traditionally been viewed as continua that gradually change in a downstream direction (Vannote et al. 1980, Fullerton et al. 2015). However, streams often display extensive spatial variability that is better described as a mosaic of patches rather than continuous longitudinal gradients (Pringle et al. 1988, Townsend 1989, Poole 2002). A riverscape perspective characterizes this variability continuously in space and time across multiple scales (Fausch et al. 2002, Lowe et al. 2006). As a result, the concept of riverscapes builds on earlier models of stream ecosystems to incorporate additional complexity that emerges from considering multiple scales, hydrological connectivity, and heterogeneity in processes among locations that collectively control stream function and response to human activities (Fausch et al. 2002, Allan 2004, Humphries et al. 2014). Although riverscape ecology has provided key conceptual and theoretical advances, application of these ideas in practice has proven more challenging (Carbonneau et al. 2012).

Thermal regimes of riverscapes drive ecological processes and are a primary factor influencing the decline of threatened cold-water adapted species (Magnuson 1979, Poole and Berman 2001, Poole et al. 2004, McCullough et al. 2009). Advances in understanding stream temperature across riverscapes stem from improved methods for quantifying spatial and temporal variability with remote sensing (Torgersen et al. 1999, Dugdale et al. 2016) and digital temperature dataloggers (Dunham et al. 2005). Process-based heat budget models elucidate the energetic drivers of thermal regimes (Johnson 2004, Dugdale et al. 2017) but are data intensive and, therefore, difficult to employ over broad spatial scales (Wondzell et al. 2019). Spatial stream network models account for network structure and spatial autocorrelation over broad scales and have greatly improved understanding of thermal regimes in riverscapes (Isaak et al. 2014, Fullerton et al. 2018, Gendaszek et al. 2020). However, the cumulative watershed effects of land use on stream thermal conditions remain difficult to quantify and predict (Steel et al. 2017, Ouellet et al. 2020, Erdozain et al. 2021).

Cumulative watershed effects of land use on thermal regimes in streams are well recognized (Poole and Berman 2001). For example, forest harvest can increase stream temperatures locally and downstream (Moore et al. 2005). Although downstream effects of forest harvest are of interest to managers (Beschta et al. 1987, Zwieniecki and Newton 1999, Johnson 2004, Moore et al. 2005), the spatial extent of downstream effects is highly context dependent and logistically challenging to quantify. Previous research has focused on local responses conducted at small spatial extents (e.g., Groom et al. 2011). When downstream effects have been considered, they were either limited to conditions immediately downstream from treatment locations (e.g., Arismendi and Groom 2019), or much farther downstream (e.g., > 1 km) likely beyond the spatial extent of the treatment effect (e.g., Bladon et al. 2018). New approaches are needed to continuously track longitudinal thermal patterns over broader spatial extents at the scale of entire watersheds to describe cumulative watershed effects in relation to forest harvest. Applying a riverscape approach over large spatial extents at high resolutions may more effectively capture such variability.

Here we address the question of how thinning second-growth riparian forests influences local and downstream stream temperatures at watershed extents. Thinning riparian forests has been proposed in the temperate forests in the Pacific coastal ecoregion of western North America as a restoration strategy for second-growth forests (Berg 1995, Russell 2009, Keyes and Teraoka 2014). Resource managers in the coast redwood (*Sequoia sempervirens*) forests of northern California are currently evaluating thinning of second-growth riparian forests to (1) accelerate the recovery of late-successional forest structure and composition; (2) increase stand heterogeneity; (3) provide a future source of large wood for structuring instream habitats; and (4) increase aquatic biodiversity and productivity (O'Hara et al. 2010, Teraoka and Keyes 2011, Pollock et al. 2014, Benda et al. 2016, Reeves et al. 2016, Wohl et al. 2019). However, forest harvest can affect stream temperatures (Moore et al. 2005), so it is important to understand the local and downstream thermal effects associated with proposed riparian thinning actions.

In this study, we applied a riverscape approach to evaluate the cumulative watershed effects of riparian forest thinning on stream thermal regimes at multiple spatiotemporal scales. We used a large-scale manipulative field experiment, in which patches of riparian forest were experimentally thinned along 10 stream reaches distributed across three watersheds located in coastal northern California. We combined this approach with a dense network of temperature sensors positioned upstream and downstream of each experimental thinning treatment reach as well as systematically every ~200 m through each watershed. Then, by collecting data before and after experimental thinning treatments, we addressed four objectives: (1) quantify pre-treatment spatial and temporal variability in stream temperature conditions; (2) evaluate local responses in stream temperature to riparian thinning; (3) assess the spatial extent and temporal duration of downstream effects to local responses in temperature; and (4) characterize local and downstream responses to thinning with a conceptual framework based on waveforms (sensu Humphries et al. 2014).

Conceptual framework

Stream thermal regimes are a product of multiple energetic processes that influence the gain or loss of heat (Johnson 2004, Caissie 2006). While there are many energetic processes that influence stream thermal regimes, here we focused on two primary drivers of local and downstream temperature conditions in smaller streams: radiative and advective processes. Systematic reviews by Johnson (2004), Moore et al. (2005), Caissie (2006), and Dugdale et al. (2017) provided the context on which we based our understanding of radiative and advective processes and the potential interacting factors (Table A3.1). In small, low-order streams, solar radiation is typically the primary input of heat and is regulated by riparian vegetation and topography (Johnson 2004, Moore et al. 2005, Caissie 2006). Variation in riparian forest conditions can result in local increases in stream temperature via radiative processes (Moore et al. 2005, Dugdale et al. 2017). In lotic systems, these local increases in temperature can propagate longitudinally farther downstream via advective processes (i.e., surface or subsurface streamflow; Moore et al. 2005). To quantify how thinning in riparian zones may affect local and downstream thermal conditions, we used a conceptual framework that illustrates alternative scenarios of local radiative and longitudinal advective energetic processes. We applied this framework to evaluate cumulative watershed effects and test hypotheses about how local changes in stream temperature associated with thinning propagate downstream through stream networks.

We hypothesized that local and downstream thermal responses occur as a series of waveforms (Humphries et al. 2014) that vary in shape depending on the relative strength of local radiative and longitudinal advective processes (Figure 3.1). We generalized these as four categories of response. Local responses depend on sufficient increases in radiative energy to increase stream temperatures; therefore, minor local reductions in shade may result in no effect. More intensive changes in radiative energy may result in a localized pulse but not extend downstream if advective processes are truncated, for example, during periods of low flow (Gendaszek et al. 2020). However, if advective processes are present, local responses may propagate downstream following different trajectories. Moore et al. (2005) and others have suggested that downstream effects eventually dissipate as an extended pulse due to reduced inputs of radiative energy or mediation by cold-water tributaries or upwelling groundwater (Story et al. 2003, Moore et al. 2005, Garner et al. 2014, Davis et al. 2016). However, if increases in temperature remain elevated or do not have sufficient time or space to dissipate before the water flows through another patch of thinning, then downstream thermal increases may accumulate as a cumulative effect (Reid 1998).

Methods

Study area

The study area encompassed three watersheds in the redwood forests of coastal northern California (USA) (Figure 3.2). Two watersheds (west and east forks of Tectah Creek) occurred on private timberland owned by Green Diamond Resource Company, and the third watershed (Lost Man Creek) occurred in Redwood National Park. The three study systems consisted of small watersheds (5.8-8.4 km^2) drained by steep, low-order perennial streams (bankfull widths: 3.2-6.6 m) that are located within 15 km of the Pacific Ocean and experience a cool, maritime climate (Welsh et al. 2000, Lorimer et al. 2009). Riparian forests within these watersheds consist of second-growth forests regenerated from timber harvest 40-60 years ago and include a mix of coast redwood, red alder (*Alnus rubra*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), tanoak (*Notholithocarpus densiflorus*), western red cedar (*Thuja plicata*), and vine maple (*Acer circinatum*). The stream channel in these systems is heavily shaded by riparian forests with little longitudinal variation (mean canopy closure: 94.3% ± 1.3% standard deviation). These watersheds support resident populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), coastal giant salamander (*Dicamptodon tenebrosus)*, and coastal tailed frog (*Ascaphus truei*), all of which are cold-water adapted and sensitive to changes in temperature (Huff et al. 2005).

Experimental design

Experimental thinning of riparian forests and monitoring of water temperature were implemented across the three study watersheds following a before-after-control-impact (BACI) design (Fig. 2). We collected pre-treatment data in 2016, experimental thinning treatments occurred in 2017, and then we collected post-treatment data in 2018. Riparian forests were experimentally thinned in 10 treatment reaches across the three watersheds (Table 1). Treatment reach identifiers corresponded to their watershed (West Fork Tectah = WFT, East Fork Tectah = EFT, Lost Man = LM) and the number of thinning treatments in each watershed (e.g. LM1). In the Tectah watersheds, multiple thinning treatments sometimes occurred adjacent to a single harvest unit and were assigned a lower and upper designation (e.g. WFT1_low, WFT1_up). Although this study consisted of three watersheds and 10 treatment reaches, we considered the reaches individually and collectively to better understand how site and treatment heterogeneity may affect thermal responses at local and watershed extents.

Thinning treatment prescriptions varied between landowners to meet their respective management objectives. Thinning treatments in the Tectah watersheds on Green Diamond Resource Company property took place as part of a larger riparian canopy experiment approved by Green Diamond's Aquatic Habitat Conservation Plan that allows for experimental harvests for research purposes (Green Diamond Resource Company 2016). Thinning treatment prescriptions in the Tectah watersheds were intended to reduce canopy closure within riparian zone by 50% on both sides of the active stream channel along a 200-m reach. Thinning treatments bordered upslope timber harvest units and targeted red alder and some conifer depending on the density and composition of the stand. In all treatment reaches, larger conifers were left intact as they are anticipated to contribute as an eventual source of large wood in riparian zones and in streams. Trees were removed from the riparian zone via cable yarding. Non-thinned reaches adjacent to the harvest units were protected by Green Diamond's standard riparian buffer prescription that consisted of a single-sided 45-m wide buffer with a 22.5-m wide inner zone of 85% canopy retention and 22.5-m wide outer zone of 70% canopy retention (Green Diamond Resource Company 2006). An analysis of buffered reaches relative to intact forest reference reaches documented no difference in riparian shade, light, and stream temperature conditions between buffer types (Roon et al. 2021).

Thinning treatments in the Lost Man watershed in Redwood National Park coincided with a larger restoration thinning effort intended to promote late-successional coast redwood forests and increase stand heterogeneity in the middle fork of the Lost Man Creek watershed (Teraoka and Keyes 2011, Redwood National Park 2014). Restoration thinning previously targeted upland forests, but now park foresters are interested in thinning second-growth forests within the riparian zone (Redwood National Park 2014). Riparian thinning treatment prescriptions reduced basal area by up to 40% on both sides of the active stream channel along a 100-150-m reach on slopes less than 20%. Thinning treatments targeted commercially planted Douglas-fir and red alder. Harvests followed a lop and scatter protocol leaving felled trees in the riparian zone but out of the stream channel (Redwood National Park 2014).

The intensity of thinning treatments varied between landowners due to differences in treatment prescriptions (Table 3.1). Reductions in shade over the stream channel as measured by hemispherical photography indicated that thinning treatments in the Tectah watersheds (Green Diamond property) were more intensive (reductions in effective shade over the stream channel: 19-30%) than the treatments in the Lost Man watershed (Redwood National Park) (reductions in effective shade over the stream channel: 4-5%) (Table 3.1).

Stream temperature data

We measured stream temperatures using digital temperature sensors (Onset Hobo Water Temperature Pro v2 and TidbiT Water Temperature Data Loggers, Onset Computer Corporation, Bourne, MA USA) deployed approximately every 200 m through each watershed as well as downstream of the confluence in the Tectah watersheds (n = 100). Before deployment, we checked that all sensors were calibrated following the protocol described in Heck et al. (2018). We used solar shields constructed from 5-cm diameter polyvinyl chloride (PVC) pipe ~13-cm in length. We anchored sensors to the streambed using Duckbill Earth Anchors (MacLean Civil Products, Fort Mill, SC, USA) modified with 5-mm diameter vinyl-coated galvanized steel cables in gravel and cobble dominant habitats or with waterproof epoxy (Pettit Splash Zone Marine Epoxy, Pettit Paint, Rockaway, NJ, USA) in habitats where bedrock or large boulders predominated (Heck et al. 2018). Temperature sensors recorded data hourly, and we summarized the data hourly, daily, and monthly during both the pre-treatment and post-treatment water years (October 1 – September 30).

To measure finer-scale longitudinal patterns in stream temperature, we used an AquaTuff 35100-K Waterproof Thermocouple Instrument (Cooper-Atkins, Middlefield, CT, USA) attached to a 2-m PVC pole. We measured stream temperature every 10 m through upstream reference, thinned, and downstream reaches during the afternoon in late summer (13-24 August 2018) at low flow when thermal variability was highest. We recorded fine-scale temperature measurements in the thalweg of the stream channel ~5 cm above the streambed. To detect potential thermal stratification in low-flow pools >0.3 m in depth (Nielsen et al. 1994), we took measurements near the surface and the streambed.

Data analysis

As originally envisioned (Fausch et al. 2002), a riverscape approach to understanding lotic ecosystems involves visualizing and quantifying biotic or physical responses in ways that address spatial and temporal variability throughout stream networks. In keeping with the concept of a riverscape approach we used a series of analyses that characterized conditions across multiple resolutions and extents (Reid, 1998, Lowe et al. 2006). As recommended by Reid (1998), these analyses emphasized characterizing spatial patterns (Turner 1989). This approach allowed us to explore how local changes in temperature associated with riparian forest thinning propagated in space and time, thus allowing us to evaluate patterns in light of our framework for assessing responses (Figure 3.1). First, we used semivariograms to evaluate how spatial autocorrelation varied before and after thinning. Second, we documented local and downstream thermal responses to thinning at a watershed extent across different temporal resolutions, including seasonal, daily, and diel (hourly) fluctuations. Last, we used Lagrangian analyses to track how changes in temperature traveled through space and time (Doyle and Ensign 2009, Vatland et al. 2015). For each analysis, to detect changes in thermal conditions associated with thinning, we compared conditions during pre-treatment (2016) and post-treatment years (2018). We examined how thinning influenced local and downstream temperatures between years and then related these patterns to the waveforms described in Figure 3.1. We conducted all analyses in R version 4.0.2 (R Core Team, 2020) and plotted all graphics in the ggplot2 package (Wickham 2016) unless otherwise noted.

Spatial autocorrelation—Spatial dependence is pervasive in ecological data (Levin 1992, Legendre 1993) and especially in riverscapes, which are connected longitudinally via flowing water (Ward 1989). Geostatistical tools quantify spatial autocorrelation and structure in watersheds (Ganio et al. 2005). We used semivariograms of summer degree days to determine the presence of spatial autocorrelation and how that spatial structure related to thinning treatments (Torgersen et al. 2004, Ganio et al. 2005). We selected summer degree days as a cumulative measure of thermal exposure that has implications for wide range of ecological processes (Steel et al. 2012, Benjamin et al. 2016, Campbell et al. 2020). We constructed semivariograms for each watershed using summer cumulative degree days for all locations distributed in the sensor network, and we compared how spatial dependence changed before and after thinning. We generated semivariograms in the gstat package in R (Pebesma 2004).

Temporal variation of local and downstream responses—To evaluate baseline spatial variability and how thinning influenced longitudinal patterns, we examined watershed-scale longitudinal profiles at different time steps. We plotted summer cumulative degree days for each of the temperature sensors during pre- and post-treatment years to explore longitudinal patterns in stream temperature over the entire summer season (July 1 – September 30). To track the spatial extent of downstream propagation of local increases in temperature associated with thinning, we applied a modified distance-to-edge approach following the combined methods described in Harper and Macdonald (2001) and Arismendi and Groom (2019). Using summer degree days, we set the before-after difference in temperature at the upstream end of each thinning reach (n = 10) to 0 and quantified temperature increases locally by comparing the difference at the downstream end of the thinned reach. Then, to track how any local increase in temperature propagated downstream, we determined the distance that temperatures remained elevated.

To evaluate the spatial extent and temporal duration of local and downstream effects of thinning at a daily time step, we examined daily maximum temperatures over the entire water year (October 1 – September 30) using spatiotemporal heatmaps constructed in the geom_raster function in the ggplot2 package. We compared pre- and post-treatment water years for each watershed to see how spatiotemporal patterns of temperature changed with thinning.

To explore the response of diel temperature fluctuations to thinning, we plotted watershed-scale longitudinal profiles of hourly data for each watershed on the warmest day of the year during our pre-treatment (30-July-2016) and post-treatment (25-July-2018) years. We selected the warmest day of the year to maximize the potential signals revealed in diel temperature fluctuations, which should be expected when fluctuations are greatest. Diel fluctuations intended to characterize how thinning influenced thermal variability, which can have implications for biota and ecological processes (Fraterrigo and Rusak 2008, Steel et al. 2012)

Lagrangian analyses—In addition to measuring stream temperature responses at fixed locations (i.e., an Eulerian approach), we tracked changes in temperature through space and time using a Lagrangian framework (Doyle and Ensign 2009, Vatland et al. 2015). First, to determine how temperature responses associated with thinning moved through these watersheds over time, we tracked the timing of maximum temperatures on the warmest day of the year as an indication of spatiotemporal thermal variability (Fullerton et al. 2018). We noted the hour of the day when temperature peaked for all locations in the temperature sensor network, and we plotted the distribution of those times using kernel density functions. We tested for differences using non-parametric Kolmogorov-Smirnov tests which examine if the distribution of observations (in this case timing of maximum temperatures) varied between years ($\alpha = 0.05$).

Second, to quantify how temperature responses moved through the watersheds over space, we mapped fine-scale longitudinal temperature patterns through upstream reference, thinned, and downstream reaches. This approach was inspired by Moore et al. (2005) and allowed us to observe the magnitude of temperature increases, where they peaked within thinning reaches, and how these increases dissipated downstream under intact forest cover. To standardize comparisons among treatment reaches, we set the temperature above the upstream reference reach to 0 and quantified longitudinal variation in upstream, thinned, and downstream reaches. We then compared fine-scale empirical measurements with locally estimated scatterplot smoothing (LOESS) regression lines.

Results

Spatial autocorrelation

Semivariograms documented widespread spatial autocorrelation that varied among watersheds and after thinning treatments (Figure 3.3). Pre-treatment semivariograms indicated stronger spatial dependence in West Fork Tectah than in East Fork Tectah and Lost Man. In contrast, post-treatment semivariograms showed increased spatial heterogeneity in East Fork

Tectah and West Fork Tectah that corresponded to the spacing of the thinning treatments, but Lost Man remained unchanged (Figure 3.3). Post-treatment spatial heterogeneity increased the most in West Fork Tectah, with an elevated sill, shorter range, and steeper ascending limb with stepped sills indicating increased patchiness at multiple scales. Spatial heterogeneity also increased in East Fork Tectah but to a lesser extent.

Temporal variation of local and downstream responses

Longitudinal profiles of summer degree days in the pre-treatment year (2016) documented inherent spatial variation, with maximum longitudinal differences in degree day accumulation ranging from 66 to 112 °C within each watershed (Figure 3.4). Thermal heterogeneity increased during the post-treatment year (2018) within each watershed by 20 to 139 °C degree days over the summer season, but the magnitude of responses varied between watersheds (Figure 3.4). In the Tectah watersheds, post-treatment temperatures increased locally in thinned reaches and frequently remained elevated farther downstream (Figure 3.4). In parts of the Tectah watersheds where thinning reaches occurred farther apart (greater than ~400 m), temperature increases dissipated downstream (Figure 3.4). However, in other parts of the Tectah watersheds where thinning treatments occurred closer together (less than ~400 m), temperature increases did not dissipate completely before encountering next thinning reach. In contrast, in the Lost Man watershed, post-treatment temperature responses were minimal in thinned reaches and showed no evidence of downstream propagation (Figure 3.4).

Distance-to-edge analyses indicated consistent local increases in summer degree days associated with thinning treatments, but the magnitude of responses varied widely among watersheds (Figure 3.5). Local temperatures increases associated with riparian thinning were most evident in treatment reaches in the Tectah watersheds, accumulating between 45 to 115 °C additional degree days over the summer compared to the treatment reaches in the Lost Man watershed, which only accumulated between 10 to 15 °C degree days (Figure 3.5). Propagation of local temperature increases downstream of treatment reaches showed a consistent cooling pattern, but the spatial extent of downstream propagation varied and depended on the magnitude of local increase (Figure 3.5). Treatment reaches where temperature increases associated with riparian thinning were smaller, such as in the Lost Man watershed, had shorter travel distances, ranging from 75 m to 150 m downstream, but treatment reaches with larger temperature increases such as in the Tectah watersheds had longer travel distances downstream, ranging from 300 m to nearly 1,000 m (Figure 3.5).

Spatiotemporal heatmaps of daily maximum stream temperatures during the pre-treatment water year showed minimal longitudinal variation within each watershed along the x-axis but greater seasonal variation along the y-axis (Figure 3.6). Pre-treatment seasonal patterns indicated that thermal conditions stayed relatively cool fall through spring, with stream temperatures peaking as expected during summer months especially in July and August (longitudinal maximums ranged: 13.2-17.4 °C) (Figure 3.6). Post-treatment heatmaps indicated increased spatial and temporal variability, but responses differed between watersheds. Increased spatiotemporal variability occurred exclusively in the Tectah watersheds, with no responses visible in the Lost Man watershed. Post-treatment temperatures increased the most in the thinned reaches in the Tectah watersheds (maximum temperatures in thinned reaches ranged: 16.8-21.8 °C), but also extended downstream of each thinning reach (Figure 3.6). The temporal duration of these temperature responses lasted the longest within thinning treatments and often persisted from May through September and decreased downstream from each thinning reach (Figure 3.6). The spatial extent of downstream effects varied seasonally peaking during summer months especially in July and August and ranged from 200 to over 1,200 m (Figure 3.6). No local or downstream responses in space or time were evident in the Lost Man watershed (Figure 3.6).

Longitudinal profiles of diel fluctuations on the warmest day of the year indicated inherent spatial variability, with pre-treatment diel fluctuations ranging from 0.3 to 2.4 °C (Figure 3.7). Post-treatment diel fluctuations displayed increased thermal heterogeneity, causing diel fluctuations to range from 0.3 to 8.7 °C (Figure 3.7). Post-treatment diel fluctuations increased the most within thinning reaches but also remained elevated downstream. Local and downstream post-treatment responses increased the most in the Tectah watersheds, whereas no responses were evident in the Lost Man watershed (Figure 3.7). In the Tectah watersheds, when thinning reaches occurred farther apart (greater than ~400 m), local increases in diel fluctuations dissipated as they continued downstream. However, when thinning reaches occurred closer together (less than ~400 m), local increases remained elevated, sometimes resulting in larger subsequent increases in temperature (Figure 3.7).

Lagrangian analyses

Lagrangian analyses indicated that thinning shifted the timing of maximum temperatures on the warmest day of the year (Figure 3.8). Pre-treatment kernel density distributions showed that maximum temperatures peaked over a shorter window of time in the late afternoon between 14:00 to 19:00 in the Tectah watersheds and 12:00 to 19:00 in the Lost Man watershed (Figure 3.8). In the post-treatment year, kernel density distributions indicated that the timing of maximum temperatures peaked over a broader temporal window, especially in the Tectah watersheds. Locally within thinning reaches, the timing of maximum temperatures occurred earlier in the afternoon, most frequently peaking at 12:00 to 13:00 (Figure 3.8). As this pulse of warmed water traveled downstream, it delayed the timing of maximum temperatures, most frequently peaking in downstream locations at 18:00 to 21:00 (Figure 3.8). These shifts in timing differed between years (Kolmogorov-Smirnov test: $p<0.05$). No shifts in timing occurred between years in the Lost Man watershed (Kolmogorov-Smirnov test: $p>0.05$) (Figure 3.8).

Fine-scale longitudinal profiles during the post-treatment year showed distinct patterns in upstream reference, thinned, and downstream reaches, but responses varied between watersheds (Figure 3.9). In all watersheds, fine-scale temperature patterns in upstream reference reaches remained constant or cooled downstream. In the Tectah watersheds, stream temperatures in thinned reaches continuously warmed with distance downstream, increasing 2.0 to 4.7 °C (Figure 3.9). Local increases in temperature extended into downstream reaches but exhibited distinct cooling trajectories. In some treatment locations, temperatures returned to initial conditions by the end of the downstream reach (e.g., EFT1_low, EFT1_up, WFT1_low, WFT2_low), whereas in other locations, temperatures dissipated partially (e.g., EFT2, and WFT1_up, WFT2_up, WFT3) (Figure 3.9). In some downstream reaches, abrupt drops in temperature in the downstream reach coincided with low-flow pools (e.g., WFT1_low, WFT2_low, EFT2, EFT1_up) followed by cooler temperatures farther downstream (Figure 3.9). In contrast, treatment reaches in the Lost Man watershed showed no change longitudinally in thinned or downstream reaches (Figure 3.9).

Discussion

We found the combination of a riverscape approach (Fausch et al. 2002), guided by interpretations from our conceptual framework of management responses (Reid 1998, Humphries et al. 2014) proved effective in providing an actionable assessment of the influences of riparian thinning on stream thermal regimes across watersheds. This study design was particularly effective for quantifying and envisioning patterns of heterogeneity in stream temperatures (Steel et al. 2017). Although we observed inherent spatial variation in thermal conditions in our study watersheds (Fullerton et al. 2015, Leach et al. 2017), we observed that riparian thinning increased thermal heterogeneity beyond the natural range of variation in pre-treatment conditions, a finding consistent with previous studies (Fraterrigo and Rusak 2008, Steel et al. 2017, Fullerton et al. 2018). Increases in thermal heterogeneity occurred across multiple spatiotemporal scales and varied between watersheds with different intensities of riparian thinning. Elucidating these responses required several lines of analyses informed by our conceptual framework for describing cumulative watershed effects (Figure 3.1, Table 3.2).

Riparian thinning altered longitudinal patterns in spatial autocorrelation

Spatial autocorrelation of stream temperature cumulative degree days indicated distinct post-treatment responses among watersheds. In the Tectah watersheds, where more intensive thinning treatments occurred, riparian thinning resulted in increased heterogeneity (i.e., higher variance and patchiness) at multiple spatial scales. Heterogeneity increased the most in the West Fork Tectah watershed where the most thinning treatments occurred ($n = 5$). The East Fork Tectah watershed displayed similar patterns of increased heterogeneity at multiple scales, but to a lesser extent than in the West Fork watershed, which coincided with fewer thinning treatments ($n = 3$). In contrast, semivariograms for the Lost Man watershed exhibited a pure nugget effect (i.e., no increase in semivariance with separation distance) during both pre- and post-treatment years. Other studies have shown semivariograms with shapes similar to the ones we observed (i.e., pure nugget effect, spherical, and nested) for fish counts (Torgersen et al. 2004, Ganio et al. 2005), water chemistry (McGuire et al. 2014), and stream temperature (Gendaszek et al. 2020). However, few studies have applied semivariograms for change-detection purposes (but see Dent and Grimm 1999, Johnson et al. 2010). Our study results highlight that semivariograms are effective tools for detecting land-use impacts, in this case documenting increased thermal heterogeneity associated with experimental riparian thinning treatments.

Riparian thinning increased local and downstream temperatures across multiple scales

Watershed responses to riparian thinning indicated that stream temperatures increased the most within thinned reaches, but the magnitude of thermal responses varied with treatment intensity. In the Tectah watersheds, which experienced more intensive thinning treatments, we observed larger thermal responses across each temporal scale considered. We observed this pattern as abrupt peaks in seasonal and daily longitudinal profiles as well as distinct hotspots in spatiotemporal heatmaps. Not only did thinning increase the magnitude of stream temperatures, but it also altered the thermal regime in other ways, as evidenced by increased thermal variability in diel fluctuations and as prolonged temporal durations in spatiotemporal heatmaps during summer low flows (Steel et al. 2017, Roon et al. 2021). In contrast, we observed minimal or no thermal responses in the Lost Man watershed, which experienced less intensive thinning treatments. These patterns corroborate other studies documenting that the magnitude of stream temperature responses to forest harvest correspond with the extent of changes in riparian shade and solar radiation (Johnson 2004, Moore et al. 2005).

Downstream propagation of local responses was evident at every temporal scale we considered, but the spatial extents of downstream effects ranged widely and often depended on the magnitude (i.e., increase in temperatures) of local responses to thinning. Distance-to-edge analyses of summer degree days showed that treatment reaches in the Tectah watersheds (where local increases in temperature were larger) extended farther downstream (300-1,000 m), while treatment reaches in the Lost Man watershed (where local increases were much smaller) did not extend downstream very far (≤ 100 m). Spatiotemporal heatmaps of year-round daily maximum temperatures revealed that the spatial extent of downstream effects fluctuated seasonally and peaked during July and August, reflecting the timing of local responses associated with thinning treatments. Tracking downstream effects year-round and across multiple temporal scales provided valuable insights not possible from a single scale (Fausch et al. 2002, Lowe et al. 2006).

Although downstream effects of forest management have been a focus in research and management (Moore et al. 2005), knowledge gaps still remain. Multiple studies describe responses immediately downstream of treatment locations (e.g., Shrimpton et al. 1999, Story et al. 2003, Arismendi and Groom 2019), often documenting downstream propagation, but there are relatively few attempts to track the spatial extent of those effects. Wilzbach et al. (2005) detected downstream effects in the Tectah watershed extending up to 430 m downstream of treatments that completely removed the riparian canopy along a 100-m reach. Davis et al. (2016) applied Newton’s law of cooling to model the downstream effects associated with a range of riparian buffer widths (6-50 m wide) in the Oregon Coast Range and found that ~50% of local increases persisted at 300 m downstream, similar to our observations in the Tectah watersheds. In contrast, Zwieniecki and Newton (1999) estimated that downstream temperatures cooled to initial conditions within 150 m of harvests that included a ~ 20-m wide riparian buffer along a 350-1,600-m reach. However, they derived these estimates relative to an averaged longitudinal trend line that did not account for the effects of inherent longitudinal thermal variability (Johnson 2004, Fullerton et al. 2015). Bladon et al. (2018) also observed minimal downstream effects from upstream harvests that consisted of a 15-m wide riparian buffer in watersheds located in the Oregon Coast Range, but positions of downstream monitoring stations varied in spacing from treatments and did not allow for detailed analysis of spatial patterns. The spatial extents of downstream effects that we measured in this study occurred at intermediate scales (100-1,200 m), which are often most relevant to management and biota (Fausch et al. 2002, Bladon et al. 2018, Arismendi and Groom 2019). These results highlight the value of a riverscape approach that combines high resolution data across a broad spatial extent to provide a more spatially and temporally continuous view of downstream changes.

Riparian thinning altered stream temperatures through space and time

Our Lagrangian analyses complemented patterns observed in watershed-scale analyses that relied on fixed locations otherwise known as a *Eulerian* perspective (Doyle and Ensign 2009). By applying a Lagrangian perspective, we successfully tracked how temperature changes associated with riparian thinning treatments moved through time and space, documenting increased spatiotemporal heterogeneity (Vatland et al. 2015). We found that thinning increased thermal asynchronies in space and time (Malcolm et al. 2004, Vatland et al. 2015, Fullerton et al. 2018) where maximum temperatures peaked earlier in thinned reaches but peaked later in downstream locations; these findings are consistent with the advective transfer of heat downstream (Moore et al. 2005). The emergence of these thermal asynchronies varied with treatment intensity, where shifts in timing were more dramatic in the Tectah watersheds (which had greater treatment intensity) than in the Lost Man watershed. Added thermal complexity in space and time as documented by Lagrangian analyses likely have implications for ecological processes and biota in these watersheds (Fraterrigo and Rusak 2008, Steel et al. 2017, Fullerton et al. 2018).

Fine-scale longitudinal profiles at a spatial resolution of 10 m revealed how quickly stream temperature increased downstream through a patch of thinning and how these increases dissipated farther downstream. As predicted by Moore et al. (2005), stream temperature continued to increase through the thinning reach, peaking at the downstream end. However, in some downstream reaches, we observed abrupt decreases in temperature that corresponded with low-flow pools, which were often thermally stratified (Nielsen et al. 1994, Ouellet et al. 2017). The mechanisms driving this pattern are complex and difficult to quantify directly (e.g., mediation by upwelling groundwater or small amounts of warmed water interacting with a larger volume of cooler water), but the end result was a buffering effect on upstream increases in temperature that limited further downstream propagation. These results illustrate the value of high-resolution approaches that can reveal fine-scale patterns of thermal heterogeneity, such as remote sensing (Torgersen et al. 1999, Fullerton et al. 2015, Vatland et al. 2015, Dugdale 2016) or distributed temperature sensing (DTS) (Roth et al. 2010, Hall et al. 2020).

Application of conceptual framework

A key objective of this study was to provide insights afforded by a riverscape approach and apply them within a conceptual framework based on waveforms that allows for interpretations that are directly relevant for managers (Figure 3.1). When we compare our results to the waveforms in Figure 3.1 (Humphries et al. 2014), we see a series of distinct waveforms develop that varied in shape depending on the intensity, scale, and proximity of thinning treatments. Waveforms in the Tectah watersheds were most frequently characterized as an extended pulse in which localized increases in temperature extended downstream of the riparian treatments but eventually dissipated at variable distances. Extended pulses appeared in the thermal responses to thinning in watershed-scale longitudinal profiles, distance to edge analyses, spatial-temporal heatmaps, and fine-scale longitudinal profiles, especially when thinning reaches were spaced farther apart (> 400 m). Extended pulses have been described in other studies, but the mechanisms responsible for driving this eventual downstream cooling and the rates at which they cool vary among systems (Shrimpton et al. 1999, Rutherford et al. 2004, Moore et al. 2005, Garner et al. 2014, Davis et al. 2016, Erdozain et al. 2021). For example, Story et al. (2003) and Moore et al. (2005) suggested that downstream cooling in extended pulses may be due to mediation by cooler inputs such as conduction with the streambed, upwelling groundwater, hyporheic flow, or junctions with cold-water tributaries. However, by using a process-based energy budget model Garner et al. (2014) determined that patterns of downstream cooling were not necessarily due to mediation by cooler inputs, but instead were more likely caused by reductions in solar energy under closed canopies that reduced the rate of heating as water flowed downstream.

Overall, we observed no evidence of cumulative watershed effects at the downstream extent of each of our study watersheds. However, responses in the Tectah watersheds showed cumulative effects (Reid 1998) between thinning treatments where thinning treatments occurred close together (<400 m apart), and local increases in temperature did not dissipate completely before entering another patch of thinning. Alternatively, apparent cumulative effects observed between thinning treatments may represent superimposition of two or more extended pulses from upstream thinning treatments. The subsequent increase in temperature was sometimes greater in magnitude, suggesting a compounding effect. Although Beschta et al. (1987) suggested that increases in temperature associated with timber harvest may continue to increase in a downstream direction, little empirical evidence has supported this hypothesis (Shrimpton et al. 1999, Johnson 2004, Moore et al. 2005, Fullerton et al. 2015, Erdozain et al. 2021). Our data suggest that cumulative effects were limited to locations that occurred between patches of thinning. However, given sufficient space, or if no additional thinning treatments were encountered, downstream cooling then followed as an eventual extended pulse.

In contrast to the waveforms observed in the Tectah watersheds, waveforms in the Lost Man watershed were generally characterized as “no effect”. This is most likely explained by minimal changes in solar radiation associated with the less intensive thinning treatments. Alternatively, the coastal climate, pervasive hyporheic flow, and upwelling groundwater characteristic of the Lost Man watershed may have offset the small increase in solar radiation (Welsh et al. 2000). Distance to edge analyses of cumulative summer degree days did, however, show a localized pulse with a highly truncated extended pulse ~100 m downstream. We did not observe this pattern at shorter temporal scales (e.g., daily, diurnal), suggesting that this waveform only occurred across broader seasonal windows.

Waveforms depicting local radiative and longitudinal advective processes were useful for evaluating and characterizing local and downstream changes in thermal conditions. Although we applied this conceptual framework to specifically evaluate the local and downstream thermal effects associated with riparian thinning treatments, the framework could be used to examine cumulative effects of other disturbances that alter riparian forest conditions in lotic systems that have the potential to propagate downstream. While this approach may be applied most directly to parameters that propagate easily with flow, such as temperature or water chemistry (McGuire et al. 2014, Abbott et al. 2018), it could also be applied to biological responses (e.g., Feijo-Lima et al. 2018).

Biological implications

Stream thermal conditions drive ecological processes in aquatic ecosystems (Magnuson 1979, Cassie 2006, McCullough et al. 2009), so it is crucial to consider the biological implications of the thermal responses we observed to riparian thinning. These watersheds support resident populations of coastal cutthroat trout, coastal giant salamander and coastal tailed frog, all of which are sensitive to changes in temperature (Huff et al. 2005, Bury 2008). While temperature increases exceeded common cold-water thresholds of 15 °C and 20 °C (Fullerton et al. 2018) for prolonged durations during summer months and the realized thermal niche for each species (Huff et al. 2005), they did not exceed the critical thermal maxima for any species (de Vlaming and Bury 1970, Bury 2008, McCullough et al. 2009).

Thermal heterogeneity influences a wide range of species behavior including their distribution, habitat use, growth and development, and movement patterns (Torgersen et al. 1999, Ebersole et al. 2003, Armstrong et al. 2013). In contrast to previous studies documenting the importance of thermal heterogeneity as cold-water refuges in otherwise warm-water systems (Torgersen et al. 1999, Ebersole et al. 2003, Brewitt et al. 2017, Fullerton et al. 2018, Yang et al. 2020), the increases in thermal heterogeneity that we observed added warm-water patches to otherwise cool-water systems. However, it is challenging to predict the effects of this heterogeneity on thermally sensitive ectotherms in these watersheds. First, the extent of thermal fluctuations in space and time vary seasonally. While warm patches may be problematic during summer months when temperature increases exceed the thermal tolerance of the cold-water adapted species, these temperature changes may not cause stress during cooler seasons and instead may actually increase growth rates (Benjamin et al. 2020). Second, the species that occupy these watersheds are highly mobile organisms and have the capacity to avoid warm patches assuming sufficient longitudinal connectivity (Schlosser 1995). In addition, thermal stratification observed in low-flow pools may provide finer-scale thermal refuges in thinned and downstream reaches (Schlosser 1991, Nielson et al. 1994). Third, the ecological effects of temperature increases on ectothermic animals depend on the availability of sufficient prey resources to support increases in metabolism (Schlosser 1991, Hughes and Grand 2000, Armstrong et al. 2013). The collective influences of these factors could be addressed by modeling frameworks that integrate these local and landscape influences on multiple responses (e.g., Railsback et al. 2009, Penaluna et al. 2015).

Management implications

Riparian forests play an important role in regulating stream temperatures (Moore et al. 2005). Thus, it is important to evaluate the potential for cumulative watershed effects when considering changes in riparian forest conditions (Reid 1998, Erdozain et al. 2021). This is especially relevant for resource managers considering thinning and other restoration strategies (e.g., gaps, variable retention buffers) for second-growth riparian forests recovering from previous harvest. In our watershed experiment, we gained valuable insights from a riverscape approach that have direct application to the management of cumulative watershed effects. These considerations include the intensity, scale, spatial proximity, and ecological context of the riparian management actions.

First, downstream effects depended on sufficient local increases in solar radiation and reductions in shade to cause a thermal response. Downstream effects were most pronounced in the Tectah watersheds, which experienced more intensive thinning treatments (20-30% loss in shade) compared to the Lost Man watershed (~4% loss in shade). These results support the hypothesis that thinning less intensively can ameliorate thermal loading of streams – similar to the findings of sufficiently wide riparian buffer widths (Anderson et al. 2007, Groom et al. 2011). As a result, one way to minimize the potential for downstream effects is to thin less intensively. Second, fine-scale Lagrangian profiles indicated that temperatures continued to increase as water traveled through the thinned reaches, peaking at the downstream end of the reach. This suggests that limiting the spatial exposure to the stream channel by reducing the extent of treatments (treating shorter reaches of stream) may be an effective strategy to minimize local and downstream temperature changes. For example, recent studies have shown smaller temperature responses with small-scale riparian gaps < 30 m in length (Coats and Jackson 2020, Swartz et al. 2020). Third, we observed distinct waveforms emerge depending on the spatial proximity of thinning treatments. Cumulative effects only occurred when thinning treatments were spaced close together (< ~400 m apart). Thus, spacing treatments farther apart (~1,000 m or more) could minimize the chances of cumulative effects developing (Reid 1998). Fourth, fine-scale longitudinal profiles indicated that downstream effects were associated with finer-scale habitat features such as low-flow pools formed by old-growth redwood logs that reduced downstream propagation of temperature increases. As a result, geomorphic and hydrologic conditions inherent in the system may influence responses that contribute to the context dependency observed among studies. Consideration of such conditions (e.g., underlying lithology, geomorphology, hydrology, watershed attributes, reach-scale attributes, climate, etc.) provide ecological context to better understand responses to change (Moore et al. 2005, Burnett et al. 2007, Leach et al. 2017, Bladon et al. 2018, Coats and Jackson 2020).

Conclusions

In conclusion, we believe our approach of pairing complementary analyses of spatial and temporal patterns of heterogeneity in a stream network with an interpretive framework is an effective means of bridging the gap between research and management as originally envisioned by the concept of riverscapes (Fausch et al. 2002). Overall, results of this study point to the value of framing management questions so that the relevance of insights revealed by a riverscape approach are immediately apparent. Furthermore, insights afforded by a riverscape approach can reveal emergent patterns that are not easily envisioned within the confines of applied frameworks, which for the sake of implementation are often based on simplified representations of reality (Poole et al. 2004). Arguably it is not reasonable to expect any generalized set of management objectives or criteria to address every conceivable scenario posed by the complex interplay of patterns and processes in riverscapes, so explicitly pairing these perspectives is an effective means of overcoming limitations of each. We believe the approach developed here can be adapted to more broadly to inform decisions regarding influences of human alterations of riverscapes at multiple scales.

Acknowledgements

We thank the project landowners Green Diamond Resource Company and Redwood National Park for guiding the questions addressed in this research, implementing the experimental treatments, and providing access to the study watersheds. We appreciate the financial and logistical support provided by Green Diamond Resource Company, Save the Redwoods League, the Department of Fisheries and Wildlife at Oregon State University, the Bureau of Land Management, and the US Forest Service Pacific Northwest and Southwest

Research Stations. The project depended upon the help of OSU field technicians and aquatic biologists at Green Diamond Resource Company for assistance with field work. We thank Bret Harvey, Dede Olson, Matt Kaylor, and anonymous reviewers for the helpful reviews that greatly improved the quality of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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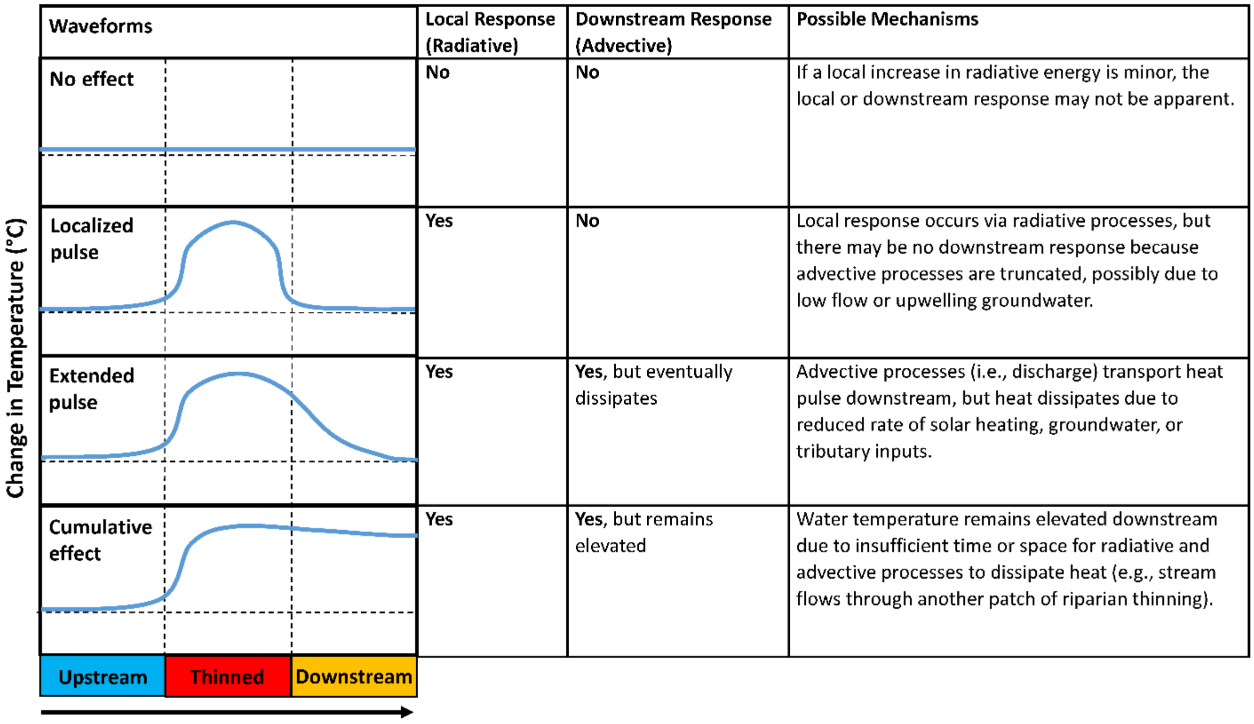
Table 3.1. Physical characteristics for experimental thinning treatment reaches nested within study watersheds.

Watershed	**Watershed area (km^2)**	**Treatment reach**	**Watershed position (m)**	**Treatment reach length (m)**	**Mean bankfull width (m)**	**Change in riparian shade (%)**	**Change in light (%)**	**Local change in summer MWMT (°C)**
West Fork Tectah (GD)	8.4	WFT1_low	140	225	6.6	-25.5	34.8	3.6
		WFT1_up	535	175	6.0	-24.0	32.8	2.1
		WFT2_low	2,750	205	4.7	-26.2	26.4	3.5
		WFT2_up	3,320	195	3.7	-27.2	32.6	4.2
		WFT3	3,840	220	3.2	-23.6	18.2	2.7
East Fork Tectah (GD)	7.8	EFT1_low	4,50	195	5.3	-19.8	21.8	2.8
		EFT1_up	990	170	6.1	-19.2	18.7	1.8
		EFT2	1,850	225	4.6	-30.5	31.2	3.8
Lost Man (RNP)	5.8	LM1	1,450	135	4.5	-4.1	2.7	0.3
		LM2	2,300	140	4.1	-4.7	5.3	0.4

Abbreviations: GD = Green Diamond, RNP = Redwood National Park, WFT = West Fork Tectah, EFT = East Fork Tectah, LM = Lost Man, MWMT = Maximum of the weekly average of the maximum temperature. See experimental design section for explanation for treatment reach abbreviations. Watershed position indicates how far upstream treatment reach occurred from the confluence (in meters). Changes in riparian shade, light, and summer MWMT estimated as the differences between post-treatment and pre-treatment years. See Roon et al. (2021) for more details on methods for shade, light, and stream temperature responses.

Table 3.2. Local and downstream thermal responses associated with thinning at multiple spatiotemporal scales. Descriptions of waveforms are provided in Figure 3.1.

Perspective	Spatial scale	Temporal scale	Response variable	Magnitude of local response	Spatial extent of downstream propagation	Temporal duration	Waveforms
Eulerian	Watershed	Seasonal	Cumulative summer degree days	Tectah: +45 – 115 °C Lost Man: +10 – 15 °C	Tectah: 300 – 1,000 m Lost Man: 75 –150 m	Summer season	Tectah: Extended pulse, Cumulative effect between treatments ≤ 400 m apart Lost Man: Localized pulse
Eulerian	Watershed	Daily	Daily maximum	Tectah: +0.0 – 8.5 °C Lost Man: no change	Tectah: 200 – 1,200 m Lost Man: no change	Tectah: May – September Lost Man: no change	Tectah: Extended pulse, Cumulative effect between treatments ≤ 400 m apart Lost Man: No effect
Eulerian	Watershed	Hourly	Diel fluctuation	Tectah: +2.2 – 6.5 °C Lost Man: no change	Tectah: 200 – 1,200 m Lost Man: no change	Tectah: +0 – 10 hours on warmest day of year Lost Man: no change	Tectah: Extended pulse, Cumulative effect between treatments ≤ 400 m apart Lost Man: No effect
Lagrangian	Watershed	Hourly	Timing of maximum temperature	Tectah: occurred earlier (12:00 – 13:00) Lost Man: no change	Tectah: occurred later (18:00 – 21:00) Lost Man: no change	Tectah: +0 – 4 hours on warmest day of year Lost Man: no change	Tectah: Extended pulse, Cumulative effect between treatments ≤ 400 m apart Lost Man: No effect
Lagrangian	Fine-scale (every 10 m)	Seconds	Instantaneous temperature	Tectah: +2.0 – 4.7 °C Lost Man: no change	Tectah: 150 – 200+ m Lost Man: no change	Tectah: Warm afternoons at low flow Lost Man: no change	Tectah: Extended pulse, Cumulative effect between treatments ≤ 400 m apart Lost Man: No effect



Waveforms	Local Response (Radiative)	Downstream Response (Advective)	Possible Mechanisms
No effect	No	No	If a local increase in radiative energy is minor, the local or downstream response may not be apparent.
Localized pulse	Yes	No	Local response occurs via radiative processes, but there may be no downstream response because advective processes are truncated, possibly due to low flow or upwelling groundwater.
Extended pulse	Yes	**Yes**, but eventually dissipates	Advective processes (i.e., discharge) transport heat pulse downstream, but heat dissipates due to reduced rate of solar heating, groundwater, or tributary inputs.
Cumulative effect	Yes	**Yes**, but remains elevated	Water temperature remains elevated downstream due to insufficient time or space for radiative and advective processes to dissipate heat (e.g., stream flows through another patch of riparian thinning).

Figure 3.1. Four conceptual models for how local changes in temperature associated with riparian thinning propagate downstream. Potential waveforms (far left panels) illustrate different local and downstream thermal responses associated with a patch of riparian thinning and mechanisms via local radiative and longitudinal advective energetic processes.

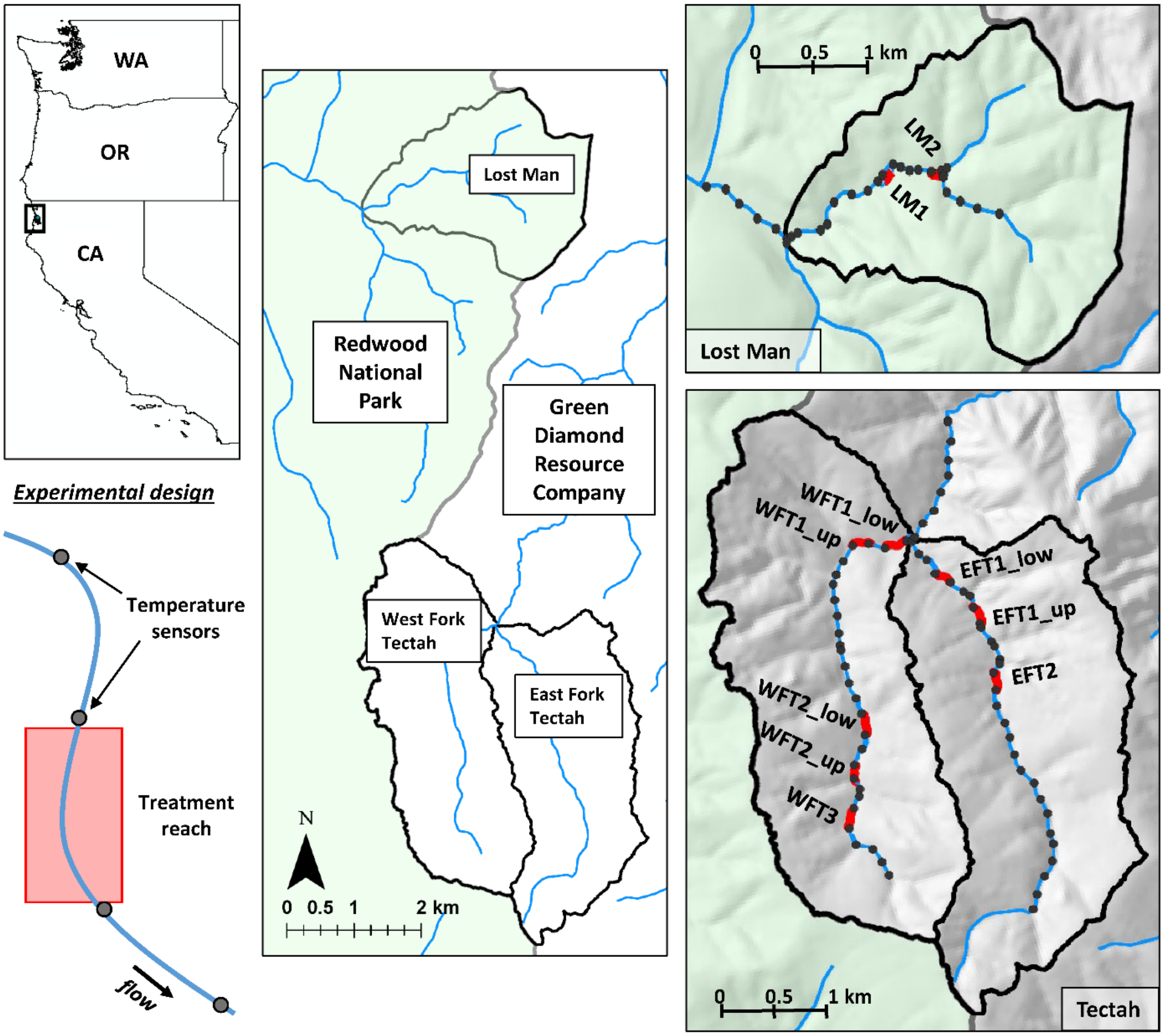


Figure 3.2. Study watersheds, treatment reaches, and experimental design in northern California (USA). Experimental riparian thinning treatments occurred along ~100-200-m reaches of stream in 10 locations distributed across three watersheds. Abbreviated names and red lines on maps indicate the position of treatment reaches in study watersheds. See Table 1 for physical characteristics of treatment reaches and experimental design section in Methods for description of treatment reach abbreviations. Points indicate the positions of temperature sensors ($n = 100$) deployed at upstream and downstream extents of treatment reaches as well as systematically every ~200 m through each study watershed. The high-density sampling design was used to quantify spatial variability, local temperature responses associated with thinning, and downstream propagation of local responses. Data were collected before and after experimental thinning treatments during pre-treatment (2016) and post-treatment years (2018).

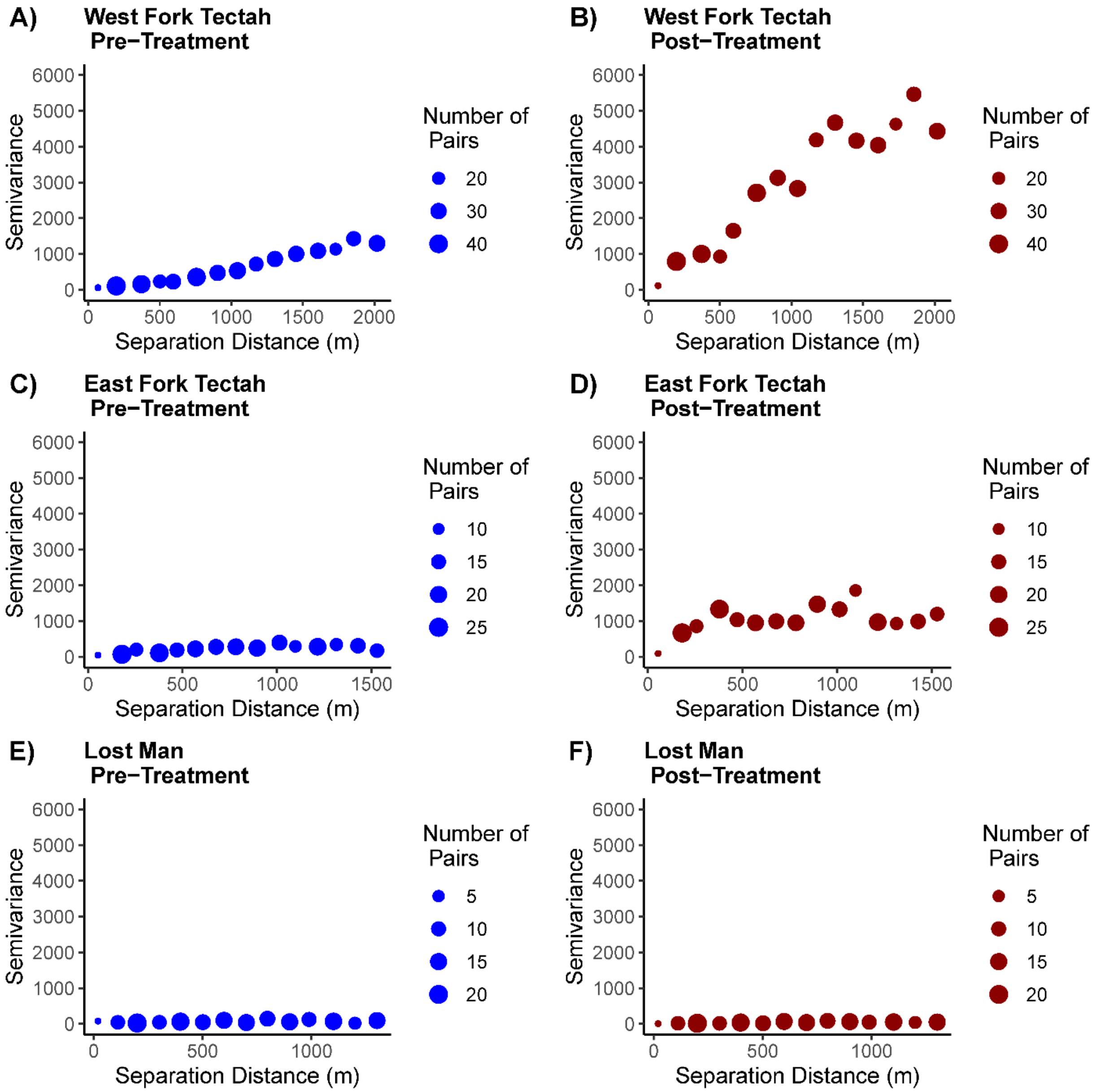


Figure 3.3. Semivariograms depicting spatial autocorrelation in stream temperature (cumulative summer degree days) for each watershed before and after thinning. Size of points indicates the number of pairs at that separation distance.

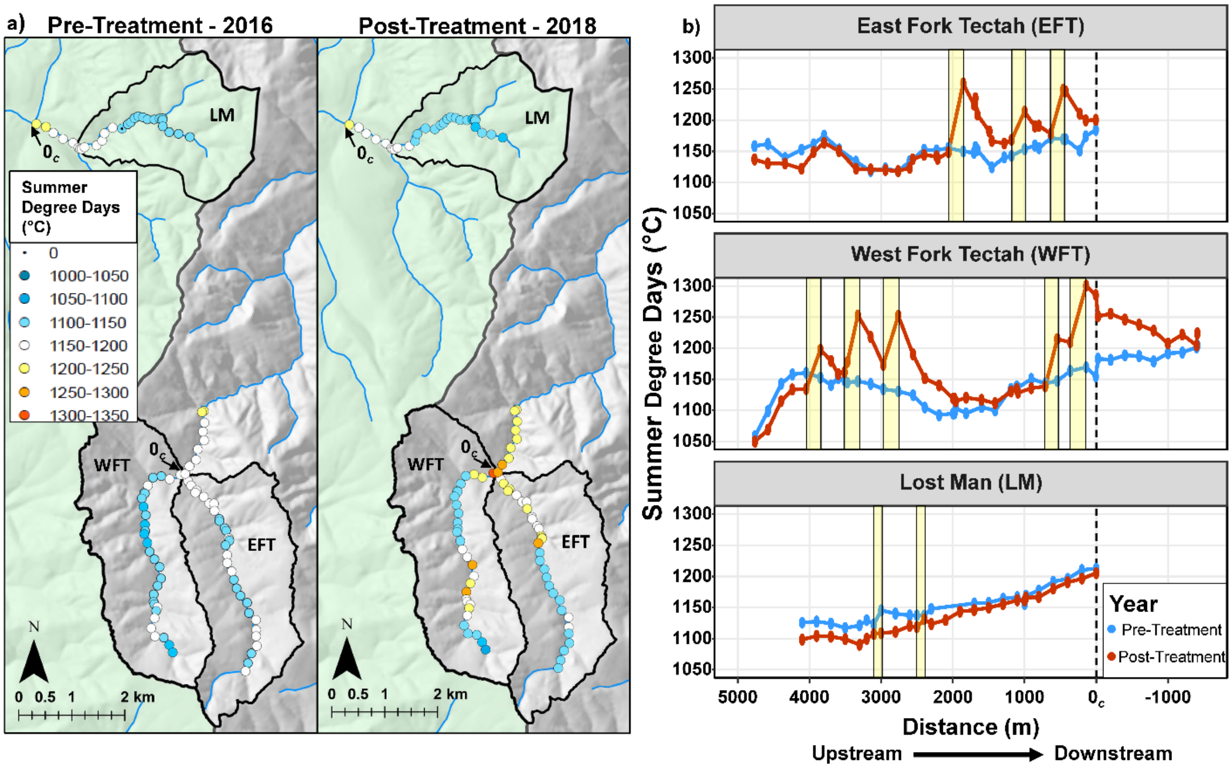


Figure 3.4. Watershed-scale spatial patterns of stream temperature as indicated by summer cumulative degree days during pre-treatment and post-treatment water years. a) Spatial patterns of cumulative degree days between July through September during pre-treatment and post-treatment years. b) Longitudinal profiles of cumulative degree days between July through September for each watershed during pre-treatment and post-treatment years. Points (a) indicate temperature sensors, spatial position in watershed, and conditions during pre- and post-treatment years. Yellow polygons (b) indicate the positions of experimental thinning treatment reaches. X-axis (b) shows the distance upstream from the major confluence (distance = 0_c) in each watershed indicated by a dashed vertical line; the direction of flow (left to right) is shown by the horizontal arrow (b).

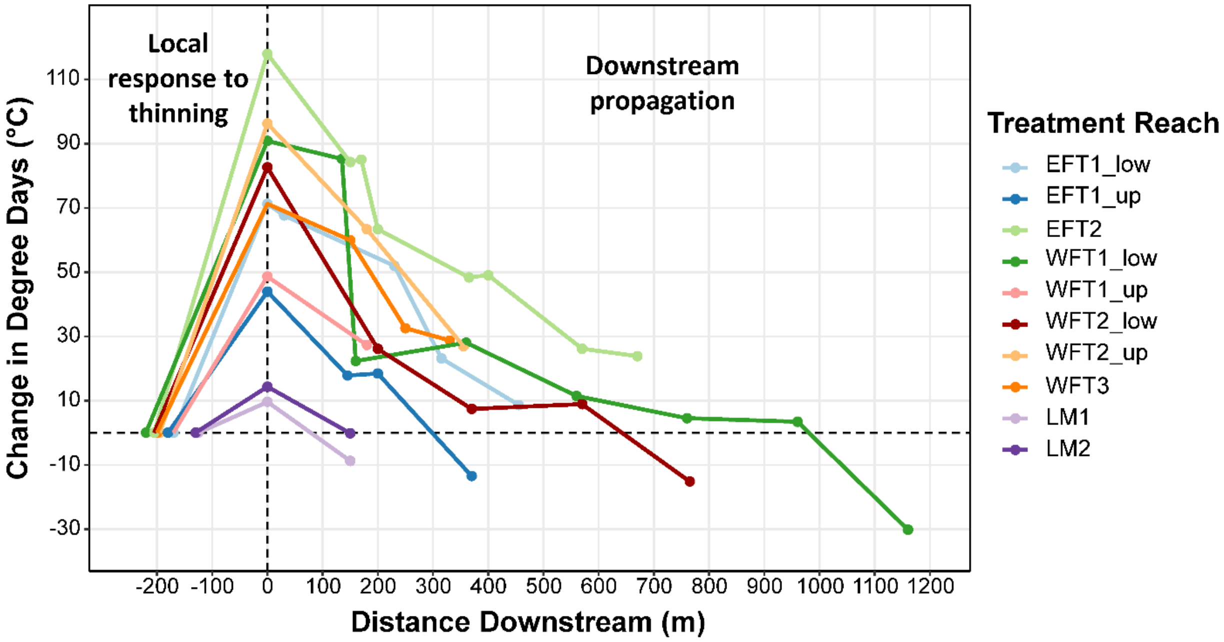


Figure 3.5. Longitudinal profiles of changes in summer cumulative degree days depicting local temperature responses to riparian thinning, downstream propagation of local responses, and variation among treatment reaches. Changes in summer cumulative degree days calculated as before-after differences in temperature where conditions at the upstream end of each thinning reach set to 0 to standardize across treatment reaches. Each line indicates the local response and downstream dissipation of temperature changes associated with treatment reaches (*n* = 10). The magnitude of temperature increase associated with thinning is plotted on the y-axis. Distance downstream from the thinned reach plotted on x-axis where to the left of 0 is position within thinned reach (negative numbers) and to the right of 0 is downstream of treatment (positive numbers).

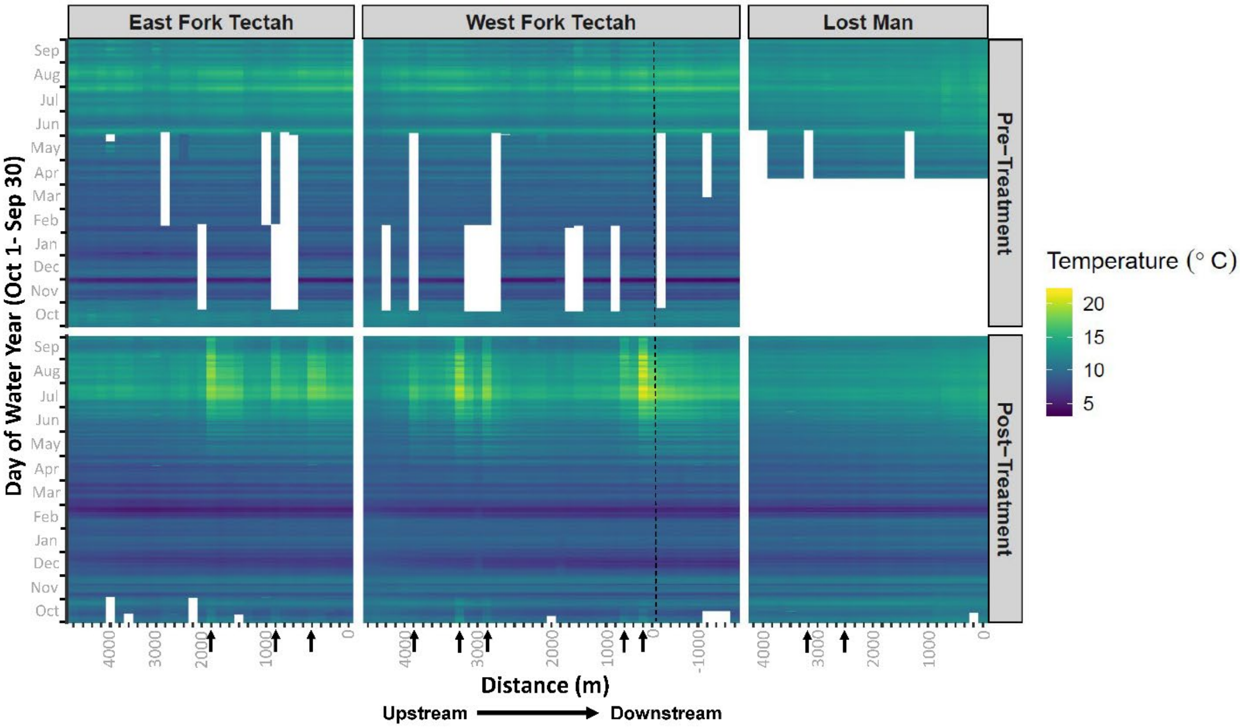


Figure 3.6. Spatiotemporal patterns of daily maximum stream temperature in the study watersheds for pre- (first row) and post-treatment (second row) water years. For each watershed, time is a daily timestep in the water year (Oct 1-Sep 30) on the y-axis, and the spatial position in the watershed (distance upstream from the confluence) is on the x-axis. Direction of flow (left to right) is shown by horizontal arrow. Vertical arrows on the x-axis show the positions of experimental thinning treatments in each watershed. White spaces indicate no data. Dashed vertical line marks stream confluences.

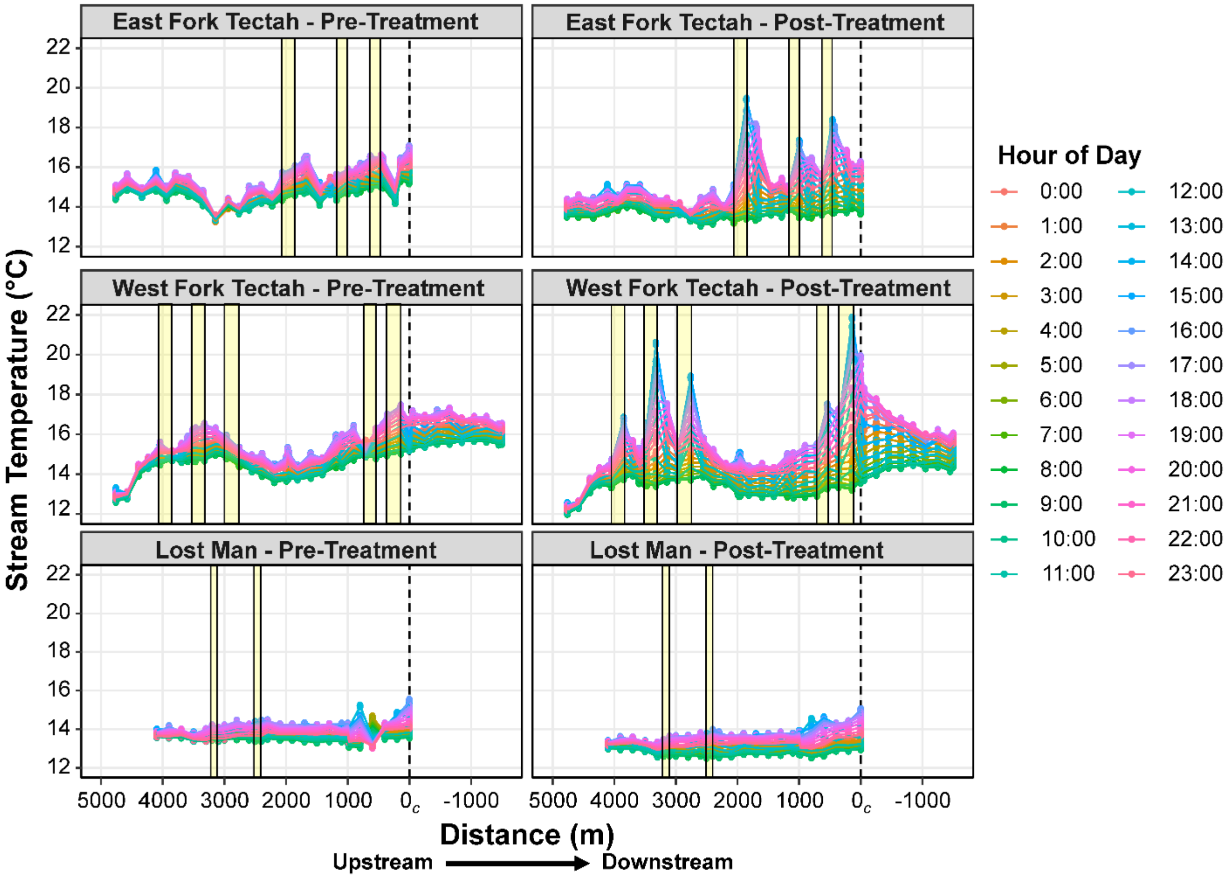


Figure 3.7. Watershed-scale longitudinal profiles of diel fluctuations in hourly temperatures on the warmest day of the year during pre- (30 Jul 2016) and post-treatment years (25 Jul 2018). Yellow polygons indicate the positions of experimental thinning treatments. X-axis shows distance upstream from major confluence (distance = 0_c) in each watershed indicated by dashed vertical line; the direction of flow (left to right) is shown by the horizontal arrow.

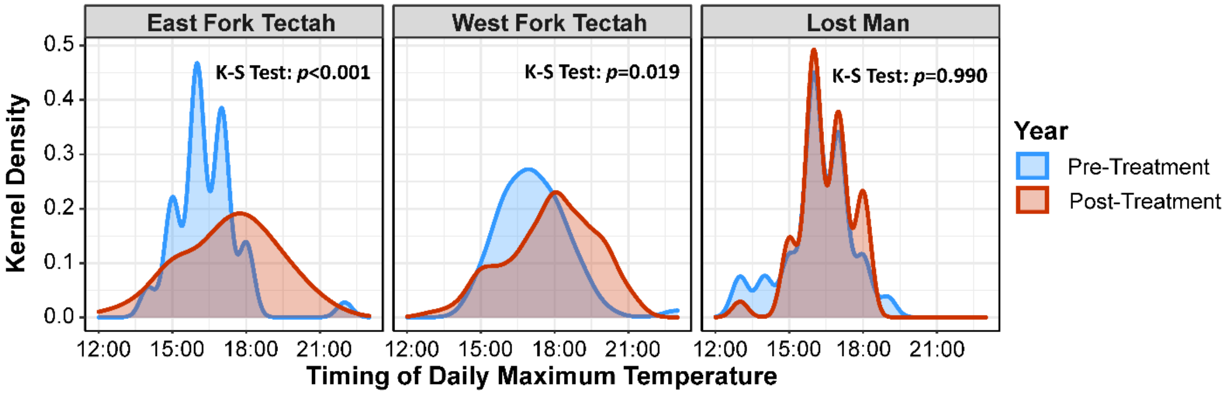


Figure 3.8. Kernel density distributions of the timing of daily maximum temperatures for study watersheds on the warmest day of the year during pre- (30 Jul 2016) and post-treatment years (25 Jul 2018). Non-parametric Kolmogorov-Smirnov (K-S) tests indicate whether the kernel density distributions differed between years (α=0.05).

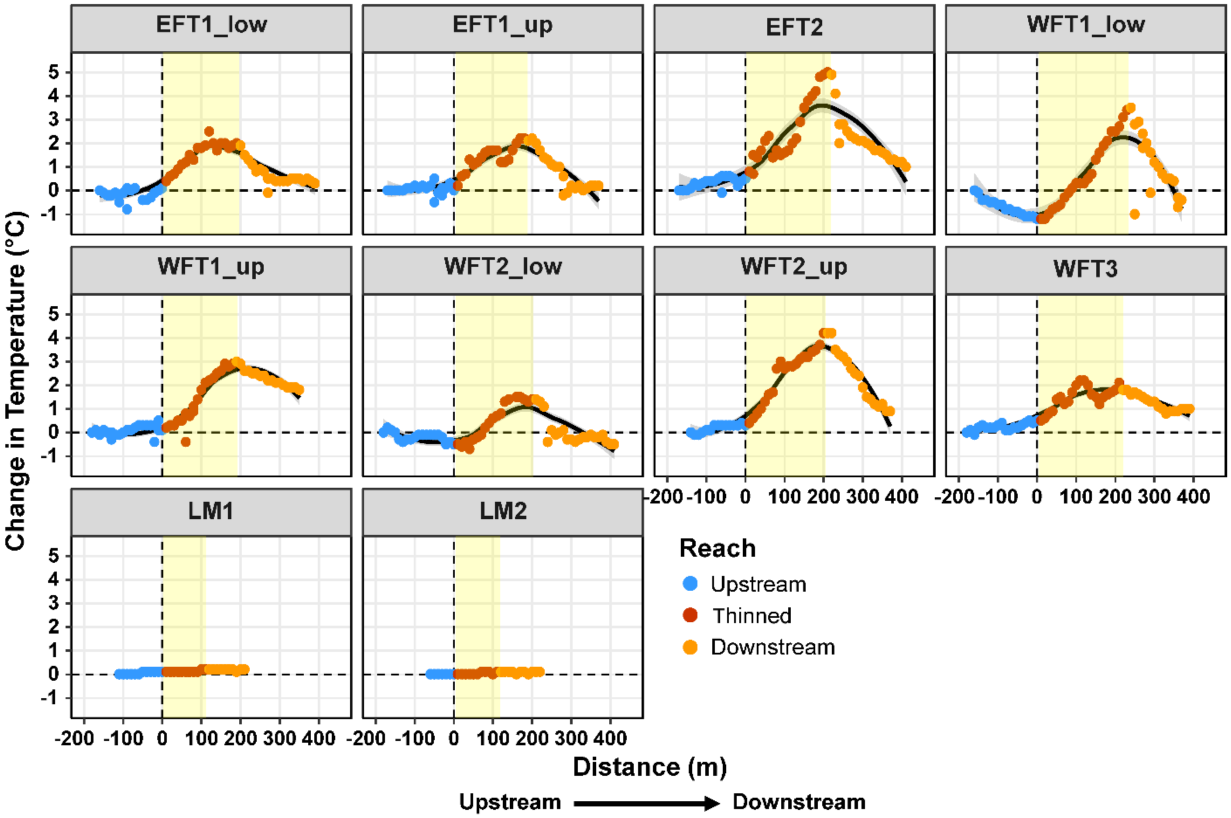


Figure 3.9. Fine-scale Lagrangian longitudinal profiles at 10-m resolution in upstream reference, thinned, and downstream reaches at low-flow during the post-treatment year on 13-24 Aug 2018. Change in temperature on y-axis determined relative to conditions at upstream extent of upstream reference reach. Distance on x-axis set to 0 at upstream extent of thinned reach indicated by dashed vertical line. The boundaries of the thinned reach are highlighted by yellow polygons. Direction of flow (left to right) indicated by horizontal arrow. Smoothed regression line (LOESS) is shown with standard error (grey envelope).

CHAPTER 4: EFFECTS OF RIPARIAN THINNING ON TROPHIC PATHWAYS SUPPORTING STREAM FOOD WEBS IN SECOND-GROWTH REDWOOD FORESTS OF NORTHERN CALIFORNIA

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Abstract

Resource managers seek to thin second-growth riparian forests to increase light to enhance aquatic productivity in watersheds of the Pacific Northwest (USA). However, increases in aquatic productivity depend on and can be mediated by complex food web dynamics that link riparian forests to streams. To determine the extent to which increases in light associated with riparian thinning shifted the trophic pathways supporting stream fish and amphibians, we employed a manipulative field experiment in three watersheds in second-growth redwood forests of northern California. Experimental thinning treatments increased light to the stream, but the magnitude of treatments varied widely between and within watersheds. When we related these increases in light to stream food webs (including stream periphyton, macroinvertebrates, and stream fish and amphibians) we observed limited influences of thinning. Thinning did not change stream periphyton standing stocks on natural substrates, but increased periphyton accrual on ceramic tiles during late-summer, especially under more intensive treatments. Evidence from experimental tiles suggested that periphyton accrual was partially muted due to top-down effects from invertebrate grazers, which were more abundant in thinned reaches. However, macroinvertebrate prey in the diets of the top predators in these streams - coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*) - did not change in quantity, quality, composition, or structure in response to thinning. Community analyses indicated that invertebrate prey resources varied more strongly seasonally and between predators than due to thinning treatments. Stable isotopes supported findings from other analyses indicating that thinning had limited influence on energy flow pathways. Shifts in carbon ($\delta^{13}C$) signatures of stream periphyton due to thinning were reflected to varying extents by primary consumers, but these responses did not propagate up to top predators. Collectively, these results suggest that alleviating light limitation via riparian thinning does not necessarily shift trophic pathways supporting top predators in forested streams, and thus system context should be taken into account when considering thinning as a restoration strategy for riparian and stream ecosystems.

Introduction

Stream ecosystems in forested landscapes are highly dynamic, relying on a combination of energy sources derived locally from within the stream, laterally from the riparian forest, and transported from up and downstream locations via advective processes and species movements (Power and Dietrich 2002, Wipfli and Baxter 2010). The relative importance of these energy sources varies seasonally and spatially within stream networks often depending on streamflow conditions for transport (Humphries et al. 2014). Traditionally, forested headwater streams were thought to rely most on subsidies from the riparian forest in the form of terrestrial leaf litter (Hynes 1975, Vannote et al. 1980, Wallace et al. 1997). Although abundant, allochthonous inputs are of relatively low quality and commonly exported downstream during high-flow events, and so may not contribute as much to the overall energy flow of stream food webs as previously thought (Power and Dietrich 2002, Cross et al. 2005, Marcarelli et al. 2011). A growing body of evidence suggests that autochthonous primary production supports a significant amount of the energy flow in stream networks, even in heavily shaded forested systems (Minshall 1978, Bilby and Bisson 1992, Finlay 2001, Thorp 2002, Rosi-Marshall et al. 2016).

Given their role in modulating energy inputs to streams, changes in riparian forest conditions can directly affect trophic pathways supporting stream food webs (Bilby and Bisson 1992, Hill et al. 1995, Kiffney et al. 2004, Warren et al. 2016). Among a variety of factors that can alter riparian forests, the influences of forest harvest practices have received the most attention. Historically, timber harvest practices that clearcut riparian forests increased autochthonous primary production (Gregory et al. 1987). Resulting shifts in stream food webs towards increased reliance on autotrophic sources of energy can lead to consequences for multiple trophic levels (Murphy and Hall 1981, Gregory et al. 1987, Bilby and Bisson 1992, Wilzbach et al. 2005, Kaylor and Warren 2017). However, riparian forest harvest can increase stream temperatures and elevate fine sediment inputs to streams, which can degrade aquatic habitat conditions (Murphy et al. 1981, Moore et al. 2005, Ashton et al. 2006). Contemporary forest practices now require greater protections for riparian zones (Moore et al. 2005). Intact riparian zones mitigate the effects of adjacent timber harvest on stream temperature and inputs of fine sediment (Moore et al. 2005) and can provide many other ecological functions (Richardson et al. 2012). In response to these protections, riparian zones in much of the Pacific Northwest (USA) have regenerated resulting in dense stands of riparian vegetation that heavily shade streams. Recent research has begun to explore the consequences of such stands for stream ecosystem dynamics (Warren et al. 2016, Kaylor and Warren 2017 and 2018).

Just as historical forest harvest practices motivated concerns over the loss of riparian vegetation, afforestation of riparian zones in response contemporary protective measures has motivated a series of new questions regarding their management. For example, resource managers in the U.S. Pacific Northwest have suggested that thinning of regenerating second-growth riparian forests may achieve multiple restoration objectives (Berg 1995, Pollock et al. 2014, Benda et al. 2016, Reeves et al. 2016). First, thinning may increase heterogeneity in dense, homogenous stands to accelerate the recovery of old-growth forest structure within riparian zones (Russell 2009, O'Hara et al. 2010, Teraoka and Keyes 2011, Keyes and Teraoka 2014). Second, thinning may shift the composition of these forests away from early-seral species like red alder (*Alnus rubra*) towards conifer to promote an eventual source of large wood, which can be important for structuring instream habitats (Pollock et al. 2014, Benda et al. 2016). Both transitions in species composition and delivery of large wood are long-term ecological processes spanning centuries. On shorter timescales, questions emerge about whether thinning may strike a balance between minor increases in stream temperature yet still allow some additional solar radiation to filter through the canopy to enhance aquatic productivity (Wilzbach et al. 2005). Some have even gone so far as to suggest that riparian forests should be managed specifically for increasing the productivity of salmonid fishes (Newton and 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 canopy conditions (Bilby and Bisson 1992, Wilzbach et al. 2005, Kaylor and Warren 2017), we know far less about the effects of more subtle changes in riparian forests. Some recent studies have documented similar outcomes for more subtle changes in riparian canopies (Wootton 2012, Studinski et al. 2015, Heaston et al. 2018), however, other studies point to minimal trophic responses to contemporary forest management practices such as riparian buffers (Kiffney et al. 2003, Bateman et al. 2016, Jensen 2017).

This uncertainty can be partially attributed to the complexity of stream-riparian systems (Gregory et al. 1987, Nakano and Murakami 2001, Baxter et al. 2005, Naiman et al. 2010) where responses can depend on and be mediated by the trophic dynamics that link streams and riparian forests (Lindeman 1942, Power and Dietrich 2002, Bascompte 2010). Management goals often focus on the productivity of target species such as salmonid fishes, but the productivity of a single species 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). Additionally, inherent spatial and temporal variation in environmental conditions and food web structure across stream networks can lead to context dependency in trophic responses (Power and 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 and mechanistic understanding of stream ecosystems and can more effectively address whether thinning enhances aquatic productivity in forested streams (Bascompte et al. 2010, Naiman et al. 2012, Bellmore et al. 2017).

In this study, we evaluated how riparian thinning affected the trophic pathways supporting stream food webs in three watersheds in the 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 in stream food webs including basal resources, macroinvertebrate and amphibian primary consumers, and top predators – coastal giant salamander (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*). To address this objective, we combined data on light, stream periphyton, diets of the top predators, and stable isotopes to track pathways of energy flow. Given that food webs are seasonally and spatially dynamic (Hawkins and Sedell 1981, Polis et al. 1997, Power and Dietrich 2002, Rundio and Lindley 2008, Humphries et al. 2014), we considered 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 objective 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

4.1). First, we hypothesized that increased solar radiation 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 these food webs. Although periphyton is naturally abundant in spring months before deciduous canopies leaf out (Hill 2001), we predicted that thinning would extend the availability of periphyton into summer and fall, thereby increasing the proportion of grazing macroinvertebrates (Gregory et al. 1987, Bilby and Bisson 1992). This in turn would increase the prevalence of grazers in the diets of top predators, thereby shifting energetic pathways supporting upper trophic levels towards autotrophic resources later in summer and fall (Rundio and Lindley 2008, Li et al. 2016). Given their differences in habitat use and foraging behaviors, we predicted differential responses to thinning by top predators. 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 (Parker 1994, Rundio 2002, Falke et al. 2020). 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 towards search-foraging and increasingly rely on inputs of terrestrial invertebrates, so we predicted they would respond less strongly to thinning (Rundio 2002, Harvey and Railsback 2014, Falke et al. 2020). We predicted that local responses to thinning could propagate downstream via increased invertebrate drift and therefore local responses to thinning would be reflected in downstream reaches to a lesser extent (Gregory et al. 1987).

Methods

Study systems

This study took place in three watersheds in the coast redwood forests of northern California (Figure 4.2). 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 (less than 10 km^2), drained by small low-order streams, within 15 km of the coast, that experienced a temperate, maritime climate heavily influenced by coastal fog (Welsh et al. 2000). Study streams exhibited highly seasonal streamflows typical of rain-fed streams of the coastal Pacific

Northwest (Ziemer and Lisle 1998) with peaks during fall through spring months followed by a period of descending summer low flows supplemented by coastal fog, groundwater, and hyporheic flow (Ziemer and Lisle 1998). Thermal regimes largely reflected the seasonality of streamflow: relatively cool in fall through spring months and warmer in summer (Roon et al. 2021).

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

These watersheds supported resident populations of stream fish and amphibians, but the species composition varied between watersheds. Sites in the Tectah watersheds supported coastal cutthroat trout as well as coastal giant salamanders and coastal tailed frogs (*Ascaphus truei*), while sites in the Lost Man watershed occurred above a fish barrier and so only supported stream amphibian species. 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 collected data for this study following a before-after-control-impact (BACI) design (Underwood 1994), where we experimentally manipulated riparian canopy conditions and monitored conditions before and after in reference and treatment locations. We collected data in upstream reference, thinned, and downstream reaches 100-200 m in length and repeated this three-reach design at seven total sites distributed across three watersheds (Figure 4.2, Table 4.1). We collected data during one pre-treatment (2016) and one post-treatment (2018) year. 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 stream food webs (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).

Thinning treatment prescriptions varied between land owners. In the Tectah watersheds, thinning treatments were part of a larger riparian canopy experiment and targeted a reduction to 50% canopy closure within the riparian zone on both sides of the stream channel along a 200 m reach. Thinning treatments targeted red alder and left large conifers that would contribute an eventual source of large wood. Thinning treatments bordered upslope harvest units and removed trees from both sides of the stream channel 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 buffer prescription. In the Lost Man watershed, thinning treatments corresponded with a larger restoration thinning effort to promote the recovery of old-growth redwood forest, and targeted a reduction up to 50% of basal area on both sides of the channel along a 100-150 m reach 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 the streambanks but out of the stream channel. See Roon et al. (2021) for more details on treatment prescriptions.

Light

To quantify changes in light associated with riparian thinning treatments, we measured solar radiation using silicon pyranometers, a broad-spectrum light sensor, deployed above and below the riparian canopy to estimate the amount of light that filters to the stream. We measured solar radiation mid-summer 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

We collected water samples to characterize nutrient concentrations because nutrients can co-limit primary production of stream periphyton (Warren et al. 2017). We collected water samples seasonally from the downstream end of thinned reaches during the pre-treatment year and from the 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

To determine if changes in light associated with thinning influenced periphyton abundance we measured stream periphyton ash-free dry mass (AFDM) on natural substrates (Ambrose et al. 2004). 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.

In the laboratory, we processed samples for AFDM following Hauer and Lamberti (2011). We filtered thawed samples onto pre-weighed 47-mm Whatman 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.

To determine how top-down effects from invertebrate grazers might 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 (1983 and 1985), we deployed unglazed ceramic tiles (225 cm^2) to measure periphyton accrual and invertebrate colonization. To see if invertebrate grazers affected periphyton accrual we manipulated tile elevation, placing half of the tiles on the streambed (more accessible to invertebrate grazers) and the other half on elevated platforms (less accessible to invertebrate grazers). 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 ~ five weeks in late-summer (late July to end of August). At the end of the experiment, we rinsed invertebrates from tiles onto a 500-micron sieve and stored invertebrates in a whirlpak with 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 glass fiber filter folded in quarters, wrapped in foil. All samples were kept frozen before analysis

In the laboratory, we processed AFDM samples following the methods described above. 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 placed 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 to extract chlorophyll *a*. 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 and 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 regressions (Table A4.1).

Macroinvertebrates in diets of stream predators

Rather than tracking the availability of prey sources in the environment, given that predators rely on multiple sources of prey and that availability does not always reflect consumption patterns (Allan et al. 2003, Romero et al. 2005), we directly quantified invertebrate prey in diets of top predators. To evaluate how potential increases in periphyton abundance associated with thinning affected macroinvertebrate prey communities supporting the top predators in these streams, we collected diet samples from coastal giant salamanders and cutthroat trout. 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 to 3 systematically-spaced 40-m sections isolated at the downstream and upstream extents using fine-mesh block nets. Then using a Smith-Root LR 24 electrofisher (Smith-Root Inc., Vancouver, WA USA), we collected amphibians and fish with a single pass moving in an upstream direction (Bateman et al. 2005). We separated species and lifestages in separate buckets to avoid artificial intraguild predation and kept captured amphibians and fish for short periods before processing either in 5-gallon 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 anesthetized trout using AQUI-S 20E (AquaTactics Fish Health, Kirkland, WA USA) and salamanders using MS-222. Once sufficiently anesthetized, we measured length (to the nearest mm) and weight (to nearest 0.1 g) of all individuals captured. We collected diet samples from a random subsample of each species via non-lethal gastric lavage using a 10ml Minipet Aqueous Pipettor, (SP Bel-Art, Wayne, NJ USA) by gently flushing water down the throat until all stomach contents were collected in a whirlpak filled with 90% ethanol. To account for well-documented individual variation (Li et al. 2016, Falke et al. 2020), we collected 10-15 replicate samples for each species per reach at all sites for all three seasons during pre- and post-treatment years for a total sample size of 2499. We then allowed salamanders and trout to recover completely before returning them to the sites of capture.

In the laboratory, we identified, enumerated, and measured the length of all prey items in diet samples to estimate biomass using published length-weight regressions (Table A4.1). We generally identified aquatic invertebrates to family, and to genus in certain families in order to distinguish scraper versus shredder functional feeding groups (Merritt and Cummins 2002). We identified terrestrial invertebrates to order. Composition of macroinvertebrates present in diets were examined and their functional feeding group assigned to infer association with riparian (terrestrial invertebrates and shredders) or freshwater (scrapers, collector-gatherers, collector-filterers, predators, emerged adults, aquatic vertebrates, or unclassified taxa) energy sources following Merritt and Cummins (2002). No reliable sources were found to estimate the biomass of aquatic vertebrates in diets from their length, 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 hours to generate length-weight relationships to estimate biomass (See derived values in Table A4.2). We then converted estimates of dry mass into units of energy density (calories) following the conversions in Cummins and Wuycheck (1971), Hartman and Brandt (1995), and Utz and Hartman (2006) to determine the total amount of energy consumed by trout and salamanders and how that potentially changed with thinning.

Stable isotopes

To complement diet sampling which provides snapshots of prey consumption during specific times of year, we used stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to gain a better understanding of how thinning may affect energy pathways assimilated over broader windows of time (Finlay et al. 2001). Previous research has indicated carbon ($\delta^{13}C$) can be used to distinguish the source material (riparian vs. freshwater) and nitrogen ($\delta^{15}N$) provides an indication of trophic level (Finlay et al. 2001).

We collected materials from each of the major components of the food web predicted to support stream amphibians and fish in sites in the Tectah watersheds. For basal resources, to represent riparian energy sources we collected alder and redwood leaf litter both senesced on the streambank and conditioned in the stream. To represent freshwater energy sources we collected stream periphyton from the streambed by scraping material off rock surfaces with a wire brush. We also collected filamentous algae that appeared in thinned reaches during the post-treatment year. We collected several functional feeding groups of invertebrates and multiple taxa were collected from each group as taxa present varied seasonally and between sampling sites: scrapers (Heptageniidae mayflies, *Juga* snails, Uenoidae caddisflies), shredders (Pteronarycidae stoneflies, Limnephilidae caddisflies), predators (Perlidae stoneflies), emerged adult aquatic insects (adult stoneflies), and terrestrial invertebrates (adult Carabidae beetles, Geometridae moth larvae, Tenthrednidae sawfly wasp larvae, spiders, and millipedes). For stream fish and amphibians we collected a small non-lethal fin or tail clip from costal tailed frog larvae, coastal giant salamanders, and coastal cutthroat trout. 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 increases in variation in carbon and nitrogen 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 4050. All samples were frozen until later analysis. In the lab, 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 abundances of stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) at the UC Davis Stable Isotope Facility (Davis, CA, USA).

Data analysis

BACI analysis

To evaluate the effects of thinning on stream food webs, we applied two approaches. First, we conducted a categorical BACI analysis using linear mixed-effects of models for responses in light, stream periphyton, the quantity (biomass) and quality (energy density) of prey items in the diet, and carbon isotope signatures. BACI models included the fixed effects of Reach Type (upstream reference, thinned, and downstream) and Year (pre-treatment and post-treatment), and an interaction term of Reach Type*Year. To account for spatial variation among sites ($n = 7$), we included a random effect of Site. To determine an effect of thinning we looked for a significant Reach Type*Year interaction ($\alpha = 0.05$). We then estimated BACI responses for thinned and downstream reaches using the following formulas:

BACI response in thinned reaches = (TH2018 – TH2016) – (US2018 – US2016)

BACI response in downstream reaches = (DS2018 – DS2016) – (US2018 – US2016)

We estimated BACI responses with 95% confidence intervals. If 95% confidence intervals did not overlap 0, we considered the effect significant. Some models did not initially meet assumptions of normality or equal variance, so we log-transformed values variables when necessary. Linear mixed effects models were run in the nlme package in R (Pinheiro et al. 2020).

Second, because thinning treatments resulted in a wide range of light responses (Roon et al. 2021), we examined how food web responses related to light as a continuous predictor. To do this, we plotted the relationships between the before-after differences in each food web response variable for upstream reference, thinned, and downstream reaches against before-after responses in light.

Tile experiment

To determine how stream periphyton accrual and invertebrate colonization on ceramic tiles varied between reach types (upstream reference, thinned, and downstream) and to evaluate the top-down effects from invertebrate grazers indicated by manipulating tile elevation (streambed vs. elevated), we used linear mixed-effects models with the fixed effects of Reach Type, Tile Elevation, and a Reach Type*Tile Elevation interaction and random effect of Site. We analyzed linear-mixed effects models using the nlme package in R (Pinheiro et al. 2020).

Community analyses

To determine how thinning affected the composition and structure of macroinvertebrate communities in the diet, we conducted 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 lifestages of aquatic invertebrates, invertebrate shredders, terrestrial invertebrates, and invertebrates of unknown origins. Second, we used non-metric multidimensional scaling ordination (NMS) to visualize how the structure of prey communities varied between watersheds, seasons, predator species, and the BACI design Reach Type*Year. To do this, we used percent composition by biomass data of invertebrate prey communities at family or order level depending on aquatic or terrestrial origin as indicated above. Third, to test for differences according to these factors we applied permutational multivariate analysis of variance tests (perMANOVA). To do this, we constructed a matrix of the relative abundance of invertebrate taxa in the diets based on the percent composition by biomass for all taxa consumed by predators in a reach. We repeated this across all sites, seasons, species and years for a total of 186 observations. Fourth, we used the community matrix to conduct 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 BACI design of Reach Type*Year. All community analyses were plotted in ggplot2 (Wickham 2016); 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 2020) in R (R Core Team 2020).

Stable isotopes

We ran into two issues that prevented use of the traditional mixing model approach to partition energy sources (Jardine et al. 2012, Phillips et al. 2014). First, the carbon signatures of the basal resources (periphyton and riparian leaves) overlapped. Second, the carbon signatures for upper trophic level consumers exceeded the range of the basal resources, even after accounting for trophic enrichment (Phillips et al. 2014). Therefore, we instead evaluated the extent to which changes in carbon signatures of stream periphyton associated with thinning were reflected by higher trophic levels. To do this, we compared BACI responses in $\delta^{13}C$ in stream periphyton to primary consumers, including tailed frog tadpoles and invertebrate grazers (Heptageniidae mayflies, *Juga* snails, and Uenoidae caddisflies), and top predators including Perlidae stoneflies, coastal giant salamander, and coastal cutthroat trout.

Results

Light

Under pre-treatment conditions only a small amount (~5%) of solar radiation reached the stream channel during mid-summer. BACI differences indicated that light levels increased in thinned reaches post-treatment, but responses ranged widely among sites (Figure 4.3). In the

Tectah watersheds thinning increased light levels by a mean of 25% (95% confidence intervals: 18, 33), but in the Lost Man watershed thinning increased only by a mean of 3% (95% confidence intervals: 0, 6) (Figure 4.3).

Nutrients

Nutrient concentrations varied seasonally and among sites, but did not differ due to thinning (Figure A4.1). Pre-treatment data indicated that concentrations of nitrate (NO3-N) in thinned reaches were slightly higher overall and showed more seasonal variation in the Tectah watersheds relative to the Lost Man watershed (Figure A4.1). Post-treatment data indicated that nitrate concentrations increased in the Tectah watersheds in summer relative to pre-treatment conditions, but did not differ in a consistent direction between upstream and thinned reaches (Figure A4.1). Concentrations of phosphate (PO4-P) were slightly lower in Lost Man than Tectah, but otherwise did not vary seasonally or differ between upstream and thinned reaches during post-treatment year (Figure A4.1).

Stream periphyton

Periphyton biomass on natural substrates varied seasonally, but did not differ among reach types during any season (spring, summer, or fall) in either the Tectah or Lost Man watersheds (Figure 4.4). BACI differences indicated that stream periphyton biomass on natural substrates did not increase in thinned or downstream reaches relative to upstream reference reaches during any season ($p > 0.05$) (Figure 4.4). When we related before-after differences in periphyton biomass to continuous increases in light, we found no evidence of relationships between the two variables during any season (spring: $R^2 = 0.12$, $p = 0.27$; summer: $R^2 = 0.01$, $p = 0.71$; fall: $R^2 = 0.01$, $p = 0.65$) (Figure 4.4).

In contrast to standing stocks on natural substrates, in the Tectah watersheds periphyton accrued ~2-4x more late-summer biomass on experimental tiles in thinned reaches relative to upstream and downstream reaches as both AFDM ($p < 0.001$) and chlorophyll *a* ($p < 0.001$) (Figure 4.5a and b). Periphyton accrual also increased by ~60% in thinned reaches in the Lost Man watershed, but did not differ relative to upstream and downstream reaches (AFDM: $p = 0.58$, chlorophyll *a*: $p = 0.64$) (Figures 4.5a and b). Within thinned reaches, periphyton accrual correlated positively with light for AFDM (elevated tiles: $R^2 = 0.56$, $p = 0.054$; streambed tiles: $R^2 = 0.44$, $p = 0.10$), but not for chlorophyll *a* (elevated tiles: $R^2 = 0.00$, $p = 0.97$; streambed tiles: $R^2 = 0.01$, $p = 0.81$), (Figures 4.5a and b). Elevated tiles less accessible to invertebrate grazers supported ~20% more periphyton accrual than streambed tiles more accessible to grazers (AFDM: $p = 0.002$) (Figures 4.5a and b).

Accordingly, tiles in the thinned reaches supported more invertebrate biomass relative to upstream and downstream reaches (Figure 4.5c and d). Invertebrate biomass increased by ~2.5x on the more-accessible streambed tiles ($p < 0.001$) and by ~90% on elevated tiles in the Tectah watersheds, or but did not change for either tile elevation in the Lost Man watershed (Figure 4.5c). This increase in invertebrate biomass in thinned reaches correlated positively with light (streambed: $R^2 = 0.51$, elevated: $R^2 = 0.40$) and periphyton biomass accrual for both streambed and elevated tiles (streambed: $R^2 = 0.46$, elevated: $R^2 = 0.44$). Thinning shifted the composition of invertebrate communities on streambed tiles, toward a greater percentage of invertebrate scrapers (~75% of overall composition) on streambed tiles in thinned reaches relative to upstream and downstream reaches (~60% of overall composition) (Figures 4.5d).

Macroinvertebrates in diets of stream predators

Prey in the diets of coastal giant salamander and coastal cutthroat trout varied seasonally and between predator species, but we observed few differences due to thinning (Figure 4.6). In general, scraper biomass in diets peaked in spring relative to summer and fall for both predators, but BACI differences indicated that salamanders in the Tectah watersheds consumed 0.5 mg/g (95% CI: -1.1, -0.1) or ~2x less scraper biomass in spring in thinned reaches relative to upstream and downstream reaches (Figure 4.6) and correlated negatively with light ($R^2 = 0.41$, $p = 0.024$) (Figure 4.6). In contrast, salamanders consumed 0.3 mg/g (95% CI: 0.1, 0.5) or ~1.5x more scraper biomass in fall in thinned reaches relative to upstream and downstream reaches in the Tectah watershed, and showed a positive relationship with light ($R^2 = 0.3$, $p = 0.019$). Scraper biomass otherwise did not differ in the diets due to thinning or correlate with light for salamanders in the Tectah watersheds in summer, salamanders during any season in the Lost Man watershed, or for cutthroat trout in the Tectah watersheds during in any season (Figure 4.6). Total aquatic biomass in the diets did not differ due to thinning for either salamanders or trout in either watershed during any season, but did show a weak positive relationship with light for salamanders in the summer ($R^2 = 0.17$, $p = 0.062$) (Figure 4.6). Total biomass in the diets did not change due to thinning for either predator for either watershed during any season (Figure 4.6).

Seasonal patterns in total energy consumed by top predators largely reflected patterns in total biomass consumption and showed that total calories in diets did not differ between reach types for either predator during any season (Figure 4.7). Total energy in diets did not correlate with light (Figure 4.7).

The composition of prey in the diets of trout and salamanders when broken down by functional feeding groups showed extensive variation seasonally, between predators, watersheds, and years, but did not vary due to the thinning treatments so results were pooled between reach types (Figure 4.8). 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%, trout: 63.3%). However, prey consumption by the two predators diverged in later seasons, when salamanders continued to rely on freshwater energy sources for over half of the biomass in their diet (summer: 57.4%, fall: 58.1%), but trout increasingly relied on terrestrial invertebrates in summer (40.9%) and fall (64.3%) (Figure 4.8). Salamanders in the Lost Man watershed largely reflected the seasonal patterns of salamanders in Tectah reaches, but relied more on terrestrial invertebrates during summer and fall (Figure 4.8). Consumption of invertebrate scrapers accounted for a substantial portion of the diet for salamanders and trout primarily in spring (11.8 to 32.5%) and continued to be important prey items for salamanders during later months, while becoming less important for trout (Figure 4.8). Top predators also consumed other aquatic vertebrates (trout fry and larval amphibians) especially during summer and fall months (6.7 to 21.3% of diet) (Figure 4.8). Seasonal patterns were largely consistent between years, with some interannual variation of certain taxa such as increased consumption of invertebrate predators and reduced consumption of emerged adult aquatic insects during the post-treatment year (Figure 4.8).

Finer-scale analyses of prey taxa in the diets of coastal giant salamanders and coastal cutthroat trout supported patterns from functional feeding groups finding that the structure of prey communities varied among seasons and between predators, but not due to thinning (Figure 4.9). NMS ordinations showed that the structure of prey communities varied between seasons and predators, but did not vary with thinning as indicated by our BACI model of Reach Type*Year (Figure 4.9). These patterns were supported by perMANOVA tests which determined that the structure of prey communities differed due to season ($p < 0.001$), and predator species ($p < 0.001$), but not due to thinning indicated by the BACI model of Reach Type*Year ($p = 0.375$) (Figure 4.9). Indicator species analyses determined that variation in community structure between seasons was primarily due to the prevalence of drifting taxa in spring (e.g., Baetidae, Ameletidae, Emphemerillidae, and Heptageniidae mayflies, and Elmidae beetles), the influx of terrestrial invertebrates, the emergence of adult aquatics, and the consumption of 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, Pteronarycidae stoneflies, and a combination of cased and free-living caddisflies (e.g., Glossostomatidae, Limnephilidae, Rhyacophilidae, and Uenoidae), while trout relied more on terrestrial taxa, emerged lifestages of adult aquatics, 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

Stream periphyton carbon δ^{13}C stable isotope ratios became more enriched post-treatment with thinning in the Tectah watersheds, although the magnitude of this response varied between seasons (Figure 4.10). BACI differences indicated that carbon signatures increased by 4.1 ‰ (95% confidence intervals: 2.2, 5.9) in spring, 1.6 ‰ (0.6, 2.5) in summer, and by 0.6 ‰ (-0.2, 1.4) in fall (Figure 4.10). These shifts in carbon signatures were partially reflected by primary consumers although responses varied between consumers and between seasons. Tailed frog tadpoles showed consistent increases in carbon signatures 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 the periphyton were not reflected by top predators during any of the three seasons we sampled. 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 were often more muted than in thinned reaches (Figure 4.10). We observed no changes in nitrogen δ^{15}N stable isotope ratios in thinned or downstream reaches.

Discussion

In this study we explored how relatively subtle changes in light associated with thinning riparian forests influenced the trophic pathways supporting stream food webs in a large-scale, replicated field experiment. Results of this work indicated limited influences of riparian thinning treatments on autotrophic pathways supporting the food webs in these forested streams in the first year following thinning. Trophic responses were largely confined to lower trophic levels: trophic pathways supporting top predators showed minimal structural changes to thinning, suggesting either that: 1) increases in light did not generate sufficient energy to propagate up to upper trophic levels; 2) resistance by top predators to changes in stream-riparian food webs; or 3) other factors may be limiting food web dynamics in these forested watersheds.

Stream periphyton responses

Light is a dominant driver of primary production in forested streams (Gregory 1980, Hill et al. 1995, Kiffney et al. 2004), yet we observed mixed responses by stream periphyton to the increases in light associated with riparian thinning. Periphyton standing stocks on natural substrates did not increase with thinning as hypothesized nor did they correlate with continuous estimates of light. In contrast, we observed ~2-4x more periphyton accrual on ceramic tiles in thinned reaches and positive relationships with light. Furthermore, we observed the emergence of filamentous algae in thinned reaches during the post-treatment year that did not otherwise occur under intact canopy conditions. Combined, these results suggest that changes in light associated with thinning were sufficient to alleviate light limitation. These results are supported by recent studies documenting that small changes in light can influence standing stocks of stream periphyton (Kiffney et al. 2003, Wootton 2012, Heaston et al. 2018). Alleviation of light limitation likely varied between watersheds. We observed algal responses only where more intensive riparian thinning treatments increased light to the stream channel by 15 to 35%. However, chlorophyll *a* did not continue to increase with more light, suggesting potential photosaturation under more intensive thinning treatments. Gregory et al. (1987) suggests photosaturation can occur at ~20% light for algal taxa adapted to low-light environments in forested streams, consistent with the increases in light observed in the Tectah watersheds. In contrast, the smaller increases in light in the Lost Man watershed of 3-5% were unlikely to alleviate light limitation and accordingly we observed minimal periphyton responses.

The differential responses we observed between natural substrates and ceramic tiles have been similarly documented by previous studies (e.g., Ambrose et al. 2004). Although Lamberti and Resh (1985) determined that ceramic tiles should approximate stream periphyton abundance found on natural substrates, discrepancies could be due to differences in assemblages where tiles are more likely colonized by early successional taxa while assemblages on natural substrates are more likely composed of more persistent taxa that could be more resistant to changes in light (Ambrose et al. 2004, Danehy et al. 2007, McIntyre et al. 2018).

Many factors beyond light can influence periphyton abundance in forested streams, including nutrients, grazing, and physical factors such as stream temperature. These influences may explain the mixed periphyton responses to thinning in these watersheds (Gregory 1980, Feminella et al. 1989, Rosemond et al. 2000). Stream periphyton is frequently co-limited by the combination of light and nutrients in forested streams (Hill and Knight 1988, Warren et al. 2017) and once light limitation is alleviated, nutrient limitation can then develop. Although nutrients varied seasonally and between watersheds, concentrations were low overall and did not change with thinning. N:P ratios averaged 6.4 (range: 1.9 to 15.5) which suggests the potential for nitrogen limitation (Stelzer and Lamberti 2001). These results are supported by nutrient limitation experiments by Ambrose et al. (2004) that revealed evidence of nitrogen limitation in some of the same study watersheds. A riparian canopy experiment by Wootton (2012) on the Olympic Peninsula determined that reductions in canopy by ~40% in watersheds where nutrients were higher resulted in larger periphyton responses and did not change when nutrients were added. In contrast, McIntyre et al. (2018) posited that the lack of periphyton responses observed over a range of canopy reduction intensities in southwestern Washington streams was likely due to low nutrient concentrations. Collectively, these results suggest that nutrients may be a key limiting factor in our study watersheds.

Top-down effects by invertebrate grazers can mute periphyton responses to changes in riparian canopies (Feminella et al. 1989, Hill et al. 1995). Our tile experiment provided evidence that periphyton accrual was indeed influenced by invertebrate grazers in that elevated tiles supported more periphyton accrual and fewer invertebrate grazers 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 grazer effects. Furthermore, invertebrate communities that colonized tiles in thinned reaches were composed of a greater percentage of grazing taxa suggesting that thinned reaches supported more scrapers consistent with hypotheses predicting strengthened autotrophic processes (Kaylor and Warren 2017). Combined, these results suggest that the lack of periphyton response on natural substrates in thinned reaches could be due in part to grazers.

Temperature can also influence primary production (Gregory et al. 1987, Rosemond et al. 2000), but it appears unlikely to have influenced our results. We observed large temperature responses associated with thinning (Roon et al. 2021), but thermal responses occurred both in thinned and downstream reaches. Given that the limited periphyton responses we observed occurred exclusively in thinned reaches and downstream reaches did not differ from upstream reference reaches provides little evidence that temperature was a major driver of periphyton conditions outside of general seasonal variation. It is unclear the extent to which these factors interact, but light, nutrients, and grazers all appear as likely factors contributing to the variable periphyton responses to thinning in these forested watersheds.

Macroinvertebrate prey community responses

Macroinvertebrates act as important trophic linkages connecting basal resources to top predators and their assemblages can be sensitive to changes in riparian forest conditions (Wallace and Webster 1996, Power and Dietrich 2002). Previous research has documented increases in macroinvertebrate abundance in response to riparian canopy reduction (Bilby and Bisson 1992, Kaylor and Warren 2017), so we predicted that thinning would increase the abundance and shift the composition of macroinvertebrates in the diets of top predators. Contrary to predictions from this hypothesis, however, we observed minimal responses in the quantity, quality, composition, or structure of macroinvertebrate prey resources in top predator diets to thinning. Instead, we found that prey resources in the diets of top predators varied more strongly seasonally and between predators rather than due to thinning treatments.

We predicted that scrapers would be the functional group most likely to respond to increases in light associated with thinning (Kaylor and Warren 2017), yet we observed minor responses in scrapers in the diets of top predators. Responses in scraper biomass consumed by coastal giant salamanders varied between seasons, where salamanders consumed more scrapers in fall, did not change in summer, and decreased in spring. In contrast, we observed no evidence of increased scrapers in diets of cutthroat trout during any season. Community analyses supported patterns in biomass and indicated limited influence of scrapers in predator diets where we observed no evidence that thinning shifted the composition of prey communities towards increased reliance on scraping taxa by stream predators. The exception to this was that indicator species analyses indicated that one of three taxa associated with thinning included a scraping taxon of caddisflies. These results contradict data from experimental tiles indicating that thinned reaches not only supported increased invertebrate colonization but also that scraping taxa composed a greater percentage of invertebrate communities.

Although we observed few effects of riparian thinning on scrapers in predator diets, coastal giant salamanders generally relied more extensively on scrapers than cutthroat trout as expected based on earlier diet studies (Rundio 2002, Falke et al. 2020). Although both predators relied on drifting scraper taxa such as heptageniid mayflies in spring, as previously documented by Parker (1994) and Esseltyn and Wildman (1997), salamanders frequently consumed a wide range of crawling scraper taxa including a large amount of *Juga* snails and stone-cased caddisflies. These taxa are often referred to as "invulnerable grazers", yet the fact they showed up so prominently in salamander diets suggests that these taxa may not act as the "trophic cul-de-sacs" as often assumed (Power and Dietrich 2002, Atlas et al. 2013). These results suggest that although we documented no changes to thinning, salamanders acted as important predators in these streams (Davic and Welsh 2004, Sanchez-Hernandez 2021), and would be more likely to benefit from increases in light than the cutthroat trout in these watersheds.

Minor increases in scraper biomass in predator diets did not affect the total amount of prey in the diets of either predator in any season. We did not detect any changes in the overall quality, quantity, composition, or structure of prey consumed by top predators. These results contradicted our predictions and observations based on findings of other studies (Bilby and Bisson 1992, Kaylor and Warren 2017) and could be attributed to several factors. First, scrapers made up a small portion of predator diets, so had little influence on overall prey consumption. Second, thinning could have increased consumer densities, so total prey consumption may not have changed because it was spread out across more individuals (i.e., increased inter and intraspecific competition). Third, increases in temperature associated with thinning could have increased the metabolic demands and consumption rates of predators, resulting an overall increase in prey consumption, but could be difficult to detect by diet sampling due to associated increases in digestive rates (Hughes and Grand 2000). Fourth, prey consumption by top predators could be limited by other factors such as fear of predation by terrestrial predators (e.g., birds and mammals), preventing salamanders and trout from feeding at their maximum rate (Harvey and Nakamoto 2013, Harvey and White 2017, Penaluna et al. 2021). It is challenging to identify which of these factor(s) may be responsible for driving these patterns, but the application of a quantitative food web approach (e.g., Bellmore et al. 2013) that can more formally incorporate top predator responses could help address predictions from some of these hypotheses.

Results from community analyses suggested that prey communities supporting top predators varied more strongly seasonally and between predators than due to thinning. This is likely due to seasonal shifts in foraging behavior in response to fluctuating streamflows (Rundio and Lindley 2008, Harvey and Railsback 2014, Humphries et al. 2014, Li et al. 2016, Falke et al. 2020). Salamanders and trout diets coincided the most in spring during high flows when benthic and drifting sources of prey likely overlapped. However, as flows receded predator diets diverged. Salamanders continued to rely on benthic invertebrates during summer and fall (Falke et al. 2020), while trout shifted foraging behaviors as drift declined with decreasing flows (Harvey and Railsback 2014, Hollis 2018) towards other prey sources such terrestrial invertebrates, adult aquatic insects, and trout fry. NMS ordinations, however, suggested that trout and salamanders continued to rely on distinct prey communities across all three seasons, suggesting niche partitioning remained between these top predators at finer-scales of taxonomic resolution (Rundio 2002, Sepulveda et al. 2012). These patterns stayed intact even after thinning, suggesting that seasonal variation in predator diets likely exceeded treatment effects due to thinning (Morley et al. 2016).

Community analyses highlighted that terrestrial invertebrates from the riparian forest acted as important prey sources for both predators in these forested watersheds (Nakano and Murakami 2001, Romero et al. 2005). Terrestrial invertebrates were more important for cutthroat trout accounting up to ~65% of their diet in the fall, as documented by many previous studies (Hetrick et al. 1998, Nakano and Murakami 2001, Romero et al. 2005, Li et al. 2016). However, terrestrial invertebrates were also surprisingly important prey resources for salamanders, more so than previously documented (Parker 1994, Esseltyn and Wildman 1997, Falke et al. 2020). Salamander reliance on terrestrial invertebrates varied between watersheds; terrestrial invertebrates composed a larger portion of their diet (~54% of diet in fall) in the Lost Man watershed where salamanders were the sole top predator than in the Tectah watershed (~28% of diet in fall), providing evidence of niche partitioning where trout and salamander co-occur (Rundio 2002, Sepulveda et al. 2012). Despite the reductions in canopy closure with thinning treatments, we observed no negative effects of thinning on terrestrial prey consumption by either predator. These results are supported by Studinski et al. (2015) that documented that terrestrial invertebrate inputs to streams increased in response to canopy treatments that removed 90% of the basal area in streams located in West Virginia. Similarly, Musetta-Lambert et al. (2019) documented either that terrestrial invertebrate abundance did not change or increased in response to timber harvest relative to reference streams in headwater systems in boreal Canada. It is unclear why terrestrial invertebrates were not affected by thinning treatments, but it could be due to increases in air temperature that influenced their metabolism and activity. Given that riparian forests tend to support unique terrestrial invertebrate assemblages (Rykken et al. 2007), their prevalence in predator diets highlights the importance of lateral sources of energy in these small forested streams even after thinning (Humphries et al. 2014).

Stable isotope responses

Carbon stable isotopes supported results from other methods finding that thinning primarily influenced lower trophic levels and 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). However, the magnitude of these shifts varied seasonally, suggesting seasonal variation in the composition of periphyton communities (Finlay 2001, McCutchan and Lewis 2001, Hill and Middleton 2006). Primary consumers sometimes reflected these shifts in carbon, but responses varied across taxa and seasons. Some responses in carbon by primary consumers (e.g., Uenoidae caddisflies, Heptageniidae mayflies) occurred during later seasons, but this could be due to differences in metabolism among primary consumers which affects the timing of their assimilation of changes in carbon sources (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 carbon signatures in stream periphyton in response to canopy treatments of similar magnitude on the Olympic Peninsula in Washington, but in their case this shift in carbon propagated up to the top consumer in the system - juvenile coho salmon. In contrast, McIntyre et al. (2018) observed no change in stable isotope signatures in response to a range of riparian buffer treatments across multiple trophic levels in Washington streams, including stream amphibians. As a result, McIntyre et al. concluded that terrestrial resources were more likely sources of energy at their study sites. Similarly, terrestrial invertebrates had some of the most enriched carbon signatures of the taxa we sampled and overlapped closely with cutthroat trout, confirming patterns in the diets that terrestrial invertebrates acted as important prey sources (Figure A4.2). While we could not run a mixing model to partition aquatic and terrestrial energy sources (Jardine et al. 2014, Phillips et al. 2014), tracking shifts in carbon signatures of stream periphyton as part of our BACI study design, which can account for both interannual and treatment-level variation, provided a useful approach for detecting changes to thinning.

Shifts in the seasonal and spatial dynamics of food webs

We predicted that increases in light associated with thinning could extend the influence of autotrophic processes – both seasonally and spatially in these watersheds. Some of our observations in thinned reaches supported this prediction of seasonal influences: increased periphyton accrual on tiles during late summer, increased scraper consumption by salamanders in fall, and shifted carbon signatures by primary consumers during summer and fall months although carbon signatures for periphyton shifted the most in spring. Most food web studies focus on summer months (e.g., Bilby and Bisson 1992) and so fewer have explored seasonal dynamics (but see Rundio and Lindley 2008, Li et al. 2016, Falke et al. 2020). In contrast, we saw little evidence of spatial influence when we examined whether local responses observed with thinning propagated into downstream reaches. We predicted that downstream propagation could occur via increased local primary production leading to increased invertebrate drift into downstream reaches. However, in contrast to the downstream effects we observed with stream temperature (Roon et al. 2021), we found no evidence that food web responses propagated downstream. This could be because local responses were minor so there was little energy to propagate or that responses did not propagate very far (Danehy et al. 2011). Alternatively, this could be due to the timing of food web responses, which were predicted to coincide with summer low flows, a time of truncated longitudinal connectivity that likely limited the chances of downstream propagation (Ward 1989, Humphries 2014, Feijo-Lima et al. 2018, Hollis 2018).

Hypotheses to explain lack stream food web responses to thinning

We propose four hypotheses that can explain the limited influence that riparian thinning had on stream food webs in the forested watersheds studied herein. First, from a second-law of thermodynamics perspective, although thinning treatments were sufficient to alleviate light limitation for primary production, they did not generate enough energy to propagate up to top predators as evidenced by prey in diets and stable isotope signatures of top predators. This hypothesis is supported by the fact that – for the variables we measured – responses were largely constrained to lower trophic levels and had little influence on top predators. While we observed some responses in basal resources in terms of periphyton biomass and in shifts in carbon isotope signatures, we saw very few if any responses reach upper trophic levels as indicated by diets or in stable isotopes. Second, it could be that top predators were largely resistant to changes associated with thinning. This is supported by the fact that despite large reductions in canopy associated with thinning treatments, consumers continued to rely on the same prey sources during different seasons. Resistance by aquatic food webs has been previously documented to other terrestrial disturbances such as wildfire (Lewis et al. 2014) or invasive species (Roon et al. 2016, 2018). Third, it could be that other factors may be limiting in the system that could have prevented food web responses to thinning. Results from periphyton responses to thinning suggests that periphyton was likely co-limited by nutrients (Warren et al. 2017). So regardless of whether thinning alleviated light limitation in these streams, if nutrient concentrations were low then it would be unlikely for effects to propagate up the food web. Alternatively, top predators could also be limited by other factors such as avoidance of terrestrial predators or territorial behavior, which may have prevented them from taking advantage of potential increases in benthic prey availability (Harvey and Nakamoto 2013, Harvey and White 2017, Penaluna et al. 2021). Finally, it could be that biological responses simply required more time to generate than we could capture in the short time frame of this study that only examined responses one year post-treatment. Future studies that monitor responses over time would help address this hypothesis.

Management implications

Natural resource managers increasingly engage in ecosystem restoration to mitigate the legacy effects of previous land-use activities (Carey 2003, Burgi et al. 2017). Disturbance, even small ones, can be a major driver of ecosystem structure in streams (Resh et al. 1988, Wootton et al. 1996), and although much research focuses on aquatic disturbances such as floods, terrestrial disturbances can also exert strong influences on stream food webs (Power and Dietrich 2002, Warren et al. 2016). An initial understanding of the structure of ecological networks is essential in order to address the complex and variable responses of ecosystems to changes ranging from disturbance to ecological restoration (Bascompte 2010). As a result, scientists are increasingly calling for the application of food web studies (Vander Zanden et al. 2006, Naiman et al. 2012, Bellmore et al. 2017) to provide a mechanistic perspective of how ecosystems respond to such changes as trophic interactions can mediate responses to disturbance (Power and Dietrich 2002, Amundrud and Serivastrava 2016, Bellmore et al. 2017, Whitney et al. 2020). By applying a food web perspective in this study we were able to address key questions about whether riparian thinning enhanced aquatic productivity via strengthened autotrophic pathways supporting stream food webs. We observed partial influence of riparian thinning on stream food webs in the first year after thinning. This could be due to a range of factors that range from co-limitation of periphyton with nutrients, limited energy did not track up to food webs, or consumers were buffered by other sources of prey (e.g., terrestrial resources). Insights from these results have direct application for managers considering whether thinning may be a viable restoration strategy. Here we suggest some implications for managers.

First, *study system context matters*. We did not see major shifts in food webs towards increased autotrophic processes with thinning. By taking a whole-system, food web perspective we were able to identify some likely constraints that could have contributed to the limited response of stream food webs in these watersheds. Our data indicated that low nutrient concentrations could in part have limited food web responses to thinning. These results suggest that outcomes do not always match initial expectations (Bateman et al. 2016, Nash et al. 2021) and that responses can be contingent upon the context of study system. Given that stream networks exhibit extensive spatial heterogeneity, it is not surprising to see different responses among locations (Whitney et al. 2020). These responses suggest that riparian thinning as a management tool to enhance aquatic productivity may be of limited benefit in low nutrient systems like coastal headwater streams. In short, understanding of system context is essential.

Second, *stream-riparian food webs are complex and rely on multiple sources of prey, not just autotrophic pathways of energy flow.* Although we saw that thinning locally increased light to the stream, we observed only minor increases on autotrophic pathways supporting the food webs in these forested watersheds. Instead we found that top predators relied on a wide range of other prey sources, including substantial support from lateral sources from the riparian forest in the form of terrestrial invertebrates especially during summer and fall. This is not a new finding on its own (Nakano and Murakami 2001, Allan et al. 2003, Romero et al. 2005), but underappreciated by recent efforts that have focused on boosting productivity in forested headwater streams that are often oligotrophic (Hetrick et al. 1998, Newton and Ice 2015). Our results emphasize the complexity of stream-riparian food webs and the fact that energy flow in these tightly coupled systems are derived from multiple sources beyond just local sources of energy (Schlosser 1991, Polis et al. 1997, Power and Dietrich 2002, Wipfli and Baxter 2010). Although previous research has examined the importance of terrestrial subsidies to forested streams much of this research has focused on lower-quality inputs of terrestrial leaf litter (Wallace et al. 1997, Collins et al. 2015, Erdozain et al. 2019). Considering that these watersheds are heavily forested (Hynes 1975), more information is needed about the sources of terrestrial invertebrates and their responses to forest harvest (but see Rykken et al. 2007, Studinski et al. 2015, Musetta-Lambert 2019). By more fully considering the complexity of stream-riparian systems that a food web perspective provides (Gregory et al. 1991), it is possible to better understand how they are structured and how they respond to change (Bascompte et al. 2010).

Ultimately, the implications of our findings depend on the objectives of resource managers. If managers are simply interested in making sure riparian management does not have adverse effects on adjacent aquatic systems and biota, then these results support the fact that thinning produced little effect on the responses considered herein. However, if managers are interested in thinning to enhance aquatic productivity, this study indicated limited benefits at least in the first year after thinning. Furthermore, given the importance of terrestrial resource subsidies for aquatic consumers combined with the limited changes in autotrophic pathways supporting food webs of top predators suggests that this may not be a realistic expectation as some claim (e.g., Newton and Ice 2015). This is especially so if other factors, such as nutrients, are limiting (Warren et al. 2017). Given that thinning can increase stream temperatures (Roon et al. 2021), future research needs to consider the interactions of thermal and trophic responses to further evaluate if thinning can actually strike a balance between the two (Wilzbach et al. 2005) or if will result in an ecological trade-off more similar to previously documented impacts with historical timber harvest practices (Murphy and Hall 1981, Bilby and Bisson 1992). The combination of that information will help managers determine if thinning is a feasible restoration strategy for second-growth riparian forests recovering from previous harvest.

Acknowledgements

We thank project stakeholders for helping frame this research, implementing experimental treatments, and providing access to study watersheds. In particular, thanks to field and laboratory technicians (Kyle Smith, Jerika Wallace, Thomas Starkey-Owens, Mary Carlquist, Ashley Sanders, Morgan Turner, Alex Scharfstein, Cedar Mackaness, and Laura

Nepstad), aquatic biologists at Green Diamond that helped with field sampling (Teal Richards-Dimitre, Dave Dimitre, Matt Kluber, Will Devenport, Matt Nannizzi, Sean Studer, Mike Zontos, Jon Pini, and Jonathan O’Connell), and student volunteers for help with field sampling in Lost Man watershed. We also thank Sherri Johnson for providing space for processing periphyton samples, the PNW Research Station and Ivan Arismendi for providing space for processing macroinvertebrate samples, Dana Warren and Matt Kaylor for guidance and lending equipment for chlorophyll *a* analysis, and Collin Eagles-Smith, Steve Perakis, and OSU Stable Isotope Laboratory for providing space to prepare stable isotope samples. This research was supported by funding from Green Diamond Resource Company, Save the Redwoods League, US Forest Service, and the Department of Fisheries and Wildlife at Oregon State University. This study was conducted according to protocols approved by OSU Animal Care and Use Permit #5037 and California Department of Fish and Wildlife Scientific Collection Permit #13298 and 6348.

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Table 4.1. Characteristics of experimental thinning reaches in the Tectah and Lost Man watersheds in northern California, USA. MWMT = Maximum weekly average of the maximum temperature.

Watershed	**Site**	**Watershed Position – distance upstream from confluence (m)**	**Reach Length (m)**	**Bankfull Width (m)**	**Change in Riparian Shade (%)**	**Change in Stream Temperature (Summer MWMT - °C)**
East Fork Tectah	EFT1	990	210	6.1	-19.2	1.8
	EFT2	1850	170	4.6	-30.5	3.8
West Fork Tectah	WFT1	535	175	6.0	-24.0	2.1
	WFT2	2750	205	4.7	-26.2	3.5
	WFT3	3840	220	3.2	-23.6	2.7
Lost Man	LM1	1450	125	4.5	-4.1	0.3
	LM2	2300	130	4.1	-4.2	0.4

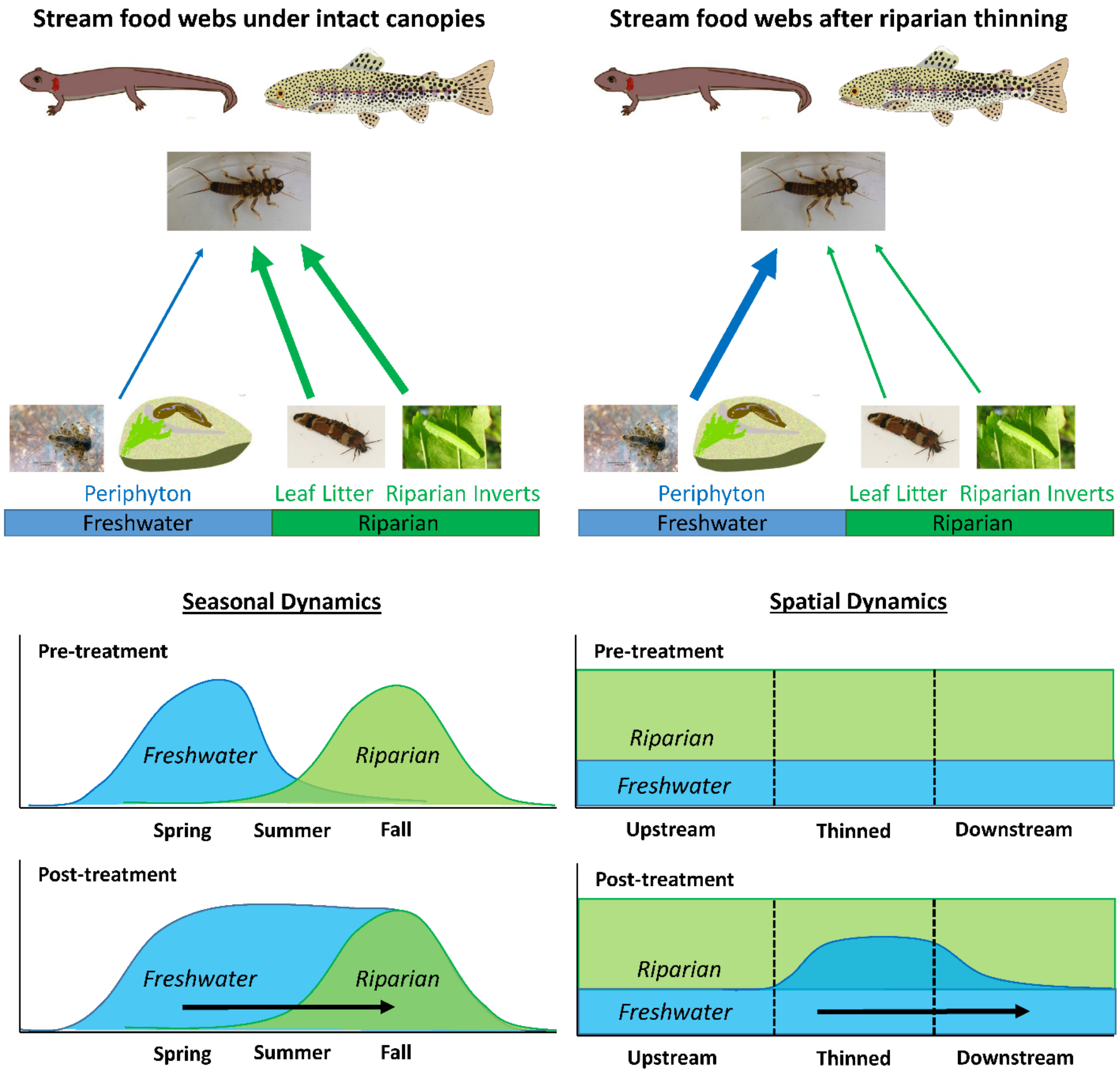

Figure 4.1. Conceptual models of (a) how riparian thinning could shift trophic pathways in stream food webs and (b) how thinning could shift seasonal and spatial dynamics of stream food webs in these forested watersheds.

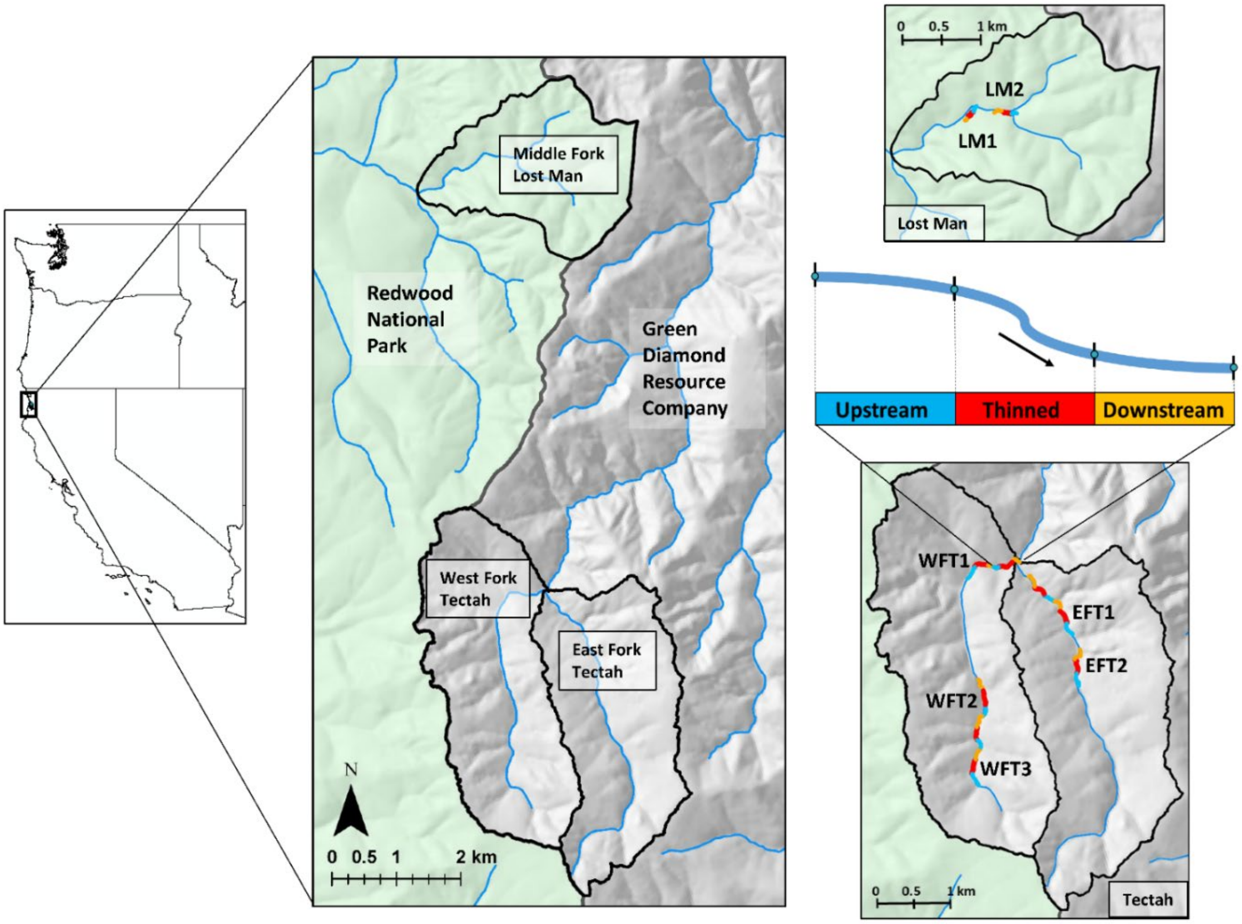

Figure 4.2. Study sites and watersheds in northern California, USA where we examined stream food web responses to riparian thinning. The inset line represents the experimental design where each study site consisted of an upstream reference, thinned, and downstream reach. This three-reach sequence was repeated across 7 total sites in three watersheds. Site names indicate watershed abbreviations: EFT = East Fork Tectah, WFT = West Fork Tectah, and LM = Lost Man.

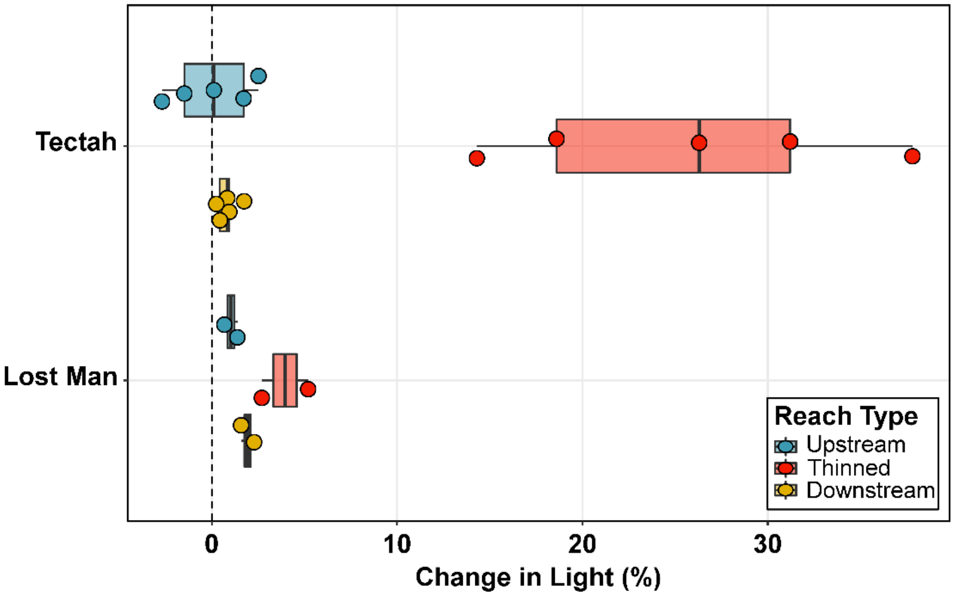

Figure 4.3. Responses of below-canopy light (%) between pre-and post-treatment years in upstream reference, thinned, and downstream reaches for sites in the Tectah and Lost Man watersheds in northern California, USA. Points represent mean values of individual sites while boxplots show the distribution of data.

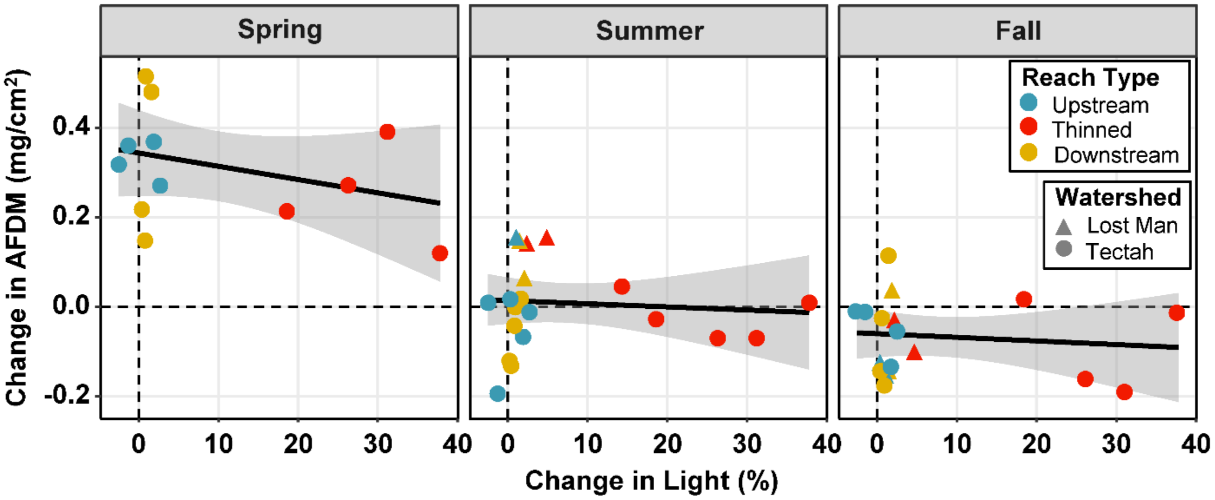

Figure 4.4. Seasonal responses of stream periphyton standing stocks on natural substrates versus responses in light in upstream reference, thinned, and downstream reaches for sites in the Tectah and Lost Man watersheds in northern California USA. Periphyton responses were characterized as the difference in ash-free dry mass (AFDM) in pre-and post-treatment years. Points represent mean values of individual sites while the trend line and associated standard error shading indicate the direction of the relationship.

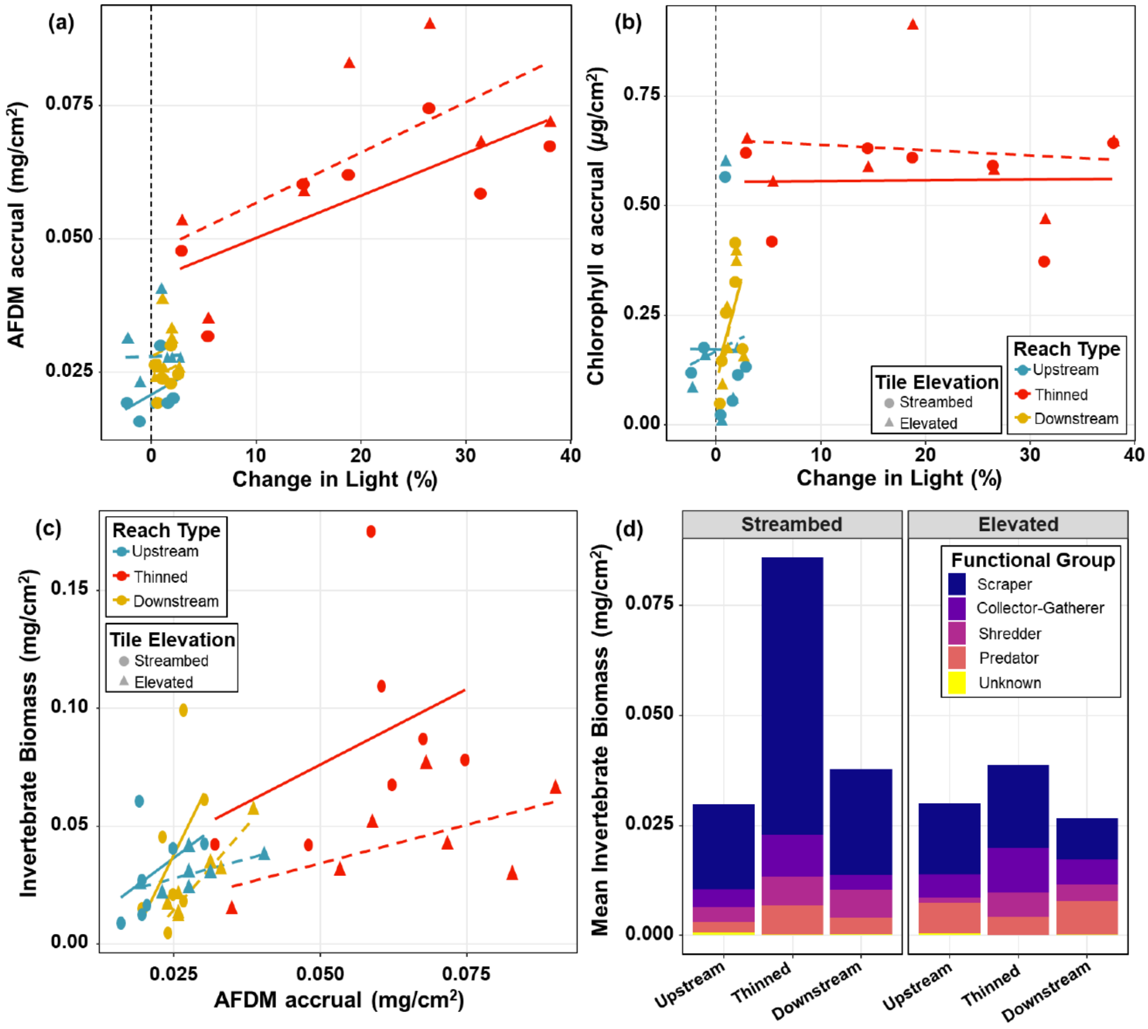

Figure 4.5. Post-treatment patterns of stream periphyton accrual and invertebrate biomass on streambed and elevated ceramic tiles during summer low flows in upstream reference, thinned, and downstream reaches in the Tectah and Lost Man watersheds in northern California, USA. Relationships between stream periphyton accrual and responses in light as (a) ash-free dry mass (AFDM) and (b) chlorophyll *a*. Points indicate mean values of individual sites where shape indicates tile elevation and color indicates reach type. The direction of the relationship indicated by trend lines with solid lines indicating trends for streambed tiles while dashed lines indicating trends for elevated tiles. Invertebrate colonization on experimental tiles characterized as (c) the relationship between invertebrate biomass and periphyton biomass following the structure described in plots a and b, and (d) the composition of invertebrate communities.

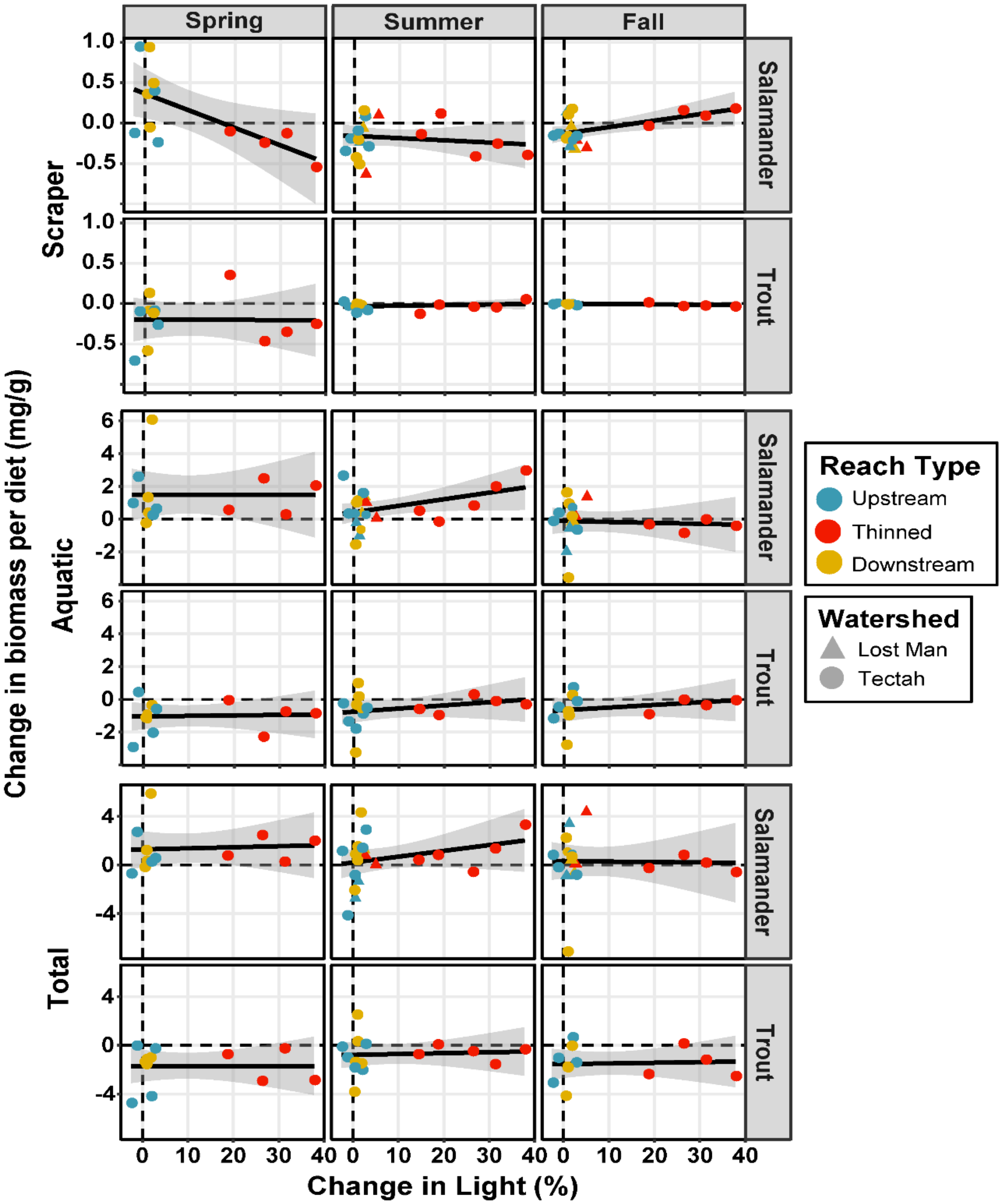

Figure 4.6. Seasonal responses of macroinvertebrate prey biomass in the diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*) versus responses in light in upstream reference, thinned, and downstream reaches for sites in the Tectah and Lost Man watersheds in northern California, USA. Macroinvertebrate prey biomass in diets characterized as (a) scraper biomass, (b) aquatic biomass, and (c) total biomass. Prey biomass (mg) in diet is standardized per gram of consumer. Points represent mean values of individual sites while the trend line and associated standard error shading indicate the direction of the relationship.

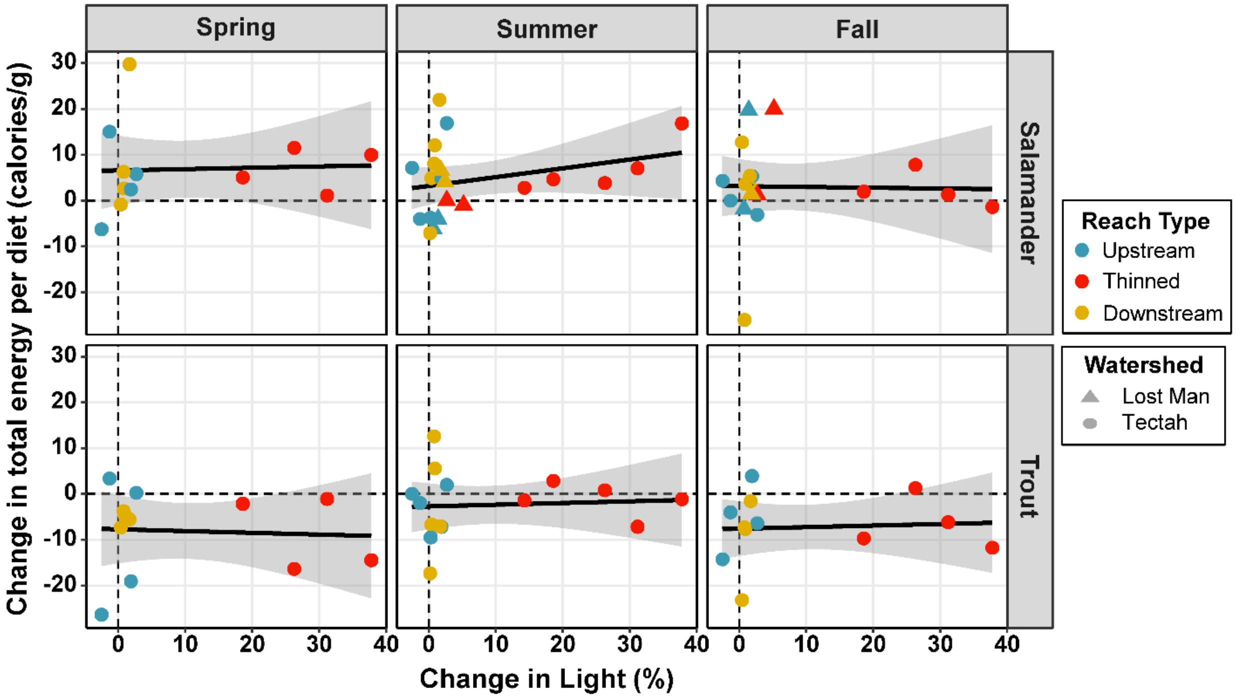

Figure 4.7. Seasonal responses of total energy of prey items in diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*) versus responses in light in upstream reference, thinned, and downstream reaches for sites in the Tectah and Lost Man watersheds in northern California, USA. Total energy (in units of calories) in diet is standardized per gram of consumer. Points represent mean values of individual sites while the trend line and associated standard error shading indicate the direction of the relationship.

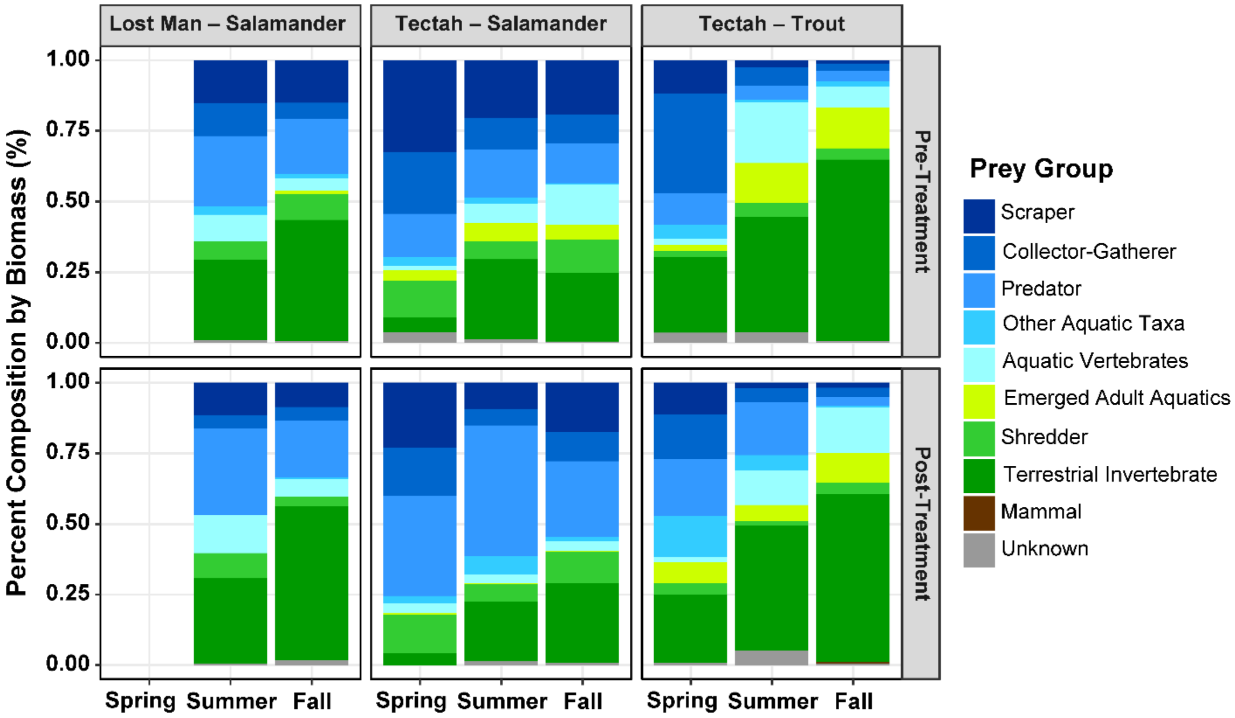

Figure 4.8. Seasonal patterns of percent composition of prey broken down by functional groups in the diets coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*) during pre and post-treatment years across for sites in the Tectah and Lost Man watersheds in northern California, USA. No differences were observed between upstream, thinned, and downstream reaches so results are pooled across reach types. Prey groups included: 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 aquatics, shredders, terrestrial invertebrate, terrestrial mammal, and taxa that we could not identify.

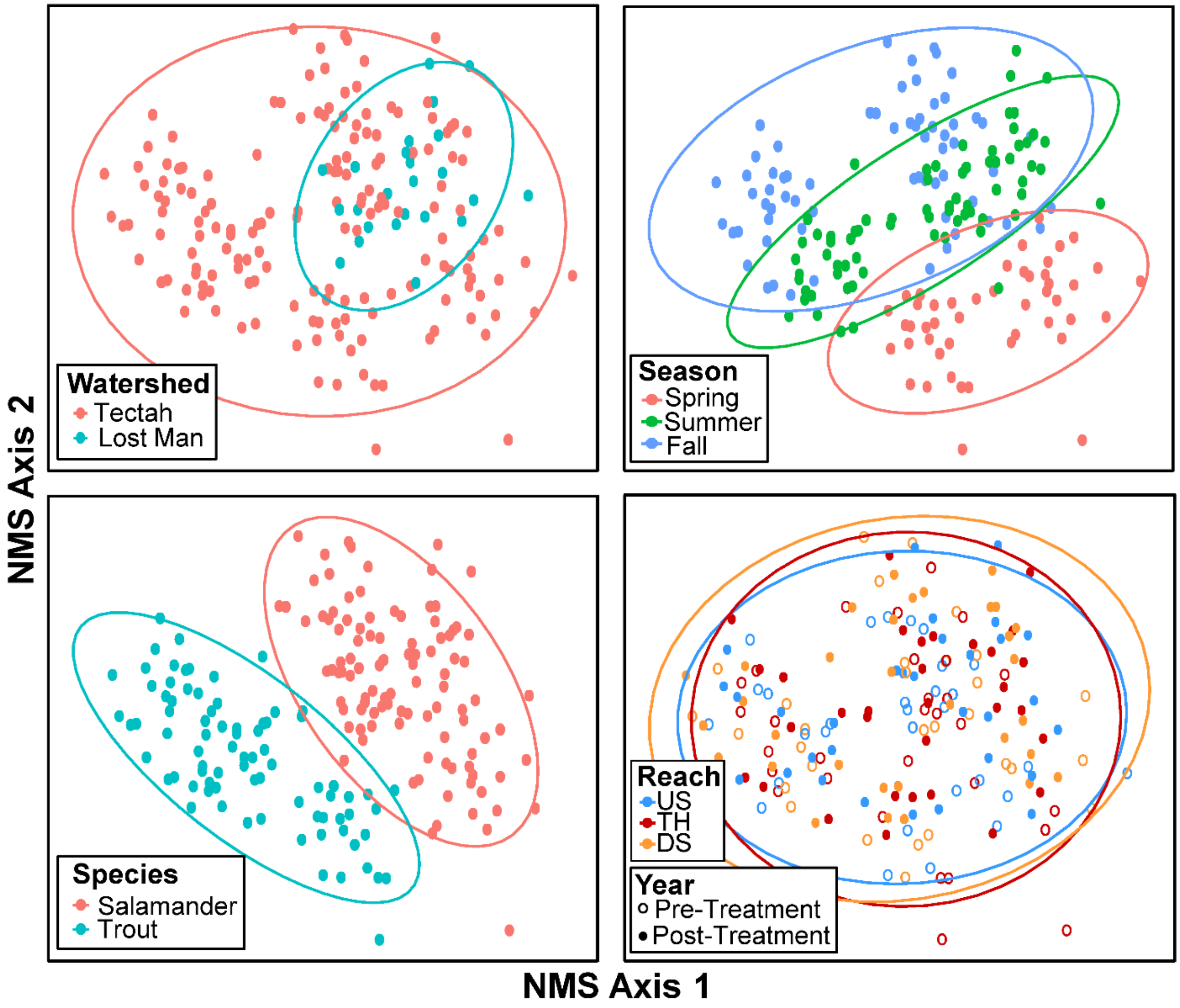

Figure 4.9. Non-metric multidimensional scaling (NMS) ordinations indicating the structure of prey communities in diets of coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarkii*) across all study sites (n = 7) in northern California, USA. NMS ordinations 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 x Year). All points represent individual communities (n=186) and the proximity of points indicates similarity of communities. Stress = 0.19. Ellipses indicate the 95% confidence intervals surrounding each grouping variable.

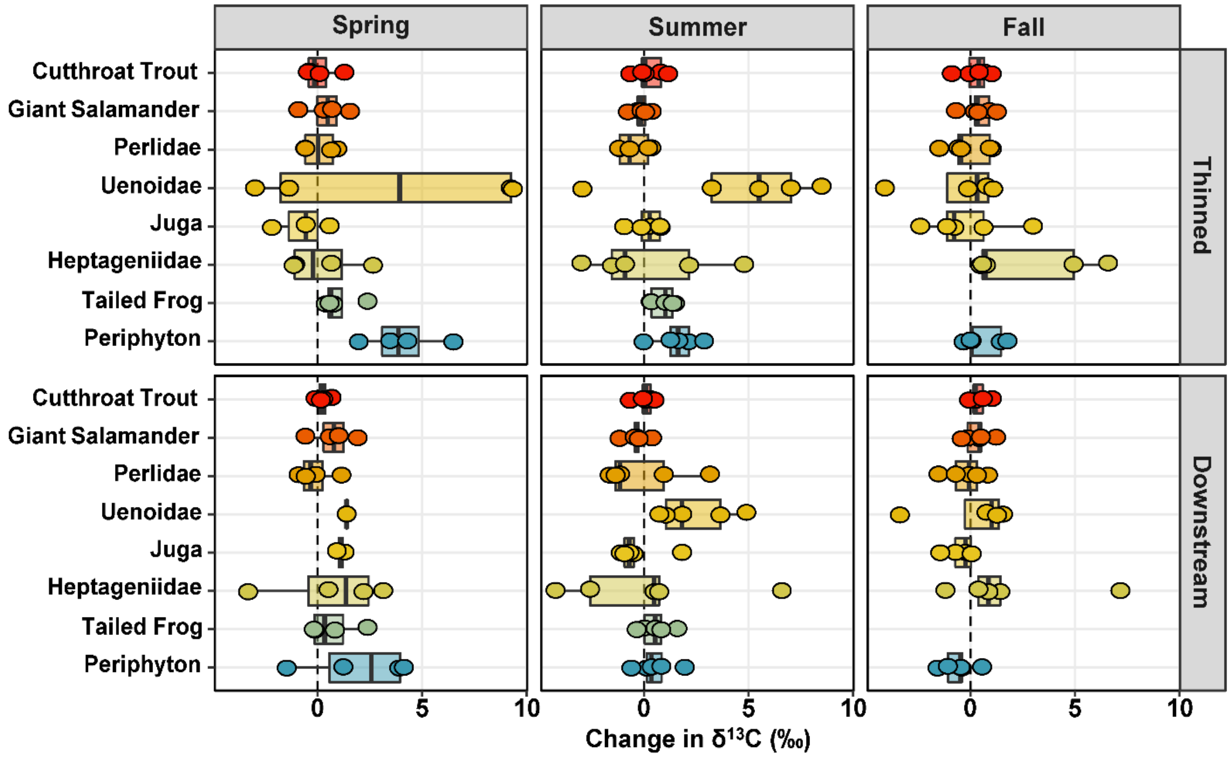

Figure 4.10. Seasonal BACI responses of carbon ($\delta^{13}C$) stable isotopes for multiple components of the food web in thinned and downstream reaches for sites in the Tectah watersheds in northern California, USA. Food web components include: stream periphyton, scrapers: (tailed frog tadpoles, heptageniid mayflies, Juga snails, uenoid caddisflies), and predators (perlid stoneflies, coastal giant salamander, and coastal cutthroat trout). Points represent mean values of individual sites while boxplots show the distribution of data.

CHAPTER 5: EFFECTS OF RIPARIAN THINNING ON THE GROWTH AND ENERGETICS OF COASTAL CUTTHROAT TROUT IN FORESTED STREAMS AT REACH AND WATERSHED SCALES

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Abstract

Resource managers are interested in more actively managing riparian forests to restore forest conditions and boost the productivity of salmonid fishes. However, previous research has indicated that opening riparian canopies can lead to ecological trade-offs where increases in stream temperature that can exceed the thermal tolerances of cold-water adapted species often co-occur with potentially beneficial increases in aquatic productivity. Whereas much research has focused on responses of streams and fish to riparian management at local scales, far less is known about how thermal and trophic processes interact at the extent of entire watersheds. In this study we explored how changes in riparian canopy conditions via experimental riparian thinning treatments affected thermal and trophic conditions and how those responses to thinning interacted to support the growth and energetics of resident populations of coastal cutthroat trout (*Oncorhynchus clarkii*) in forested watersheds in the redwoods of northern California, USA. Riparian thinning warmed streams especially during summer months. The composition of coastal cutthroat trout diets fluctuated seasonally, but overall prey energy density remained relatively stable and decreased slightly with thinning. Growth rates for age 1+ cutthroat trout varied more seasonally than due to thinning treatments and peaked in spring and overwinter relative to summer. Combining empirical observations of stream temperature, diet, and growth in a bioenergetics modelling framework at the reach-scale indicated that thinning did not alter estimates of energy intake per fish, but did increase reach-scale total energy intake largely via higher fish densities. Reach-scale estimates of relative consumption rates (pCmax) varied seasonally, peaking in spring and overwinter relative to summer, and increased with thinning especially overwinter. At a watershed-scale we found that thinning increased the growth potential for cutthroat trout at annual scales. However, when we partitioned patterns seasonally we observed that the direction of responses and driving factors varied among seasons. Increased growth potential associated with thinning in cooler seasons was likely due to enhanced trophic processes (i.e., increased consumption rates), but in summer responses were driven by the combination of thermal and trophic processes and the net outcome of responses depended on the magnitude of temperature increases. Collectively, these results indicate that the effects of thinning varied seasonally and with the scale of observation. This study illustrates the utility of process-based approaches that can capture patterns across broader seasonal and spatial extents

when trying to understand how thermal and trophic conditions associated with changes in riparian forests may interact to support the growth of stream fishes.

Introduction

Disturbances that alter riparian forests can directly affect stream fishes via aquatic-terrestrial linkages and warrant further investigation when riparian forest conditions change (Gregory et al. 1991, Warren et al. 2016, Sievers et al. 2017). In many settings, land use is regulated to minimize disturbances to riparian zones in efforts to protect stream water quality and fisheries (Gregory et al. 1991, Northcote and Hartman 2004). In the Pacific Northwest (USA), forest management is the primary terrestrial disturbance influencing riparian forests and associated stream ecosystems (Moore and Richardson 2012). Previous research has documented that historical timber harvest practices that removed riparian forests can lead to increased aquatic productivity (e.g., via warming of temperatures and increased light), but such changes can also lead to sublethal (e.g., reduced growth) or lethal consequences for coldwater-adapted species such as salmonid fishes (Murphy and Hall 1981, Murphy et al. 1981, Moore et al. 2005). Regulatory responses to these findings focused on adapting forest harvest practices to minimize the likelihood of adverse impacts on salmon and trout (Poole and Berman 2001, Poole et al. 2004, Reeves et al. 2006). Accordingly, contemporary forest management practices now require protection of riparian zones to mitigate adverse effects on stream temperature and cold-water adapted species (Moore et al. 2005). As riparian forests have recovered, however, high levels of shade associated with dense riparian canopies may have negative effects on stream fishes via reduced aquatic productivity (Kaylor and Warren 2017). This has caused some to suggest that more subtle reductions in riparian forest canopies may be able to strike a balance between smaller increases in temperature yet still allow some additional light to boost aquatic productivity (Wilzbach et al. 2005).

As riparian forests have recovered in the wake of contemporary protections, resource managers in the Pacific Northwest are increasingly interested in more actively managing them via silvicultural practices such as thinning for upland and riparian forest restoration (Berg 1995, Carey 2003). Interest in thinning ranges widely depending on the objectives of land managers, which can include: 1) accelerating the recovery of old-growth forest composition and structure (Russell 2009, O’Hara et al. 2010, Teraoka and Keyes 2011, Keyes and Teraoka 2014); 2) shifting the composition of riparian forests from early seral deciduous species to conifer to provide an eventual source of large wood (Benda et al. 2016); and 3) enhancing aquatic productivity of salmonid fishes (Wilzbach et al. 2005, Newton and Ice 2015). These potential benefits of thinning are balanced by concerns over potential negative consequences for salmon and trout, particularly the possibility of warming stream temperatures (Poole and Berman 2001). Fortunately, the effects of warming temperatures on stream fishes are particularly well-studied, with established frameworks in place such as bioenergetics models to effectively predict responses such as fish growth and consumption (Hanson et al. 1997, Deslauriers et al. 2017).

Growth is often used as a key indicator of stream fish performance because it integrates many ecological processes into a single metric (Warren 1971, Railsback and Harvey 2002). Growth is a useful indicator because it can respond rapidly to environmental changes that may be associated with thinning in riparian zones, including temperature, prey resources, and other factors that influence net energy gain such as competition for resources (Magnuson 1979, Hughes and Grand 2000, Wipfli and Baxter 2010). Previous research has often tracked fish responses to changes in riparian forests without understanding the factors driving those responses (Murphy et al. 1981, Bilby and Bisson 1992). For example, Wilzbach et al. (2005) documented increased growth rates for trout in coastal watersheds in northern California in response to opening riparian canopies, yet did not identify the causal mechanisms driving this response. Accordingly, it is important to have some means of understanding factors that likely drive observed growth patterns. To this end, process-based bioenergetics models can help elucidate the underlying mechanisms supporting growth (Hansen 1997, Railsback and Rose 1999). Bioenergetics models have been previously applied to understand how forest composition and timber harvest affect growth processes in stream fish (McCarthy et al. 2009, Leach et al. 2012), and therefore provide a useful framework for evaluating growth in ways that are not possible by empirical observations alone.

Growth regimes of stream fishes fluctuate seasonally and spatially in watersheds (Benjamin et al. 2020, Armstrong et al. 2021, Kaylor et al. 2021). Growth is often assumed to peak in summer, which is true in some locations where temperatures are particularly cold, but in more temperate coastal climates and in forested headwaters of the Pacific Northwest, growth rates can actually decrease to zero or negative values (Raggon 2010, Harvey et al. 2014, Jensen 2017, Hollis 2018). Growth studies tend to be conducted in summer, so much less is known about the year-round and seasonal growth regimes of stream fishes and further investigation is needed to partition seasonal patterns in growth (Armstrong et al. 2021, Brady et al. 2021). Moreover, stream fishes are highly mobile so understanding growth conditions beyond the local scales of typical studies is needed (Schlosser 1991, Gowan et al. 1994, Fausch et al. 2002, Kaylor et al. 2021). Ultimately, expanding the seasonal and spatial scope of analysis provides important context by quantifying temporal and spatial variation that these fish encounter and therefore would contribute a better understanding of growth responses by stream fishes to changes in the environment such as riparian thinning.

In this study, we explored how riparian thinning influenced the growth and energetics of coastal cutthroat trout (*Oncorhynchus clarkii*) in second-growth coast redwood forests (*Sequoia sempervirens*) of northern California. Coastal cutthroat trout predominate in low-order streams in the coastal Pacific Northwest - a region with a long history of timber harvest and extensive research on the interactions of the two (e.g., Aho 1976, De Groot et al. 2007, Bateman et al. 2016). We evaluated the effects of riparian thinning on cutthroat trout growth and energetics in a watershed-scale manipulative field experiment following a before-after-control-impact (BACI) design (Underwood 1994) where we collected data in upstream reference, thinned, and in downstream reaches during pre and post-treatment years. This study builds upon previously reported datasets evaluating the effects of thinning on thermal (Roon et al. 2021, Chapter 3) and trophic resources (Chapter 4). The objectives of this study were to: 1) quantify reach-scale growth rates for coastal cutthroat trout and how they responded to thinning; 2) combine reach-scale empirical data on stream temperature, prey composition and energy density in diets, and growth in a bioenergetics model to estimate energy intake and relative consumption rates (pCmax); and 3) apply the bioenergetics model to relate reach-scale estimates of relative consumption to a network of temperature sensors (Chapter 3) to estimate growth potential across study watersheds (Falke et al. 2019). We also considered the influence of body size, as this is often hypothesized to be a response to changes in riparian zones (Meeuwig et al. 1994, Gresswell and Hendricks 2007, Rosenberger et al. 2015) and can be an important factor influencing growth (Hughes and Grand 2000).

Methods

Study systems

This study took place in the west and east forks of Tectah Creek on private timberland owned by the Green Diamond Resource Company in coastal northern California (Figure 5.1, Table 5.1). Study watersheds were small and densely forested (7-8 km^2), drained by small streams (bankfull width: 3-6 m) at the top of the drainage network that eventually flow into the lower Klamath River. Study watersheds were within 15 km of the Pacific Ocean and experience a cool climate heavily influenced by coastal fog. Flow regimes follow seasonal patterns typical of a rain-driven hydrology of streams in this region, with high flows persisting fall through spring months corresponding to coastal storms followed by summer low flows supplemented by coastal fog, upwelling groundwater, and hyporheic flow (Ziemer and Lisle 1998). Thermal regimes are relatively cool (maximum temperature ~16 °C) overall, with coolest temperatures occurring fall through spring and temperatures peaking during summer low flows (Roon et al. 2021). Riparian canopies consisted of second-growth forests and included coast redwood, red alder (*Alnus rubra*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), tanoak (*Notholithocarpus densiflorus*), and western red cedar (*Thuja plicata*). Riparian forests heavily shaded the stream channel (mean canopy closure: ~95%) with little longitudinal variation along streams. Resident populations of coastal cutthroat trout co-occurred with stream amphibian assemblages including coastal giant salamander (*Dicamptodon tenebrosus*) and coastal tailed frogs (*Ascaphus truei*), as well as lower densities of southern torrent salamander (*Rhyacotriton variegatus*), northern red-legged frog (*Rana aurora*), and foot-hill yellow legged frog (*Rana boylii*).

Experimental design

We collected data for this study following a replicated before-after-control-impact (BACI) study design (Underwood 1994) where we experimentally manipulated riparian canopies and collected data before and after in upstream reference, thinned, and downstream reaches. We collected pre-treatment data in fall 2015 through spring of 2017, experimental thinning treatments occurred summer of 2017, and we collected post-treatment data in fall of 2017 through fall of 2018. We repeated sampling in these reaches seasonally in spring, summer, and fall.

Riparian thinning prescriptions targeted a reduction to 50% canopy closure in the riparian zone on both side of the stream channel up to the stream edge along 200-m treatment reaches. Thinning treatments were part of a larger riparian canopy experiment included in Green

Diamond's Aquatic Habitat Conservation Plan. Thinning treatments took place in 8 locations across the two study watersheds. Thinning treatments aligned with upslope harvest units and trees were removed from both sides of the stream channel via cable yarding. Un-thinned reaches adjacent to upslope harvest units were protected by one-sided 45-m riparian buffers that included a 22.5-m inner zone of 85% canopy retention and 22.5-m wide outer zone of 70% canopy retention. An evaluation of buffered and intact reference reaches indicated that one-sided buffers had no measurable effect on shade, light, or stream temperature relative to reaches with intact riparian forests (Roon et al. 2021).

Data collection

We collected empirical data to provide the major inputs for the Wisconsin bioenergetics model (Hanson et al. 1997; Deslauriers et al. 2017) including stream temperature, composition and energy density of trout diets, and fish growth.

Stream temperature – We measured stream temperature at two different scales using digital temperature sensors (a combination of Onset Hobo v2 and Tidbit dataloggers) (Roon et al. 2021, Chapter 3). At a reach scale, we deployed temperature sensors at the upstream and downstream extents of upstream reference, thinned, and downstream reaches (Roon et al. 2021). At a watershed scale, we deployed sensors every ~ 200 m through each study watershed and downstream of the confluence for ~ 1 km, using a total of 72 sensors (Chapter 3). We programmed sensors to record data hourly and summarized hourly data as daily mean temperatures year-round during pre-treatment and post-treatment years.

Fish sampling – We collected coastal cutthroat trout via single-pass backpack electrofishing in all study reaches. Backpack electrofishing surveys were conducted with a Smith-Root LR 24 electrofisher (Smith-Root Inc., Vancouver, WA USA) moving in an upstream direction. We subsampled each reach in two or three 40-m sections isolated with fine-mesh block nets. Captured fish were briefly held in 5-gallon buckets filled with well-oxygenated stream water and an aerator or in temporary mesh enclosures in the stream channel before processing. We anesthetized fish using AQUI-S (AquaTactics Fish Health, Kirkland, WA USA) and allowed them to recover completely before returning them to the site of initial capture. We sampled in spring, summer, and fall, during pre-treatment (2016), treatment (2017), and post-treatment years (2018).

Diet composition – To quantify the composition and energy density of trout diets, we collected diet samples using non-lethal gastric lavage with a 10-ml Minipet Aqueous Pipettor (SP Bel-Art, Wayne, NJ USA) from a subsample (n = 10-15 fish/reach) of cutthroat trout at each site during each sampling period (total sample size n = 1260) (Chapter 4). We identified, enumerated, and measured the length for all prey items and estimated biomass using published length-weight regressions (See Chapter 4 for references). We then estimated prey energy density following the categories described by McCarthy et al. (2009) and Thompson and Beauchamp (2016) (Table 5.2). No estimates of energy density were available for cutthroat trout fry or larval amphibians, so for these species we generated length-dry mass relationships following Utz et al. (2006) and used derived values of percent dry mass to estimate energy density using the equation in Hartman and Brandt (1995).

Growth – To quantify growth rates of age 1+ cutthroat trout, we measured changes in weight of recaptured individuals marked with 8- or 12-mm PIT tags. We then estimated specific growth rates using the formula: $((\ln W_t - \ln W_0)/t) * 100$, where W_t is the final mass in grams, W_0 is the initial mass in grams, and t is time in days. Of the 6124 trout we captured during this study, we tagged 1918 fish and recaptured 1058 individuals. Of those 1058 recaptures we eliminated records of individuals that moved into adjacent reaches (13 fish) and fish that we recaptured during nonconsecutive sampling dates (335 fish), leaving a sample size of 710. Of those fish we focused on the ones we recaptured during pre and post-treatment years for a final sample size of 586 individuals. We then separately estimated growth rates for: spring (April/May through July), summer (July through September/October), and overwinter (September/October through April/May).

Bioenergetics modeling

To gain a mechanistic understanding of the thermal and trophic processes supporting the growth and energetics of coastal cutthroat trout and how that varied with thinning, we used the Wisconsin Bioenergetics model (Hanson et al. 1997, Deslauriers et al. 2017) in different ways at the reach and watershed scales. We used a bioenergetics model parameterized for adult rainbow trout using published coefficients (Hanson et al. 1997, Railsback and Rose 1999) in R (R Core Team 2020).

First, at a reach-scale we estimated how energy intake or calories consumed by cutthroat trout based on thermal conditions and observed growth varied seasonally and with thinning, following the methods described by Harvey et al. (2006). To do this, we combined seasonal data on stream temperature, total prey energy density in diets, and observed growth at all sites. We then multiplied mean estimates of energy intake by fish densities to estimate total calories consumed at the reach level. We estimated total fish densities by multiplying single-pass electrofishing densities by 2-pass mark-recapture abundance estimates (*n* = 10) which yielded capture probabilities of 0.6 in summer and 0.8 in fall. Based on these estimates and channel characteristics during higher flow conditions we assumed a capture probability of 0.4 in spring.

Second, at a reach-scale we estimated relative consumption rates (pCmax) using empirical data on stream temperature, composition and energy density of prey in diets, and observed growth following the formula where: Consumption = M + W + G (Hanson et al. 1997), where:

M = Metabolism (Respiration + Active Metabolism + Specific Dynamic Action)
W = Waste (Fecal Egestion + Urinary Excretion)
G = Growth (Somatic + Gonad Growth)

Estimates of consumption were then used to estimate relative consumption rates (pCmax) by dividing them by Cmax – the maximum physiological rate at which fish are able to feed (Railsback and Rose 1999, Beauchamp 2009). We estimated pCmax for all recaptured fish at each reach. We repeated this during three seasonal windows: spring (April – July), summer (July – September), and overwinter (September – April) as well as before and after thinning.

Third, at the watershed-scale we related reach-scale estimates of relative consumption rate (pCmax) to temperature data at all locations within the sensor network to estimate growth potential using the formula: Growth Potential = pCmax - M - W (see abbreviations above). We then estimated growth potential at all sensor locations throughout study watersheds (*n* = 72) and repeated these estimates before and after thinning during the following seasonal windows based on the general timing of field sampling: spring: April 15 – July 14, summer: July 15 – September 14, and overwinter: September 15 – April 14. Because body size can influence growth responses, we separately estimated growth potential for three size classes of cutthroat trout based on size-frequency distributions: small (5 to 20 g), medium (20 to 40 g), and large (40 to 65 g). We estimated watershed-scale patterns of growth potential under two different scenarios. First, we considered the effects of temperature alone by using empirical temperature conditions at each sensor location during pre- and post-treatment years but set relative consumption rates and prey composition (seasonal means) constant across all locations in study watersheds. Second, we considered the combined effects of temperature and reach-scale estimates of relative consumption rate and prey composition during the post-treatment year. Finally, we summarized responses annually to understand how thinning influenced growth potential for cutthroat trout across an entire year.

Data analysis

Although most of this study focused on modeling growth, we were also able to empirically evaluate measured growth and to statistically evaluate patterns of estimated consumption. At the reach-scale, we evaluated the effects of thinning on empirical growth rates, bioenergetics estimates of energy intake and relative consumption rates (pCmax) following a BACI design. We compared conditions in upstream reference, thinned, and downstream reaches and determined if those changed during pre-treatment and post-treatment years. To do this, we characterized mean responses and 95% confidence intervals before and after thinning during spring, summer, and overwinter seasonal windows and we compared whether 95% confidence intervals overlapped between thinned and downstream reaches relative to upstream reference reaches. At the watershed scale, we arranged bioenergetics estimates of growth potential according to spatial position in the watershed and visually compared how longitudinal profiles differed between pre and post-treatment years and how that corresponded to thinning reaches. To infer whether growth responses to thinning were a function of thermal or trophic processes, we compared post-treatment growth estimates between model simulations that considered the effects of temperature to simulations that considered the combined effects of temperature and relative consumption rates.

Results

Stream thermal regimes

Stream thermal regimes during the pre-treatment year showed inherent extensive seasonal variation ranging between 4 °C in winter and 16 °C in summer (Figure 5.2). Post-treatment stream thermal regimes increased with thinning primarily in summer, less so in spring, and showed minimal changes overwinter (Figure 5.2).

Composition and energy density of prey in diets

Prey in cutthroat trout diets varied more in composition than by total energy density and showed minimal responses to thinning (Figure 5.3). Diet composition fluctuated widely between seasons. Cutthroat trout relied primarily on aquatic larva and nymphs and adult beetles in spring, a mix of aquatic and terrestrial invertebrate and vertebrate prey in summer, and terrestrial invertebrates in fall (Figure 5.3). Total prey energy density in cutthroat trout diets ranged between 4200 and 5200 J/g, and was relatively stable between seasons and years, although in the post-treatment year energy density decreased slightly by ~ 200 J/g in thinned and downstream reaches relative to upstream reference reaches (Figure 5.3).

Growth

Individual growth rates of age 1+ cutthroat trout varied more seasonally than among reach types or between pre and post-treatment years (Figure 5.4). During both pre- and post-treatment years, growth rates were highest in spring and overwinter and lowest in summer (Figure 5.4). Thinning did not affect growth rates during the post-treatment year. Growth rates appeared slightly elevated in thinned and downstream reaches in overwinter (increasing by 42% and 33% respectfully), but did not differ significantly during any season (Figure 5.4).

Energy intake at a reach-scale

Bioenergetics-modeled estimates of mean energy intake per fish indicated that calories consumed by cutthroat trout were largely stable between seasons and reach types during the pre-treatment year and ranged from 140 to 230 calories per day (Figure 5.5). Estimates of total energy intake per reach did not differ between reach types during the pre-treatment year. During the post-treatment year mean energy intake varied more seasonally and was slightly higher in spring and overwinter periods than summer. Mean energy intake increased slightly in thinned reaches relative to upstream and downstream reaches, especially in overwinter increasing by 45%, but did not differ significantly in any of the three seasons (Figure 5.5). Total energy intake was consistently higher in thinned reaches relative to upstream and downstream reaches during the post-treatment year across all three seasons (spring: 23%; summer: 68%; overwinter: 76%), but did not differ during any season (Figure 5.5).

Relative consumption rates at a reach-scale

Reach-scale estimates of relative consumption rates (pCmax) varied seasonally during pre-treatment year and were lowest in summer (mean pCmax = 0.122, range: 0.09 – 0.182) and highest in spring (mean pCmax = 0.147, range: 0.119 – 0.177) and overwinter (mean pCmax =

0.166, range: 0.138 – 0.194 seasonal windows (Figure 5.6). During the post-treatment year, seasonal patterns remained intact where relative consumption was highest in spring and overwinter and lowest in summer. Post-treatment relative consumption rates tended to be higher in thinned and downstream reaches relative to upstream reaches in all seasons (spring: 12% in thinned reaches, 7% in downstream reaches; summer: 12% in thinned reaches, 9% in downstream reaches; overwinter: 27% in thinned reaches, 17% in downstream reaches), but only differed significantly in overwinter (Figure 5.6).

Growth potential at a watershed-scale

Watershed-scale longitudinal profiles of cutthroat trout growth potential during the pre-treatment year indicated greater seasonal variation (higher in spring and overwinter than summer) and due to body size than spatially in these watersheds (Figure 5.7). Within each season, potential growth was highest for small size classes of cutthroat trout relative to medium and large size classes. Summer showed greater longitudinal variation than other seasons, whereas spring and overwinter showed minimal longitudinal variation (Figure 5.7). Post-treatment responses to thinning in longitudinal profiles varied depending on inputs from the bioenergetics model. In model simulations where we only considered the effects of post-treatment temperatures and assumed a constant pCmax, longitudinal profiles remained unchanged in spring and overwinter, yet shifted in summer where growth potential consistently decreased by 40-80% in thinned reaches and recovered after ~ 400 m (Figure 5.7). However, in model simulations where we combined post-treatment temperatures with reach-scale estimates of pCmax, the effects of thinning on growth potential varied between seasons. Growth potential consistently increased in thinned reaches by 15-28% in spring and 47-100% in overwinter and local increases recovered after ~ 400 m. However, responses in summer were mixed. Growth potential increased by 27-72% in thinned reaches with smaller changes in temperature, while growth potential decreased by 14-28% or remained unchanged in locations with larger changes in temperature (Figure 5.7). Responses to thinning varied by body size, where small fish exhibited smaller responses in spring and overwinter relative to medium and large size classes, yet showed larger responses in summer (Figure 5.7).

When we considered conditions across the entire year, pre-treatment growth potential varied little longitudinally, but varied more among size classes of cutthroat trout (Figure 5.8). Post-treatment longitudinal profiles indicated consistent increases in growth potential that corresponded with thinning reaches and dissipated within 400 m (Figure 5.8). Increased growth potential varied among size classes of fish; growth potential for small fish increased by 32%, medium fish increased by 51%, and large fish increased by 92% (Figure 5.8).

Modeled vs. empirical growth

Cutthroat trout growth estimates from the bioenergetics model reflected annual and seasonal variation in empirical growth rates, but modeled estimates were smaller and less variable than measured growth (Figure 5.9). Modeled growth estimates also documented post-treatment increases in thinned reaches at annual and seasonal scales (especially in spring and overwinter), but were not evident in empirical growth rates (Figure 5.9).

Discussion

This study indicates that the thermal and trophic resources supporting the growth and energetics of coastal cutthroat trout in our forested watersheds were seasonally dynamic, and this seasonal variation often exceeded the effects of riparian thinning. At a reach-scale we found that stream temperatures, prey composition and energy density in diets, and growth rates all varied strongly across seasons. When these inputs were combined in a bioenergetics model at a reach-scale, estimates of mean and total energy intake and relative consumption rates frequently reflected this seasonal variation. Responses to thinning were comparatively smaller in magnitude and statistical significance. When we combined estimates of relative consumption rates with a watershed-scale network of temperature sensors, longitudinal profiles indicated that annual growth potential consistently increased locally with thinning, but such patterns did not reveal important seasonal variation. When partitioned seasonally, the direction and magnitude of growth potential in response to thinning often shifted, supporting the importance of year-round studies that can consider seasonality.

Thermal and trophic resources

Stream thermal regimes fluctuated more seasonally than spatially in these forested watersheds, likely due to the high levels of riparian shade and the limited spatial extent of each watershed (~ 5-6 km in length), which resulted in little longitudinal variation pre-treatment (Roon et al. 2021). Responses to thinning were limited to summer months during low flows and not evident during spring and overwinter seasons when stream flows were higher (Roon et al. 2021). Thinning effects on stream temperatures were also relatively small in magnitude:

temperatures never exceeded 16.5 °C and remained within thermal optima for coastal cutthroat trout (Huff et al. 2005, McCullough et al. 2009). This could be due in part that in this analysis we focused on mean daily temperatures which showed more muted responses than other components of the thermal regime such as maximum temperatures, variability, duration, and frequency (Roon et al. 2021).

Coastal cutthroat trout relied on a diversity of prey types that varied seasonally in composition and energy density. Seasonal variation in prey composition was largely driven by the timing in reliance of aquatic and terrestrial invertebrate prey items where aquatic invertebrates were more prominent in diets in spring and terrestrial invertebrates were more prevalent in fall (Chapter 4). We did not see changes in prey composition due to thinning (Chapter 4), which contrasts with other work on indicating that increases in light can shift community composition and structure towards increased prevalence of taxa that rely on freshwater energy sources (Bilby and Bisson 1992, Mihuc and Minshall 2005, Kaylor and Warren 2017). We found that energy density in the diets did not vary as much seasonally as prey composition, but decreased slightly each season due to thinning (by ~ 100-250 J/g), especially overwinter. This slight reduction in energy density associated with thinning was not observed in a previous food web analysis (Chapter 4), but could be due in part to different classification of prey types. In general, cutthroat trout prey energy densities averaged ~4800 J/g but ranged from 3500 to 5600 J/g. These values are all substantially higher than what is typically observed in trout diets or applied in bioenergetics models. For example, Railsback and Rose (1999) assumed a prey energy density of 2500 J/g for rainbow trout in inland northern California streams. Leach et al. (2012) separately assumed the same prey energy density of 2500 J/g for cutthroat trout in southwestern British Columbia. Given that prey energy density is likely to vary between species and systems and has major consequences when estimating consumption, these discrepancies demonstrate the value of collecting empirical data whenever conducting bioenergetics analyses.

Growth

Seasonally, growth rates of cutthroat trout peaked in spring and overwinter seasons, while trout grew little in summer. Summer growth averaged around zero during both pre and post treatment years with ~55% of fish showing negative growth. Intuitively, it may seem reasonable to assume that growth should peak in summer for many stream fishes based on temperatures and potential prey availability, but our observations are consistent with low to no growth in summer reported for cutthroat trout in similar coastal streams in the Pacific Northwest (Raggon 2010, Harvey et al. 2014, Jensen 2017, Hollis 2018). Summer growth for cutthroat trout in small streams can be limited by low flows where adult fish are more exposed and less likely to feed at maximum rates due to predation risk (Railsback and Harvey 2002, Harvey and White 2017, Penaluna et al. 2021). We did not see growth rates differ statistically with thinning, but responses tended to be elevated relative to upstream reference conditions in overwinter – a period of higher flows, cooler temperatures, and when invertebrate drift rates are higher (Romero et al. 2005, Harvey and Railsback 2014). Although we did not sample during winter months, Hollis (2018) indicated that growth rates were evenly elevated during early (October – February) and late winter (February – April) in these watersheds. These results illustrate the value of year-round studies that attempt to partition growth seasonally (Tattam et al. 2016) and not just consider summer conditions.

Reach-scale patterns of energy intake and relative consumption

When we combined stream temperature, prey energy density, and observed growth in a bioenergetics model to estimate energy intake, we observed differential responses between our per-capita and total-reach scale estimates. Mean per-capita energy intake indicated some seasonal variation especially during the post-treatment year, but this was lower in magnitude relative to growth responses and showed minimal responses to thinning. However, when we multiplied these values against cutthroat trout densities, total reach-scale estimates of energy intake indicated a consistent increase of 23-76% in the amount of calories consumed per reach associated with thinning across all three seasons, although these increases did not differ significantly. These results suggest that because thinning reaches tended to support higher densities of cutthroat trout, as a result, more overall calories were consumed per reach. Wilzbach et al. (2005) also documented evidence of increased trout densities in response to canopy treatments that completely removed riparian vegetation along 100-m reaches in some of the same study watersheds. Although the mechanisms responsible for increased salmonid densities in response to thinning remain unclear, the response has been observed in several studies (Murphy and Hall 1981, Hawkins et al. 1983, Bilby and Bisson 1992). Increased densities could explain the lack of growth or total energy in diet responses to thinning simply because resources were spread across more individuals (i.e., more inter and intraspecific competition) (Hughes and Grand 2000). However, recaptures of marked individuals provided limited evidence of movement between reaches, consistent with other work on this species (Gresswell and Hendricks 2007). Moreover, density estimates were relatively low overall and even with thinning peaked at only ~0.5 fish/m^2 so unlikely approaching levels where density dependent effects would be expected (Dunham and Vinyard 1997, Ramirez 2011).

Bioenergetics estimates of relative consumption rates (pCmax) exhibited greater seasonal variation than due to thinning. Estimates of relative consumption rates in this study were much lower (range: pCmax = ~ 0.1 to 0.2) than what has previously been documented for trout in streams. For example, Leach et al. (2012) assumed an annual relative consumption rate of 0.27 for cutthroat trout in southwestern British Columbia, which exceeded our highest seasonal estimates of relative consumption. McCarthy et al. (2009) estimated relative consumption rates to range from 0.15 to 0.5 for steelhead inland northern California streams. Similarly, Railsback and Rose (1999) estimated relative consumption to range between 0.25 and 0.5 for rainbow trout in Sierra Nevada streams in northern California. Differences among studies in estimates of prey energy density could partially account for these differences in relative consumption. These results suggest that cutthroat trout in our study system could feed at lower rates because they consumed higher quality prey, assuming all else to be equal. Relative consumption rates tended to be higher with thinning during the post-treatment year, but only differed significantly during overwinter. These increases in relative consumption rate associated with thinning were likely due to reductions in prey energy density in diets which was greatest in overwinter, demonstrating the sensitivity of relative consumption estimates in the bioenergetics model to energy density as an input. Similarly, in a sensitivity analysis Jensen (2017) found that relative consumption rates were much more sensitive to changes in energy density than temperature or growth. These results show that directly measuring prey energy density in the diets can provide improved consumption estimates for stream fishes in bioenergetics analyses.

Watershed-scale patterns of growth potential

Relating estimates of relative consumption rates to a network of temperature sensors allowed us to generate estimates of growth potential for cutthroat trout both seasonally and longitudinally through our study watersheds, similar to recent works by Falke et al. (2019) and Kaylor et al. (2021). When these longitudinal patterns were considered annually and seasonally, different patterns emerged. Longitudinal profiles of annual growth potential showed consistent localized increases with thinning across all thinning treatments for all three size classes of cutthroat trout we considered. However, when growth potential was partitioned seasonally, responses to thinning varied accordingly. In spring and overwinter, growth potential consistently increased locally with thinning for all three size classes of cutthroat trout. However, in summer, responses in growth potential varied among size classes of fish, where larger fish experienced negative growth potential, whereas positive growth potential was limited to the smaller size classes, a finding that is consistent with laboratory studies of cutthroat trout exposed to variable thermal regimes (Meeuwig et al. 1994, Beauchamp 2009, Dalhke et al. 2020)

Watershed-scale longitudinal profiles revealed that the effects of thinning on growth potential via thermal and trophic processes varied seasonally. Trophic processes had greater influence in spring and overwinter corresponding to the timing of thinning-associated increases in consumption rates. This was illustrated by the differential responses between our bioenergetics scenarios. Scenarios that only considered the effects of temperature showed no effect of thinning during these times of year. In contrast, scenarios that considered the combined effects of temperature and consumption documented growth potential to consistently increase in thinned reaches, demonstrating the importance of trophic processes during cooler times of year when temperatures were not limiting. Instead, we found that changes in thermal processes to thinning primarily influenced growth potential in summer. These results are consistent with Leach et al. (2012), who found that forest harvest primarily influenced cutthroat trout growth rates in southwestern British Columbia via trophic processes fall through spring while growth was primarily influenced by thermal processes in summer. However, the net effect of thermal processes on summer growth potential in this study was highly variable. This variability in summer responses to thinning appear largely due to the magnitude of temperature change associated with thinning treatments and how that interacted with trophic responses in consumption. When only temperature was considered in the model (consumption is held constant), increases in temperature alone caused negative effects on growth potential in summer that varied magnitude depending on intensity of treatment (Roon et al. 2021). However, in scenarios where we combined post-treatment temperature effects with reach-scale consumption estimates, the direction of responses depended on the relative strength of both influences across reaches within watersheds. Collectively, these results illustrate that the effects of thinning on cutthroat trout growth potential varied seasonally and could be context dependent depending on the relative strength of thermal and trophic processes.

Longitudinal patterns in growth potential indicated that responses to thinning were largely localized in watersheds with little evidence of downstream propagation (~ 400 m). Even in summer, when temperature responses to thinning were most prominent, we observed minimal evidence of downstream propagation. This could be due to the fact that the spatial extent of downstream propagation observed in Chapter 3 depended on the magnitude of local increase and when we characterized thermal conditions as mean daily temperatures in this study, the extent of increase was lower in magnitude so there was little thermal energy to propagate. We observed less inherent longitudinal variation in thermal conditions in our study watersheds relative to other studies such as Falke et al. (2019) or Kaylor et al. (2021), but those studies took place at much larger spatial extents, and were therefore more likely to capture greater heterogeneity (Ranta et al. 1997). Longitudinal variation in thermal conditions was greatest in summer both before and after thinning. Summertime increases in temperature associated with thinning often varied in magnitude depending on position in the watershed and intensity of treatment resulting in context dependency in responses. These results highlight the value of watershed-scale evaluations that can more effectively capture the spatial extent of responses in the context of entire watersheds (Schlosser 1991, Fausch et al. 2002, Fullerton et al. 2018).

While the longitudinal profiles of growth potential suggested that thinning could facilitate faster growth for cutthroat trout, we saw little evidence of responses in empirical growth rates to thinning. Comparisons of modeled and empirical growth rates also indicated that the bioenergetics model consistently underestimated cutthroat trout growth rates during each of the seasons we considered. However, the model did predict seasonal variation in growth rates relatively well. These discrepancies could be due to a variety of real-world constraints encountered by fish not captured in the bioenergetics model we used (Chipps and Wahl 2008). For example, we were not able to account for the costs of swimming (Boisclair and Leggett 1989), which we assumed are more likely important in spring and overwinter when flows are higher. In spite of this, growth was lower in summer, which may be related to reduced foraging activity attributed to fish spending more time avoiding predators (Harvey and White 2017, Penaluna et al. 2021). There are a host of other potential uncertainties in bioenergetics models (e.g., Ney 1993), but they function as useful heuristic tools for exploring growth, which are challenging to quantify in observational field studies. In this study, knowledge of processes potentially influencing growth, as well as direct observations of growth provide complementary perspectives on how riparian thinning ultimately influenced cutthroat trout. Future research should further explore the discrepancies between modeled and empirical growth estimates to help identify other ecological processes not currently addressed by the model and to help refine modeled estimates.

Management implications

By characterizing the thermal and trophic resources supporting growth processes for cutthroat trout and how they respond to experimental thinning treatments, we can consider the implications of these responses for managers deciding whether thinning may act as a viable restoration strategy to enhance riparian and stream ecosystems. Riparian thinning treatments in this study were much less intensive than historical timber harvest practices which often removed riparian forests from the landscape across entire basins (Moore and Richardson 2012). The thinning treatments we evaluated yielded modest reductions in canopy density (~20-30% change in shade and light) on a limited spatial scale (~200-m reaches). Our findings support recent conclusions that: 1) it is challenging to detect treatment effects in heterogeneous aquatic ecosystems with extensive seasonal and spatial variation (Whitney et al. 2020; and 2) inherent spatiotemporal variability is likely to exceed treatment effects (Morley et al. 2016) when evaluating the effects of contemporary forest management practices (Bateman et al. 2016, Jensen 2017). As a result, if managers are interested in understanding how proposed riparian forest restoration actions would affect growth conditions for stream fishes, it depends on the context under which treatments would be taking place, so expectations should be tempered away from predictable or consistent outcomes (Nash et al. 2021). In this light, effort should be made to quantify seasonal and spatial variation in pre-treatment conditions to help quantify ecological context and provide a better understanding for the range of possible post-treatment responses.

Results from this work also highlight the importance of trophic pathways supporting growth processes for stream fishes. While much of the conversation surrounding riparian forest management focuses on the potential negative effects of elevated stream temperatures (Moore et al. 2005), trophic processes tend to be considered less frequently. In this study and in a more thorough temperature analyses (Roon et al. 2021), we documented that thinning treatments increased stream temperatures, yet in this analysis we found temperature changes had less influence on cutthroat trout than trophic processes represented by consumption. Changes in temperature only affected growth potential in summer and the effects were often outweighed by changes in consumption. Nonetheless, thinning decreased cutthroat trout growth potential in summer under more intensive scenarios, and so managers could make sure to thin less intensively to minimize potential negative effects on these stream fish. In contrast, changes in consumption had larger effects on cutthroat trout growth potential in spring and overwinter, which led to net increases in growth potential when we considered responses annually. These results show that growth processes supporting stream fish are highly sensitive to food web dynamics especially in cool, temperate systems where temperatures rarely exceed thermal tolerance of cold-water adapted species. Greater attention to food web processes supporting fish in addition to temperature impacts could benefit thinking about future riparian management scenarios (Bellmore et al. 2017, Whitney et al. 2020).

Conclusions

By considering the thermal and trophic processes driving growth via the bioenergetics model, we gained a more holistic understanding of the underlying mechanisms driving patterns of responses to riparian thinning by cutthroat trout in these watersheds. We learned that the thermal and trophic processes supporting growth and energetics of cutthroat trout varied in importance depending on the season and scale of inference. We found that trophic processes had greater influence during spring and overwinter while thermal processes had more influence in summer (Leach et al. 2012, Campbell et al. 2020). The relative interactions of these processes affected the direction and magnitude of responses emphasizing the value of approaches that allow for consideration of the two together (Brandt 1993, Railsback and Rose 1999). Furthermore, we saw different responses depending on the scale of analysis where annual patterns provided different inferences than seasonal ones. This scale dependency in responses highlights the importance of year-round studies that can effectively parse out conditions seasonally. Also, by scaling responses up to the entire watershed, we gained insights about the spatial extent of responses further demonstrating the likelihood of driving factors. Collectively, mechanistically linking processes as well as characterizing conditions across more continuous seasonal and spatial extents provided a more holistic understanding of how changes in riparian forests can influence growth processes for stream fishes in forested watersheds not possible from examining patterns in growth alone.

Acknowledgements

Thanks to Green Diamond Resource Company for helping to guide questions addressed in this research, conducted experimental treatments, and provided access to study watersheds. Thanks to OSU technicians that helped with field and laboratory work: Kyle Smith, Jerika Wallace, Thomas Starkey-Owens, Mary Carlquist, Ashley Sanders, Morgan Turner, Alex Scharfstein, Cedar Mackaness, and Laura Nepstad. Thanks to the aquatic biologists at Green Diamond that helped with field sampling: Teal Richards-Dimitre, Dave Dimitre, Matt Kluber, Will Devenport, Matt Nannizzi, Sean Studer, Mike Zontos, Jon Pini, and Jonathan O'Connell. Thanks to the USFS PNW Research Station and Ivan Arismendi for providing space for processing macroinvertebrate samples. Thanks to reviewers for providing feedback that strengthened the quality of this this manuscript. This research was supported by funding from Green Diamond Resource Company, Save the Redwoods League, and the Department of Fisheries and Wildlife at Oregon State University. This study was conducted according to protocols approved by OSU Animal Care and Use Permit #5037 and California Department of Fish and Wildlife Scientific Collection Permit #13298 and 6348.

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Table 5.1. Reach-scale characteristics of northern California (USA) study sites.

Watershed	Site	Distance Upstream from Confluence (m)	Reach Length (m)	Bankfull Width (m)	Change in Riparian Shade (Δ%)	Change in Stream Temperature – summer MWMT (Δ°C)
East Fork Tectah	EFT1	990	210	6.1	-19.2	1.8
	EFT2	1850	170	4.6	-30.5	3.8
West Fork Tectah	WFT1	535	175	6.0	-24.0	2.1
	WFT2	2750	205	4.7	-26.2	3.5
	WFT3	3840	220	3.2	-23.6	2.7

Table 5.2. Prey categories and energy densities used for bioenergetics modeling.

Prey Taxa	Energy Density (J/g)	Indigestibility	Reference
Aquatic larva and nymphs	3072	0.15	Thompson and Beauchamp 2016
Aquatic adults	4225	0.15	Thompson and Beauchamp 2016
Terrestrial larva	4272	0.15	Thompson and Beauchamp 2016
Terrestrial adults	5761	0.15	Thompson and Beauchamp 2016
Beetle adults	6387	0.15	McCarthy et al. 2009
Trout fry	5781	0.05	Roon et al. (Chapter 4)
Amphibian larva	3957	0.05	Roon et al. (Chapter 4)

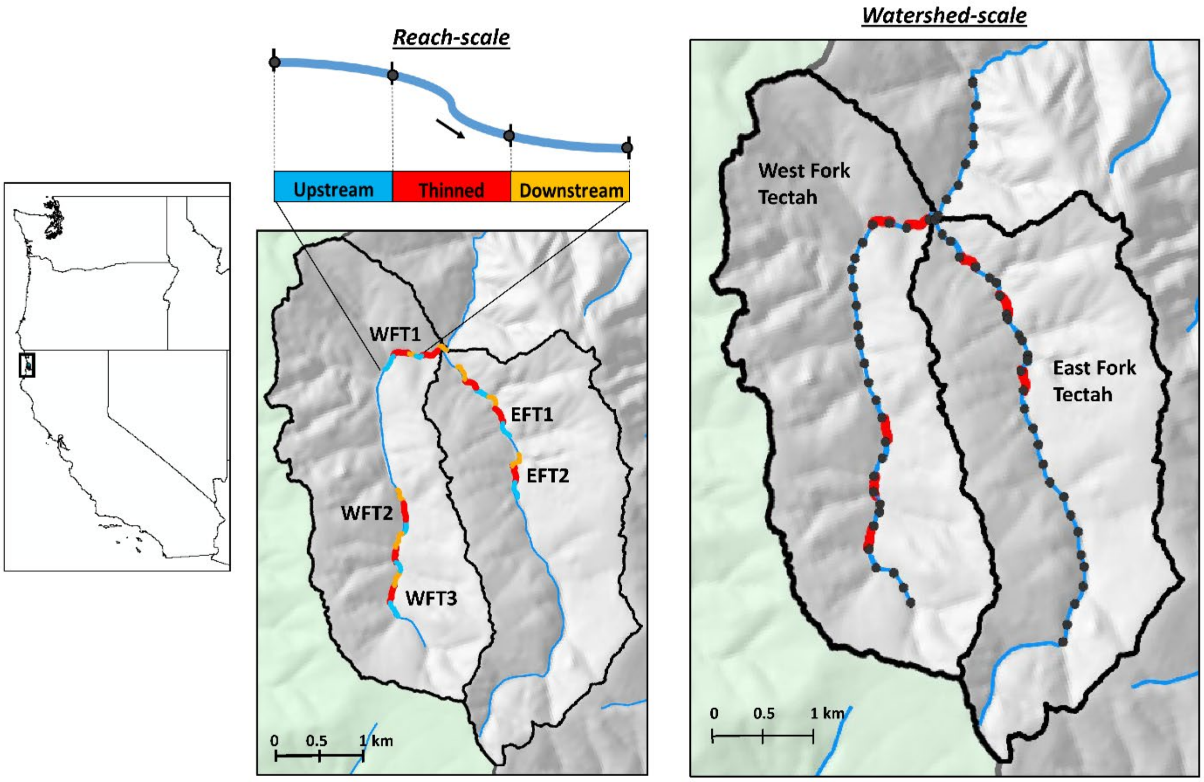


Figure 5.1. Study location, study watersheds, and experimental design at reach and watershed scales in northern California, USA. Reach-scale design where we collected stream temperature, diet, and empirical growth data in upstream reference, thinned, and downstream reaches before and after experimental thinning treatments. Position of abbreviated names on map indicate sampling sites where we collected empirical data (*n* = 5). Watershed-scale design where we measured stream temperature and applied bioenergetics model to predict growth potential for coastal cutthroat trout throughout study watersheds. Points indicate position of water temperature sensors and where we estimated growth potential in study watersheds (*n* = 72) while red blocks indicate position of thinning treatments.

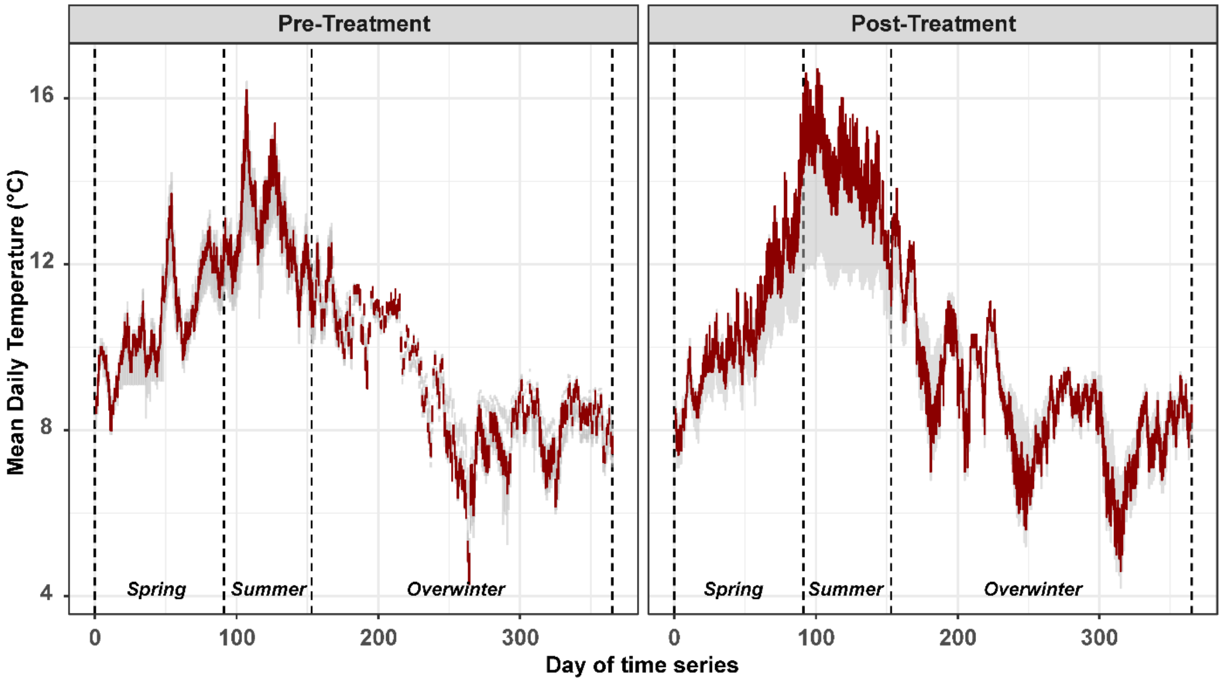


Figure 5.2. Time series of mean daily stream temperatures (°C) of all sensors in network (*n* = 72) in pre- and post-treatment years in northern California, USA study watersheds. Dark red lines indicate thermal conditions in thinned reaches while gray lines indicate thermal conditions in unthinned locations. Time series starts on April 15th and continues for an entire year. Vertical hashed lines indicate the timing of sampling events and associated seasonal windows including: Spring (April 15 – July 14), Summer (July 15 – September 14), and Overwinter (September 15 – April 14).

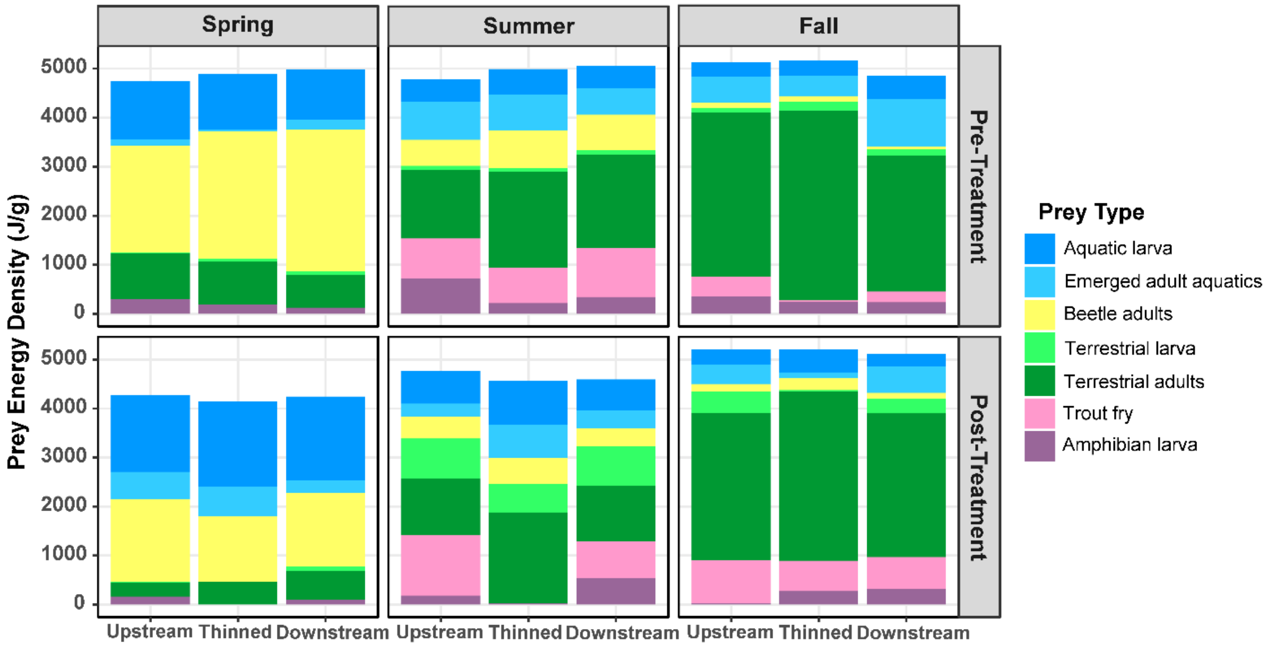


Figure 5.3. Seasonal composition and total energy of invertebrate and vertebrate prey in diets of coastal cutthroat trout (*Oncorhynchus clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in northern California, USA study watersheds. Stacked bar graphs show relative contribution of each prey type to the total energy of prey in cutthroat trout diets. Data represent mean estimates across all reach-scale sampling sites (*n* = 5).

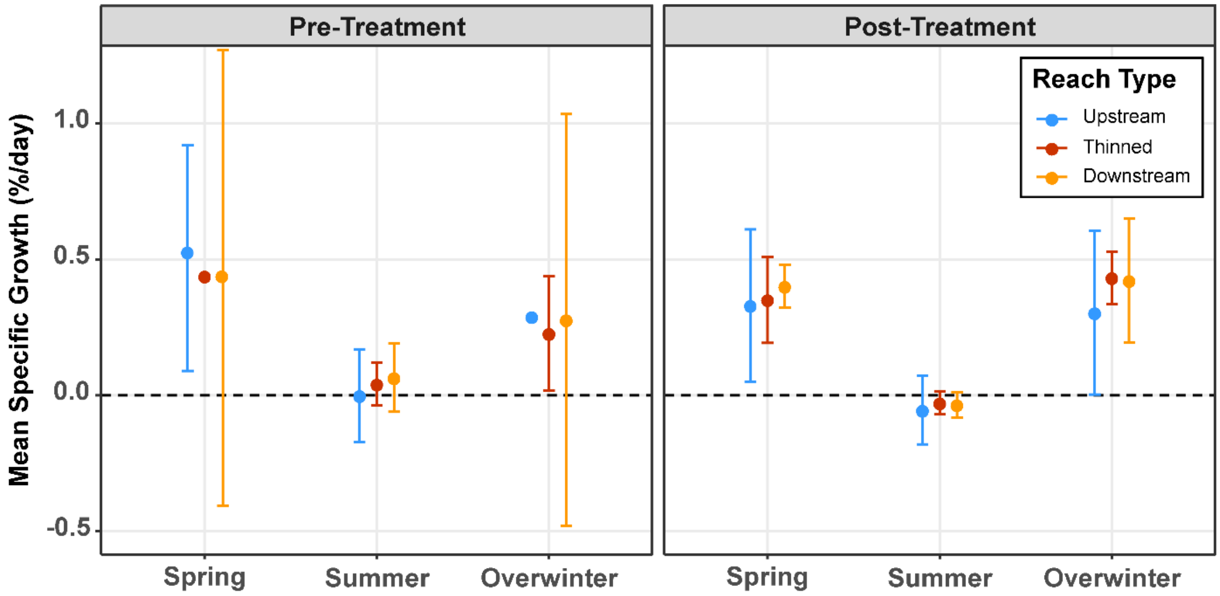


Figure 5.4. Seasonal estimates of empirical growth rates of coastal cutthroat trout (*Oncorhynchus clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in northern California, USA study watersheds. Points represent mean estimates of all reach-scale sampling sites (*n* = 5) and error bars represent 95% confidence intervals.

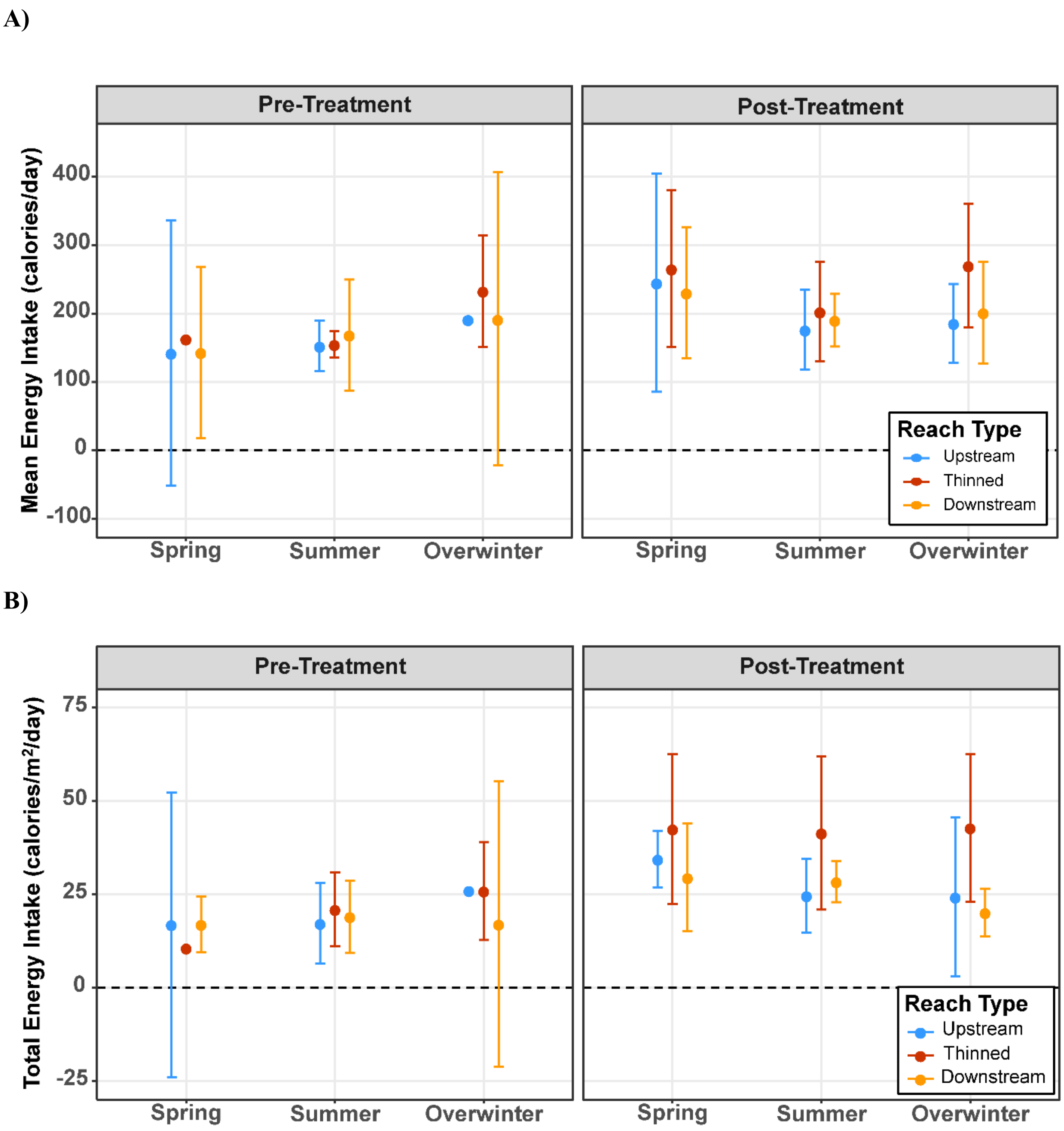


Figure 5.5. Seasonal estimates of energy intake of coastal cutthroat trout (*Oncorhynchus clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in northern California, USA study watersheds. Mean energy intake (A) indicates mean calories consumed per fish per day while total energy intake (B) indicates total calories consumed by all fish per reach per day. Estimates derived from bioenergetics model that combined reach-scale empirical data on thermal conditions, prey energy density, and growth. Points represent mean estimates of all reach-scale sampling sites ($n = 5$) and error bars represent 95% confidence intervals.

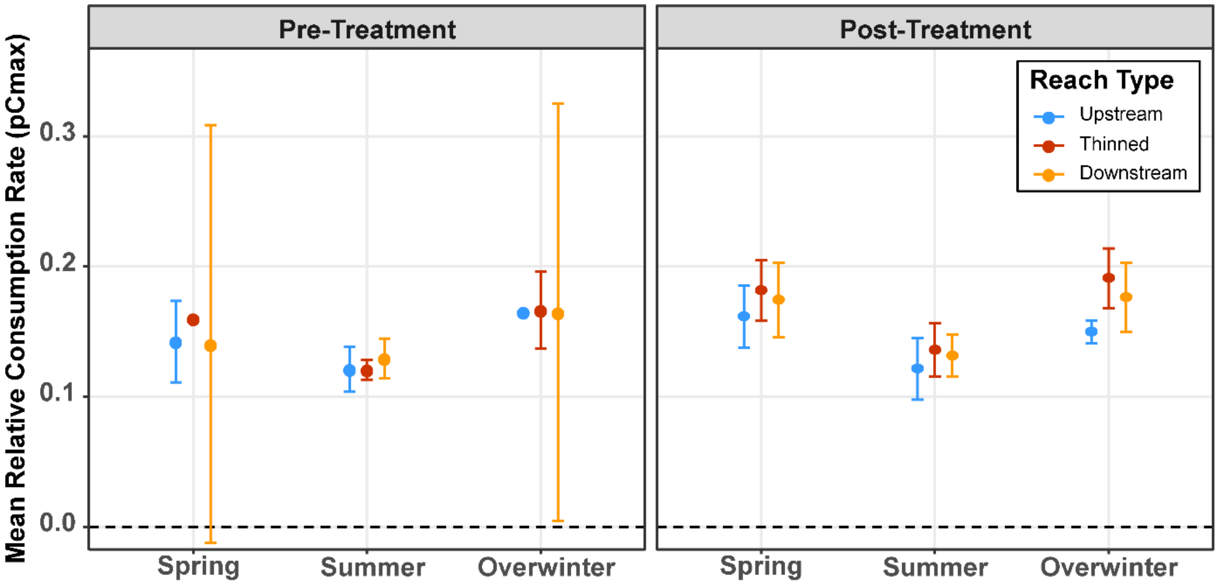
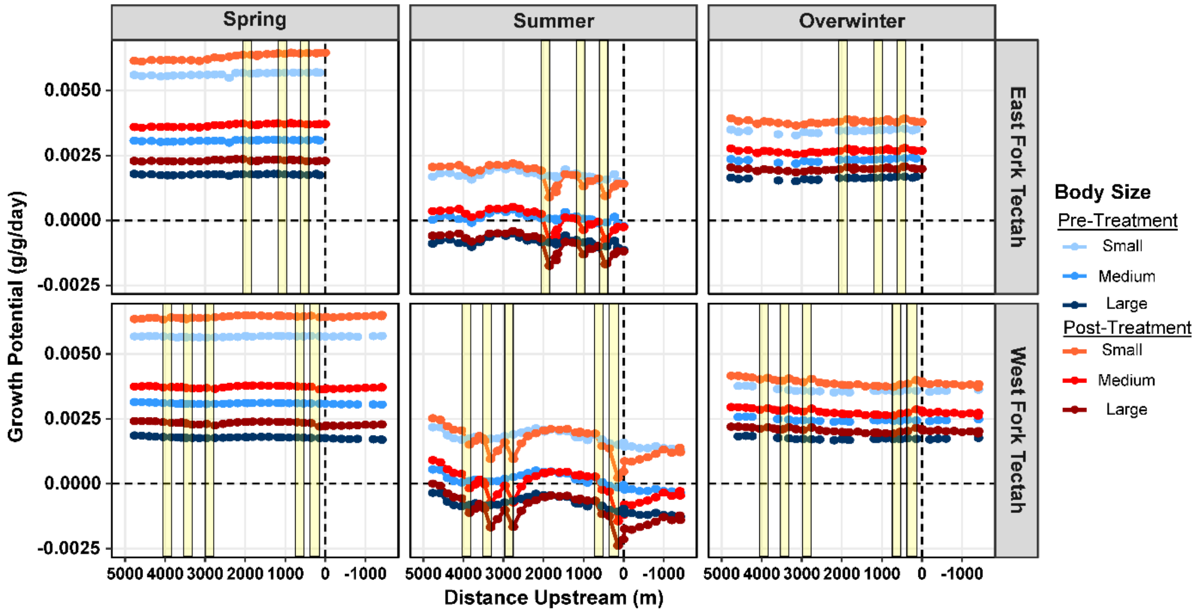


Figure 5.6. Seasonal estimates of relative consumption rates (pCmax) of coastal cutthroat trout (*Oncorhynchus clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in northern California, USA study watersheds. Estimates derived from bioenergetics model that combined reach-scale data on thermal conditions, prey composition and energy density, and growth. Points represent mean estimates of all reach-scale sampling sites (*n* = 5) and error bars represent 95% confidence intervals.

A) Temperature only



B) Temperature + Consumption

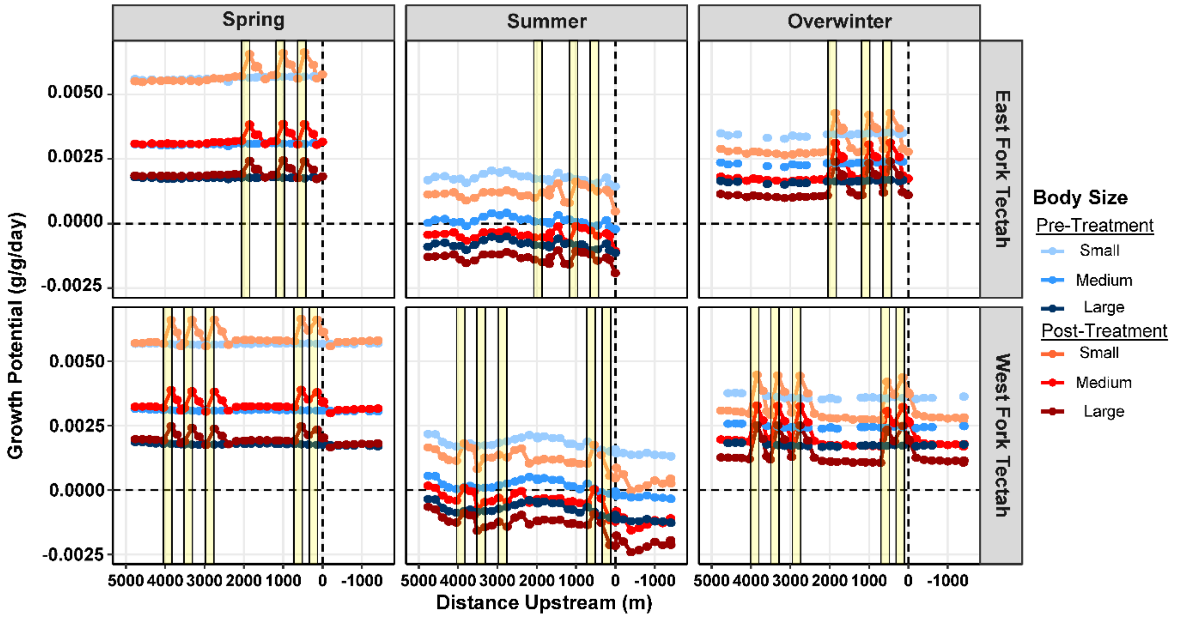


Figure 5.7. Watershed-scale longitudinal profiles of coastal cutthroat trout (*Oncorhynchus clarkii*) seasonal growth potential at different body sizes during pre- and post-treatment years in northern California, USA study watersheds. Body sizes (small: <20g, medium: 20-40g, and large: 40-60 g) indicated by different colors, with colors getting darker as body size increases. Points indicate the positions of temperature sensors where we estimated growth potential with bioenergetics model based on stream temperatures and reach-scale estimates of relative consumption rates (pCmax). Vertical yellow stripes indicate the position of experimental thinning reaches in each study watershed. We repeated modeling under two scenarios: A) temperature-only effects, and B) combined effects of temperature, relative consumption rates, and prey composition in diet.

Temperature + Consumption

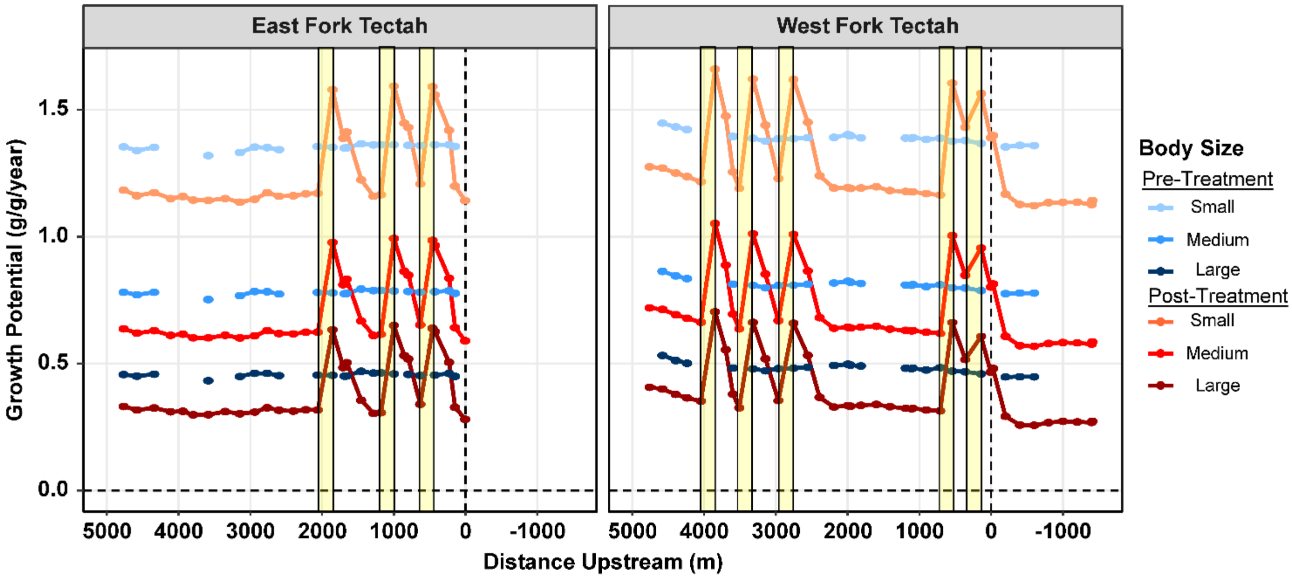


Figure 5.8. Watershed-scale longitudinal profiles of coastal cutthroat trout (*Oncorhynchus clarkii*) annual growth potential at different body sizes during pre- and post-treatment years in northern California, USA study watersheds. Body sizes (small: <20g, medium: 20-40g, and large: 40-60 g) indicated by different colors, with colors getting darker as body size increases. Points indicate the positions of temperature sensors where we estimated growth potential with bioenergetics model based on stream temperatures and reach-scale estimates of relative consumption rates (pCmax). Vertical yellow stripes indicate the position of experimental thinning reaches in each study watershed.

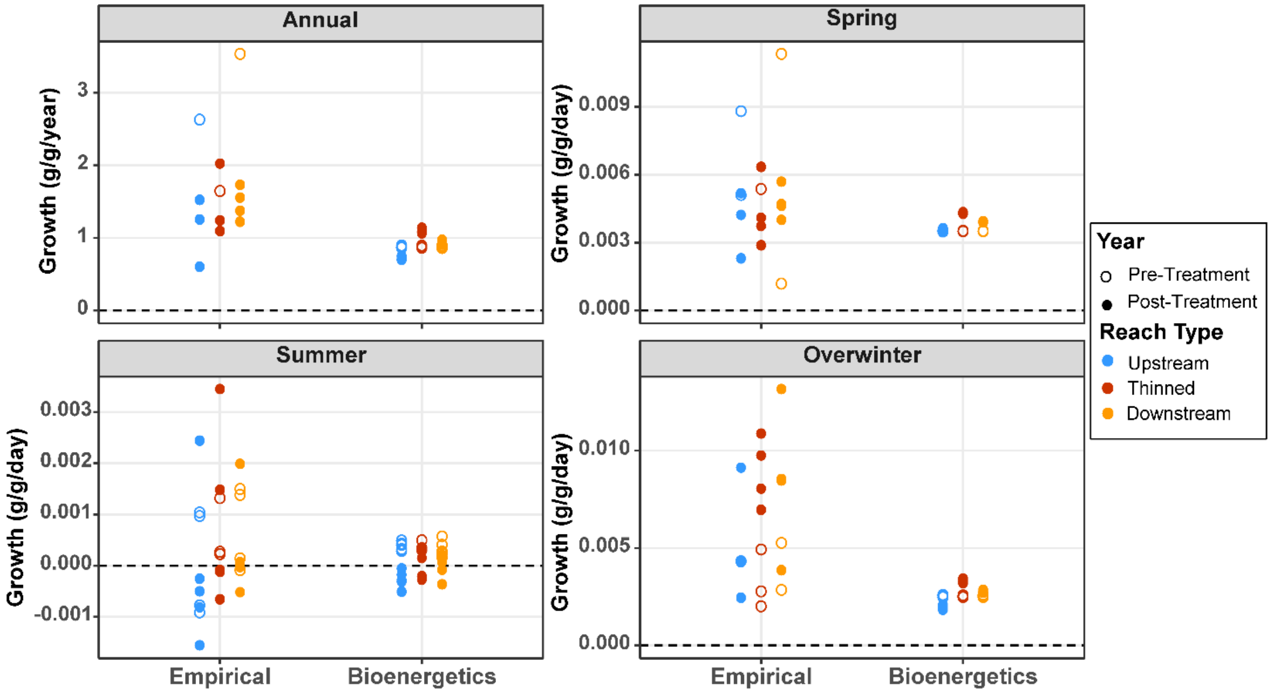


Figure 5.9. Comparisons between empirical and bioenergetics-modeled estimates of seasonal growth rates for coastal cutthroat trout (*Oncorhynchus clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in northern California, USA study watersheds. Points represent mean growth estimates of cutthroat trout of all body sizes at each of our reach-scale sampling sites (*n* = 5).

CHAPTER 6: GENERAL CONCLUSIONS

In this dissertation I explored how changes in riparian zones associated with experimental riparian forest thinning affected thermal and trophic processes in stream ecosystems. In Chapter 2, I examined how changes in shade and light associated with thinning treatments affected stream temperatures at a reach-scale across seasons and multiple components of the thermal regime. In Chapter 3, I applied a riverscape perspective to evaluate how local changes in stream temperature in response to thinning propagated downstream at watershed extents and across multiple spatiotemporal scales to quantify the spatial extent and temporal duration of downstream effects. In Chapter 4, I examined how increases in light associated with thinning affected autotrophic pathways of energy flow and the extent to which increases in periphyton were incorporated into the food webs supporting stream amphibians and fish. Finally, in Chapter 5, I looked to see how these thermal and trophic responses interacted with one another to influence the growth and energetics of coastal cutthroat trout. Through the use of a bioenergetics model, I estimated the effects of thinning on cutthroat trout energy intake, consumption, and growth potential at both reach and watershed scales. Taken together, my dissertation provides a whole-system, process-based evaluation of how stream ecosystems responded to riparian thinning. Here I provide some of the key findings, their implications for management, and suggestions for future research.

In Chapters 2 and 3, I explored the effects of thinning on stream temperatures. In Chapter 2, I found that stream temperature responses to thinning depended on treatment intensity. More intensive thinning treatments that reduced shade and increased light to the stream channel by 20-30% resulted in larger responses in stream temperature, whereas less intensive thinning treatments that only reduced shade and increased light by 3-5% had minimal influence on stream temperatures. Although the magnitude of temperature responses observed with thinning were much smaller than what was observed with historical timber harvest practices (Moore et al. 2005), increases in stream temperature were detected across multiple seasons and components of the thermal regime. Model selection analyses indicated that temperature responses to thinning were primarily driven by a combination of local radiative and longitudinal advective processes (Moore et al. 2005). In Chapter 3, I combined this conceptual framework of local radiative and longitudinal advective processes with a riverscape approach that employed a watershed-scale network of temperature sensors and characterized thermal conditions across multiple spatiotemporal scales (Fausch et al. 2002) to quantify the potential cumulative watershed effects associated with thinning (Reid 1998). From this analysis, I found that local changes in temperature to thinning frequently propagated downstream, but that the spatial extent of downstream effects depended on the magnitude of local increase, ranging from 100 to nearly 1000 m downstream, and was evident across multiple spatiotemporal scales. Downstream effects typically dissipated as an extended pulse and I saw little evidence of cumulative effects except where thinning treatments were closely spaced (<400 m) and local increases in temperature did not have enough space to dissipate before encountering another patch of thinning.

Results from these analyses of stream temperatures provide important information for how managers could minimize local and downstream temperature responses to thinning. First, I documented that more intensive thinning treatments increased stream temperatures, but less intensive thinning treatments had minimal effects. So, if changes in temperature are a concern, managers could thin less intensively. Smaller changes in temperature could also be achieved by thinning a shorter section of stream as smaller scale changes in canopy typically result in smaller temperature responses (Swartz et al. 2020). Second, in these studies I documented the importance of advective processes for transporting heat that affected both local and downstream thermal responses to thinning (Moore et al. 2005). For example, I documented that local increases in temperature frequently propagated downstream and local responses to thinning were often affected by other thinning treatments higher in the watershed. When treatments were nearby one another, upstream temperature changes caused larger increases in the subsequent downstream reach, resulting in a compounding effect. In order to avoid potential cumulative effects, thinning treatments could be spaced farther apart to ensure heat from thinning treatments has a chance to dissipate before encountering the next treatment section. Downstream distances as documented with more intensive treatments in Chapter 3 (300-1000 m) provide guidance for managers on potential spacing to avoid the potential for cumulative effects.

In Chapter 4, I explored the effects of thinning on trophic pathways linking stream-riparian food webs. I found that increases in light associated with thinning led to limited food web responses and that observable responses were largely confined to lower trophic levels. I saw no effect of thinning on stream periphyton abundance on the streambed, yet saw increased periphyton accrual on experimental tiles. These mixed effects did not appear to propagate up to top predators in these streams indicated by lack of response in invertebrate prey in the diets or reflected by stable isotopes inferring broader pathways of energy flow for coastal giant salamanders or coastal cutthroat trout. This lack of a response by top predators could be due to: 1) increases in light associated with thinning treatments did not generate sufficient energy to propagate up to upper trophic levels; 2) resistance by top predators to changes in stream-riparian food webs; or 3) other factors may be limiting food web dynamics (e.g., nutrients) in these forested watersheds. Although I did not find strong food web responses to thinning, from this study I found value in the application of process-based food web approaches that helped tease apart whether the trophic pathways by which changes in riparian canopies could increase aquatic productivity for top predators in streams actually responded with thinning (Power and Dietrich 2002, Bellmore et al. 2017). This study documented the importance of considering species interactions, the structure of ecological networks, and trophic linkages to provide a better understanding of how ecosystems are structured and respond to change (Bascompte 2010).

The results from the food web study in Chapter 4 also highlighted the fact that although many assume that increases in light associated with thinning will automatically lead to increased aquatic productivity (Newton and Ice 2015), outcomes do not always match expectations (Nash et al. 2021). Additionally, because conditions and communities within stream networks vary widely due to inherent spatial heterogeneity, it may be unrealistic to expect responses to be consistent across the landscape (Power and Dietrich 2002, Whitney et al. 2020). Part of the disconnect between expectations and reality regarding responses in aquatic productivity could be because available information is largely based on older studies that evaluated more dramatic changes in riparian canopies that had larger effect sizes (e.g., Bilby and Bisson 1992). Although more recent studies have also found evidence that smaller changes in canopy conditions can influence aquatic productivity and food webs (e.g., England and Rosemond 2004, Kaylor and Warren 2017, Heaston et al. 2018), the smaller effect sizes associated with thinning increases the chances of environmental variability exceeding treatment effects which can lead to context dependent outcomes (Morley et al. 2016). As a result, it is challenging to provide simple management recommendations about the effects of thinning on aquatic food webs, because responses are more likely to be context dependent. For example, I found evidence that even though thinning alleviated light limitation, primary production could still be limited by nutrients in this small forested watersheds (Warren et al. 2017). In this light (pun intended), making sure to collect detailed background data to quantify environmental context would help identify potential limiting factors and whether a system would be likely to respond to more subtle changes in riparian forests such as thinning.

In Chapter 5, I combined data on stream temperature, invertebrate prey in diets, and empirical growth rates of coastal cutthroat trout in a bioenergetics model to understand the effects of thinning on growth and energetics for these stream fish. In this study I frequently observed greater seasonal variation than variation due to thinning, where stream thermal and trophic conditions, growth rates, and bioenergetics estimates of energy intake and relative consumption all varied more seasonally than due to thinning (Morley et al. 2016). When I combined bioenergetics estimates of relative consumption with my watershed-scale network of temperature sensors, I was effectively able to model growth potential at a watershed-scale and how growth potential responded to thinning. Watershed-scale longitudinal profiles showed that thinning increased growth potential for cutthroat trout annually. However, when I considered patterns seasonally, I found that the responses and the driving factors depended seasonally. Increases in growth potential to thinning were largely driven by trophic processes in spring and overwinter, and effects in summer were driven by a combination of thermal and trophic processes where the net outcome depended on the relative strength of these two pathways. These results highlight the importance of trophic processes supporting growth potential for these stream fish and suggest that temperature increases associated with thinning had little negative effect on cutthroat trout growth potential only affecting these fish in summer and under the greatest temperature changes.

Results from my analysis of growth and bioenergetics found that extending the scales of analysis provided unique insights not possible from shorter periods of time or smaller spatial extents. Stream ecology studies tend to take place in summer (Brady et al. 2021) and at more localized scales (Fausch et al. 2002). I gained a more comprehensive perspective about the effects of thinning both by extending our sampling across multiple seasons and across entire watersheds. Rather than just focusing on summer, I tracked year-round patterns of stream temperature helping us determine the times of year under which thinning affected thermal conditions. I also repeated my biological sampling seasonally to help capture seasonal dynamics. By tagging cutthroat trout and sampling seasonally I effectively captured seasonal patterns in growth during spring, summer, and overwinter periods of time. I also scaled my analysis to the watershed extent through the use of a watershed scale network of temperature sensors. I used this network of sensors to track local and downstream patterns of temperature changes with thinning, but I also related this network to a bioenergetics model to estimate watershed-scale patterns of growth potential, similar to recent efforts by Falke et al. (2019). Studies at the watershed scale can allow researchers and managers gain a more spatially explicit understanding of effects at scales more directly relevant to mobile species (Schlosser 1991, Fausch et al. 2002) and to land use and disturbance effects (Allan 2004).

Future research

One major limitation of this research was that due to my limited timeframe, I could only compare one year of pre-treatment conditions to one year of post-treatment conditions. This is the nature of many graduate research projects, but this is a major limitation for two reasons. First, I was likely unable to fully capture interannual variability in pre-treatment conditions. This can add uncertainty to inferences made about post-treatment responses because I am unable to know how representative either year is in the context of the full range of variation the system naturally experiences. Second, I could only capture post-treatment responses one year after treatment. While I was effective in capturing some rapid responses such as changes in shade, light, and temperature that can respond immediately, I was not able to quantify the persistence of those changes through time. Furthermore, some of the biological responses may have taken more time to generate than I could capture within the timeframe of this research. This raises the possibility that although I did not see strong biological responses to thinning, it simply could take more time for them to develop. This seems especially likely when thinking about responses in the context of entire food webs, where multiple biological interactions need to occur before a response would propagate up to a top predator like a coastal giant salamander or coastal cutthroat trout. Longer-term studies that can monitor physical and biological responses over longer periods of time are needed to fully understand responses to changes in riparian forests such as thinning.

Future research could also benefit from exploring a broader range of riparian restoration treatments. In this research I evaluated just two intensities of treatment intensity of thinning. Under the more intensive thinning treatments in the Tectah watersheds on private timberland owned by Green Diamond, treatment reaches were thinned on both sides of the stream channel so canopy closure within riparian forests approached 50%. In contrast, the thinning treatments in the Lost Man watershed in Redwood National Park was much less intensive, where a smaller percentage of trees within the riparian zone were cut as it was a first attempt of thinning by the park and likely was approached with caution. Future research is thus warranted to explore the effects of more intermediate thinning treatments that would represent more realistic treatments if thinning were to be applied at larger scales. This includes one-sided thinning treatments as well as other riparian treatments such as canopy gaps, variable buffer widths, and variable-density thinning (Teraoka and Keyes 2011, Richardson et al. 2012, Swartz et al. 2020). A broader range of treatments that are more realistic to achieve management objectives would provide a better understanding of adding heterogeneity at a range of intensities in recovering riparian forests and the effects on aquatic ecosystems.

Finally, this research took place in three small watersheds in coastal northern California and as a result, my scope of inference regarding thinning is limited to these watersheds. While my results may apply to nearby watersheds or locations with similar conditions, I do not know how well they may apply to other locations. Therefore, in order to better understand the effects of riparian thinning there needs to be more observations under a broader range of contexts. Riparian protections often limit these type of field experiments, however, landscape experiments have been called for when trying to evaluate changes in land use such as the Northwest Forest Plan (Stankey et al. 2003, Spies et al. 2019) or more active management of riparian zones (Berg 1995, Carey 2003). I hope that the results from this field experiment inspires future research and contributes to the collective understanding of how best to restore second-growth riparian forests so they can provide important ecological functions for both stream and riparian ecosystems while they continue to recover from a legacy of previous land-use.

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APPENDICES

Chapter 2

Table A2.1. Summary of BACI Analyses. Summary of BACI models and estimated BACI differences with lower and upper 95% confidence intervals. BACI differences are indicated as statistically significant ($p < 0.05$) by bold font. No pre-treatment stream temperature data were available during fall and winter seasons for Lost Man, so BACI analyses focused on spring and summer.

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Canopy Closure – Tectah					
Intercept	1,53	6226.8	<0.0001	TH vs. US (2017)	**-18.7 (-21.0, -16.3)**
Reach	2,53	0.4	0.6758	TH vs. US (2018)	**-16.9 (-19.2, -14.6)**
Year	2,53	612.0	<0.0001	DS vs. US (2017)	0.6 (-0.7, 1.9)
Reach*Year	4,53	142.5	**<0.0001**	DS vs. US (2018)	0.5 (-1.1, 2.1)
Canopy Closure – Lost Man					
Intercept	1,8	12030.4	<0.0001	TH vs. US (2017)	-2.1 (-5.1, 1.4)
Reach	2,8	19.6	0.0008	TH vs. US (2018)	-1.9 (-5.3, 1.2)
Year	2,8	130.4	<0.0001	DS vs. US (2017)	0.5 (-2.9, 3.9)
Reach*Year	4,8	2.7	0.1046	DS vs. US (2018)	-1.5 (-4.9, 1.9)
Effective Shade – Tectah					
Intercept	1,53	1074.4	<0.0001	TH vs. US (2017)	**-25.4 (-28.6, -22.3)**
Reach	2,53	40.7	<0.0001	TH vs. US (2018)	**-23.0 (-25.8, -20.1)**
Year	2,53	331.9	<0.0001	DS vs. US (2017)	-0.9 (-2.3, 0.5)
Reach*Year	4,53	139.7	**<0.0001**	DS vs. US (2018)	-1.0 (-2.6, 0.6)
Effective Shade – Lost Man					
Intercept	1,8	30329.8	<0.0001	TH vs. US (2017)	**-4.8 (-8.0, -0.5)**
Reach	2,8	28.6	0.0002	TH vs. US (2018)	**-4.1 (-7.3, -0.3)**
Year	2,8	250.2	<0.0001	DS vs. US (2017)	-0.6 (-2.9, 3.9)
Reach*Year	4,8	4.7	**0.0300**	DS vs. US (2018)	-0.5 (-5.1, 4.0)
Light – Tectah					
Intercept	1,44	422.9	<0.0001	TH vs. US (2017)	**33.0 (27.3, 38.5)**
Reach	2,44	244.7	<0.0001	TH vs. US (2018)	**27.1 (20.4, 33.8)**
Year	2,44	63.3	<0.0001	DS vs. US (2017)	3.2 (-1.6, 4.8)
Reach*Year	4,44	45.3	**<0.0001**	DS vs. US (2018)	1.8 (-0.8, 3.9)
Light – Lost Man					
Intercept	1,8	496.7	<0.0001	TH vs. US (2017)	2.9 (-0.7, 6.5)
Reach	2,8	13.7	0.0026	TH vs. US (2018)	2.5 (-1.6, 5.6)
Year	2,8	14.6	0.0021	DS vs. US (2017)	-0.4 (-3.3, 2.5)
Reach*Year	4,8	1.5	0.2772	DS vs. US (2018)	1.0 (-1.9, 3.9)

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Stream Temperature – Fall MWMT - Tectah					
Intercept	1,33	26104.8	<0.0001	TH vs. US (2018)	**1.0 (0.5, 1.5)**
Reach	2,33	11.8	<0.0001	DS vs. US (2018)	0.3 (-0.1, 0.6)
Year	1,33	69.9	<0.0001		
Reach*Year	2,33	7.8	**0.0016**		
Stream Temperature – Winter MWMT - Tectah					
Intercept	1,33	191084.3	<0.0001	TH vs. US (2018)	-0.1 (-0.2, 0.1)
Reach	2,33	2.9	0.0672	DS vs. US (2018)	-0.1 (-0.2, 0.1)
Year	1,33	44.1	<0.0001		
Reach*Year	2,33	0.3	0.7273		
Stream Temperature – Spring MWMT - Tectah					
Intercept	1,33	22810.1	<0.0001	TH vs. US (2018)	**1.7 (0.9, 2.5)**
Reach	2,33	3.4	0.0456	DS vs. US (2018)	**1.0 (0.0, 2.0)**
Year	1,33	0.4	0.5233		
Reach*Year	2,33	9.9	**0.0004**		
Stream Temperature – Summer MWMT - Tectah					
Intercept	1,33	5255.8	<0.0001	TH vs. US (2018)	**2.8 (1.8, 3.8)**
Reach	2,33	0.5	0.6151	DS vs. US (2018)	**1.4 (0.3, 2.6)**
Year	1,33	37.4	<0.0001		
Reach*Year	2,33	15.6	**<0.0001**		
Stream Temperature – Spring MWMT – Lost Man					
Intercept	1,5	4440.2	<0.0001	TH vs. US (2018)	0.1 (-0.2, 0.5)
Reach	2,5	4.0	0.0919	DS vs. US (2018)	0.1 (-0.2, 0.4)
Year	1,5	243.6	<0.0001		
Reach*Year	2,5	0.7	0.5209		
Stream Temperature – Summer MWMT – Lost Man					
Intercept	1,5	6957.8	<0.0001	TH vs. US (2018)	0.2 (-0.1, 0.4)
Reach	2,5	3.2	0.1252	DS vs. US (2018)	0.1 (-0.2, 0.3)
Year	1,5	7.4	0.0414		
Reach*Year	2,5	2.1	0.2216		

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Stream Temperature – Fall MWAT - Tectah					
Intercept	1,33	40736.8	<0.0001	TH vs. US (2018)	0.1 (-0.1, 0.3)
Reach	2,33	449.5	<0.0001	DS vs. US (2018)	0.1 (-0.1, 0.3)
Year	1,33	362.7	<0.0001		
Reach*Year	2,33	0.7	0.5093		
Stream Temperature – Winter MWAT - Tectah					
Intercept	1,33	82065.7	<0.0001	TH vs. US (2018)	0.0 (-0.1, 0.1)
Reach	2,33	0.1	0.9868	DS vs. US (2018)	0.0 (-0.1, 0.1)
Year	1,33	31.1	<0.0001		
Reach*Year	2,33	0.1	0.9898		
Stream Temperature – Spring MWAT - Tectah					
Intercept	1,33	58402.4	<0.0001	TH vs. US (2018)	**0.5 (0.2, 0.8)**
Reach	2,33	15.2	<0.0001	DS vs. US (2018)	0.3 (-0.1, 0.7)
Year	1,33	124.5	<0.0001		
Reach*Year	2,33	7.4	**0.0022**		
Stream Temperature – Summer MWAT - Tectah					
Intercept	1,33	24385.0	<0.0001	TH vs. US (2018)	**0.9 (0.4, 1.4)**
Reach	2,33	0.8	0.2779	DS vs. US (2018)	**0.6 (0.1, 1.2)**
Year	1,33	55.1	<0.0001		
Reach*Year	2,33	7.6	**0.0020**		
Stream Temperature – Spring MWAT – Lost Man					
Intercept	1,5	13028.6	<0.0001	TH vs. US (2018)	-0.1 (-0.4, 0.3)
Reach	2,5	1.7	0.2770	DS vs. US (2018)	0.0 (-0.3, 0.4)
Year	1,5	297.9	<0.0001		
Reach*Year	2,5	0.0	0.9859		
Stream Temperature – Summer MWAT – Lost Man					
Intercept	1,5	25233.9	<0.0001	TH vs. US (2018)	0.1 (-0.1, 0.3)
Reach	2,5	2.5	0.1741	DS vs. US (2018)	0.0 (-0.1, 0.2)
Year	1,5	19.0	0.0073		
Reach*Year	2,5	3.4	0.1181		

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Stream Temperature – Fall Degree Days - Tectah					
Intercept	1,33	15969.7	<0.0001	TH vs. US (2018)	2.9 (-9.1, 14.9)
Reach	2,33	21.0	<0.0001	DS vs. US (2018)	5.6 (-6.2, 17.4)
Year	1,33	281.0	<0.0001		
Reach*Year	2,33	0.5	0.6025		
Stream Temperature – Winter Degree Days - Tectah					
Intercept	1,33	2116.7	<0.0001	TH vs. US (2018)	0.5 (-5.8, 6.8)
Reach	2,33	0.2	0.7913	DS vs. US (2018)	1.1 (-6.4, 8.7)
Year	1,33	3561.0	<0.0001		
Reach*Year	2,33	0.1	0.9525		
Stream Temperature – Spring Degree Days - Tectah					
Intercept	1,33	113187.8	<0.0001	TH vs. US (2018)	**18.6 (7.5, 29.7)**
Reach	2,33	21.7	<0.0001	DS vs. US (2018)	11.1 (-11.5, 33.8)
Year	1,33	204.4	<0.0001		
Reach*Year	2,33	5.9	**0.0066**		
Stream Temperature – Summer Degree Days - Tectah					
Intercept	1,33	78900.6	<0.0001	TH vs. US (2018)	**77.7 (48.6, 106.8)**
Reach	2,33	0.3	0.7289	DS vs. US (2018)	**48.1 (12.5, 83.7)**
Year	1,33	57.5	<0.0001		
Reach*Year	2,33	15.1	**<0.0001**		
Stream Temperature – Spring Degree Days – Lost Man					
Intercept	1,5	14830.5	<0.0001	TH vs. US (2018)	6.8 (-8.2, 21.8)
Reach	2,5	2.0	0.2303	DS vs. US (2018)	-2.3 (-17.3, 12.7)
Year	1,5	80.9	0.0003		
Reach*Year	2,5	1.3	0.3490		
Stream Temperature – Summer Degree Days – Lost Man					
Intercept	1,5	20627.2	<0.0001	TH vs. US (2018)	11.9 (-5.5, 29.4)
Reach	2,5	2.1	0.2177	DS vs. US (2018)	0.4 (-17.0, 17.8)
Year	1,5	44.8	0.0011		
Reach*Year	2,5	2.0	0.2315		

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Stream Temperature – Fall Daily Range - Tectah					
Intercept	1,33	313.7	<0.0001	TH vs. US (2018)	**0.4 (0.2, 0.5)**
Reach	2,33	0.9	0.4023	DS vs. US (2018)	0.2 (0.0, 0.3)
Year	1,33	6.9	0.0131		
Reach*Year	2,33	11.7	**0.0001**		
Stream Temperature – Winter Daily Range - Tectah					
Intercept	1,33	476.2	<0.0001	TH vs. US (2018)	0.0 (-0.1, 0.1)
Reach	2,33	4.7	0.0162	DS vs. US (2018)	-0.1 (-0.2, 0.1)
Year	1,33	62.0	<0.0001		
Reach*Year	2,33	1.1	0.3339		
Stream Temperature – Spring Daily Range - Tectah					
Intercept	1,33	262.2	<0.0001	TH vs. US (2018)	**0.5 (0.2, 0.9)**
Reach	2,33	0.1	0.8632	DS vs. US (2018)	0.3 (-0.3, 0.7)
Year	1,33	60.6	<0.0001		
Reach*Year	2,33	4.6	**0.0169**		
Stream Temperature – Summer Daily Range - Tectah					
Intercept	1,33	74.9	<0.0001	TH vs. US (2018)	**2.5 (1.6, 3.4)**
Reach	2,33	0.0	0.9700	DS vs. US (2018)	**0.7 (0.0, 1.5)**
Year	1,33	17.2	0.0002		
Reach*Year	2,33	16.8	**<0.0001**		
Stream Temperature – Spring Daily Range – Lost Man					
Intercept	1,5	165.4	0.0001	TH vs. US (2018)	0.2 (-0.4, 0.9)
Reach	2,5	0.4	0.6860	DS vs. US (2018)	-0.1 (-0.6, 0.6)
Year	1,5	1.7	0.2538		
Reach*Year	2,5	0.6	0.6069		
Stream Temperature – Summer Daily Range – Lost Man					
Intercept	1,5	1088.2	<0.0001	TH vs. US (2018)	0.1 (-0.2, 0.4)
Reach	2,5	0.2	0.8098	DS vs. US (2018)	0.1 (-0.2, 0.4)
Year	1,5	0.3	0.6197		
Reach*Year	2,5	0.4	0.6765		

BACI model				**BACI differences**	
Variable	**DF**	**F-stat**	**p-value**	**Post-hoc Test**	**Estimate**
Stream Temperature – Fall Variance - Tectah					
Intercept	1,33	66.7	<0.0001	TH vs. US (2018)	**0.1 (0.0, 0.2)**
Reach	2,33	0.3	0.7456	DS vs. US (2018)	0.0 (0.0, 0.1)
Year	1,33	2.2	0.1517		
Reach*Year	2,33	8.8	**0.0009**		
Stream Temperature – Winter Variance - Tectah					
Intercept	1,33	129.6	<0.0001	TH vs. US (2018)	0.0 (-0.1, 0.1)
Reach	2,33	4.7	0.0158	DS vs. US (2018)	-0.1 (-0.1, 0.1)
Year	1,33	48.8	<0.0001		
Reach*Year	2,33	1.0	0.3947		
Stream Temperature – Spring Variance - Tectah					
Intercept	1,33	75.2	<0.0001	TH vs. US (2018)	**0.3 (0.1, 0.5)**
Reach	2,33	0.2	0.8279	DS vs. US (2018)	0.2 (-0.1, 0.4)
Year	1,33	29.2	<0.0001		
Reach*Year	2,33	4.3	**0.0220**		
Stream Temperature – Summer Variance - Tectah					
Intercept	1,33	22.7	<0.0001	TH vs. US (2018)	**1.6 (0.7, 2.5)**
Reach	2,33	0.0	0.9913	DS vs. US (2018)	**0.5 (0.0, 1.0)**
Year	1,33	4.0	0.0546		
Reach*Year	2,33	8.4	**0.0012**		
Stream Temperature – Spring Variance – Lost Man					
Intercept	1,5	31.0	0.0026	TH vs. US (2018)	0.0 (-0.1, 0.1)
Reach	2,5	3.3	0.1197	DS vs. US (2018)	0.0 (-0.1, 0.1)
Year	1,5	1.8	0.2363		
Reach*Year	2,5	0.0	0.9883		
Stream Temperature – Summer Variance – Lost Man					
Intercept	1,5	64.0	0.0005	TH vs. US (2018)	0.0 (-0.1, 0.1)
Reach	2,5	0.9	0.4777	DS vs. US (2018)	0.0 (-0.1, 0.1)
Year	1,5	1.3	0.3119		
Reach*Year	2,5	2.0	0.2352		

Table A2.2. Model selection AIC$_c$ table ranking top ten *a priori* candidate models.

To better understand the variation in stream thermal regimes and their responses to riparian thinning we considered a range of models in a model selection analysis. In addition to the BACI model of Reach*Year we considered a broad range of environmental covariates that we hypothesized could influence stream temperatures based on previous stream temperature studies. Here we list the covariates we considered in the correlation matrix and whether or not covariates were included in candidate models in model selection. Covariates included in model selection are highlighted in bold and abbreviations of the covariate are listed next to name.

Effective Shade (ES) – shade over the stream channel (%). Accounts for the intensity of thinning treatments. Continuous estimates of shade may better represent conditions than categorical fixed effects in BACI model of Reach*Year.

Canopy Closure – another measure of shade over the stream channel (%). Accounts for the intensity of thinning treatments. Did not include in model selection because correlated with Effective Shade.

Light – below canopy light over the stream channel (%). Accounts for the intensity of thinning treatments. Did not include in model selection because correlated with Effective Shade.

Upstream Temperature (UT) – summer MWMT from the incoming upstream reach (°C). Upstream thermal conditions could be a major source of non-independent thermal behavior between sites.

Treatment Proximity (TP) – categorical variable of whether or not reach is positioned downstream from a thinning treatment (within 400m). Accounts for a lack of independence of some sites that are spatially adjacent.

Air Temperature – summer mean air temperature at the upstream reach within a site (°C). Did not include in model selection because correlated with other physical site characteristics.

Reach Length (RL) – length of stream reach (m). Accounts for the fact that the length of the reach may influence the spatial exposure of a reach to thinning.

Bankfull Width (BW) – bankfull width of the stream channel (m). Accounts for the fact that the width of the reach may influence the spatial exposure of a reach to thinning.

Gradient (GR) – gradient of the stream channel (%). Accounts for the gradient of the stream channel may influence how quickly the water may move through a reach and in turn how quickly it may heat up.

Distance Upstream – position of the reach within the watershed (m). Accounts for the position in the watershed may influence spatial exposure of a reach to thinning. Did not include in model selection because correlated with other physical site characteristics.

Aspect – orientation of the stream channel (°). Accounts for the position in the watershed may influence spatial exposure of a reach to thinning. Did not include in model selection because correlated with other physical site characteristics.

Elevation – elevation of the stream channel (m). Accounts for the position in the watershed may influence spatial exposure of a reach to thinning. Did not include in model selection because correlated with other physical site characteristics.

Summer MWMT – *Tectah*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	ES + UT	3	10	104.2	0.0	0.383
2	UT	2	9	106.8	2.6	0.103
3	ES + UT + GR	4	11	107.1	2.9	0.092
4	ES + UT + TP	4	11	107.6	3.4	0.071
5	ES + UT + RL	4	11	107.7	3.4	0.068
6	ES + UT + BW	4	11	107.7	3.5	0.068
7	UT + RL	3	10	108.7	4.5	0.040
8	UT + BW	3	10	109.7	5.5	0.024
9	UT + GR	3	10	109.8	5.6	0.024
10	UT + TP	3	10	109.9	5.7	0.023

Summer MWAT – *Tectah*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	ES + UT + TP	4	11	29.3	0.0	0.292
2	ES + UT + RL	4	11	30.8	1.5	0.137
3	ES + UT	3	10	31.1	1.7	0.122
4	ES + TP	3	10	32.0	2.6	0.079
5	ES + UT + TP + RL	5	12	32.1	2.8	0.074
6	ES + UT + TP + GR	5	12	32.4	3.1	0.062
7	ES + UT + TP + BW	5	12	33.0	3.7	0.046
8	ES + UT + RL + GR	5	12	33.7	4.4	0.033
9	ES + UT + BW	4	11	34.0	4.6	0.029
10	ES + UT + RL + BW	5	12	34.5	5.2	0.022

Summer Degree Days - *Tectah*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	ES + UT + TP	4	11	406.9	0.0	0.249
2	ES + UT + GR	4	11	406.9	0.0	0.248
3	ES + UT + TP + GR	5	12	408.6	1.6	0.109
4	ES + UT	3	10	409.0	2.1	0.089
5	ES + TP	3	10	409.8	2.9	0.058
6	ES + UT + TP + RL	5	12	410.4	3.5	0.044
7	ES + UT + TP + GR	5	12	410.4	3.5	0.043
8	ES + UT + RL + GR	5	12	410.6	3.7	0.039
9	ES + UT + BW	4	11	411.0	4.1	0.032
10	ES + UT + RL	4	11	412.1	5.2	0.018

Summer Daily Range – *Tectah*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	ES + UT	3	10	93.0	0.0	0.286
2	ES + UT + TP + GR	5	12	93.6	0.7	0.203
3	ES	2	9	95.0	2.0	0.105
4	ES + TP	3	10	96.4	3.4	0.052
5	ES + UT + TP	4	11	96.4	3.4	0.051
6	ES + UT + RL	4	11	96.4	3.5	0.050
7	ES + UT + BW	4	11	96.4	3.5	0.050
8	ES + UT + GR	4	11	96.4	3.5	0.050
9	ES + BW	3	10	98.2	5.3	0.020
10	ES + GR	3	10	98.2	5.3	0.020

Summer Variance – *Tectah*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	ES + UT + TP + GR	5	12	26.2	0.0	0.873
2	UT	2	9	32.5	6.3	0.038
3	UT + RL + GR	4	11	34.2	7.9	0.016
4	UT + GR	3	10	34.8	8.6	0.012
5	UT + TP	3	10	34.9	8.7	0.011
6	ES + UT	3	10	35.2	9.0	0.010
7	ES + UT + RL + GR	5	12	35.3	9.1	0.009
8	UT + BW	3	10	35.8	9.6	0.007
9	UT + RL	3	10	35.8	9.6	0.007
10	ES	2	9	37.8	11.6	0.003

Summer MWMT – *Lost Man*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	Intercept	1	3	-6.1	0.0	0.256
2	GR	2	4	-5.4	0.7	0.178
3	UT	2	4	-4.5	1.6	0.112
4	BW	2	4	-4.4	1.7	0.109
5	UT + GR	3	5	-4.2	1.9	0.097
6	UT + BW	3	5	-3.0	3.1	0.054
7	ES	2	4	-2.5	3.6	0.042
8	TP	2	4	-1.4	4.7	0.025
9	RL	2	4	-1.4	4.7	0.024
10	TP + GR	3	5	-1.4	4.8	0.024

Summer MWAT – *Lost Man*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	GR	2	4	-13.4	0.0	0.228
2	Intercept	1	3	-13.0	0.3	0.193
3	BW	2	4	-12.7	0.7	0.161
4	UT	2	4	-11.2	2.2	0.077
5	TP + GR	3	5	-10.7	2.6	0.061
6	TP + BW	3	5	-10.4	2.9	0.052
7	ES	2	4	-10.2	3.1	0.047
8	UT + BW	3	5	-9.6	3.8	0.034
9	TP	2	4	-8.9	4.4	0.025
10	UT + BW	3	5	-8.9	4.5	0.024

Summer Degree Days – *Lost Man*

Rank	Model	*K*	df	AIC$_c$	ΔAIC$_c$	w_i
1	UT	2	4	103.5	0.0	0.195
2	Intercept	1	3	103.8	0.3	0.169
3	ES	2	4	104.3	0.8	0.134
4	GR	2	4	104.6	1.1	0.114
5	BW	2	4	105.2	1.7	0.083
6	TP + GR	3	5	106.9	3.4	0.036
7	ES + BW	3	5	107.3	3.8	0.030
8	TP	2	4	107.3	3.8	0.029

9	TP + BW	3	5	107.4	3.9	0.028
10	UT + GR	3	5	108.1	4.6	0.020

Summer Daily Range – *Lost Man*

Rank	**Model**	***K***	**df**	**AIC$_c$**	**ΔAIC$_c$**	w_i
1	Intercept	1	3	-24.5	0.0	0.543
2	ES	2	4	-20.8	3.8	0.083
3	TP	2	4	-20.6	4.0	0.075
4	RL	2	4	-20.4	4.1	0.069
5	BW	2	4	-20.4	4.1	0.068
6	UT	2	4	-20.0	4.6	0.055
7	GR	2	4	-19.9	4.6	0.054
8	ES + TP	3	5	-15.3	9.2	0.005
9	UT + BW	3	5	-15.0	9.5	0.005
10	TP + RL	3	5	-15.0	9.6	0.005

Summer Variance – *Lost Man*

Rank	**Model**	***K***	**df**	**AIC$_c$**	**ΔAIC$_c$**	w_i
1	Intercept	1	3	-72.6	0.0	0.221
2	BW	2	4	-72.0	0.6	0.163
3	ES	2	4	-71.2	1.4	0.108
4	ES + GR	3	5	-70.4	2.2	0.073
5	GR	2	4	-70.1	2.5	0.064
6	TP	2	4	-69.7	2.9	0.052
7	ES + BW	3	5	-69.7	2.9	0.051
8	ES + UT	3	5	-69.5	3.1	0.047
9	RL	2	4	-69.5	3.1	0.047
10	ES + UT + BW	4	6	-69.3	3.3	0.042

Table A2.3. Best supported models determined by model selection. Best supported linear mixed-effects models where fixed and random effects are determined by model selection for each response variable.

Summer MWMT - Tectah

Summer MWMT ~ Effective Shade + UpstreamTemp with Random Effect of Site fit by Restricted Maximum Likelihood that includes weights argument that allows Reach and Year to vary.

Fixed Effects

	Value	SE	DF	t-value	p-value
Intercept	18.86	1.89	36	10.01	<0.0001
EffectiveShade	-0.10	0.01	36	-7.92	<0.0001
UpstreamTemp	0.43	0.08	36	5.66	<0.0001

Random Effects

Groups	SD
Site	0.317
Residual	0.509

Summer MWAT - Tectah

Summer MWAT ~ Effective Shade + UpstreamTemp + TreatmentProximity with Random Effect of Site fit by Restricted Maximum Likelihood that includes weights argument that allows Reach and Year to vary.

Fixed Effects

	Value	SE	DF	t-value	p-value
Intercept	15.31	0.73	35	21.10	<0.0001
EffectiveShade	-0.03	0.00	35	-13.42	<0.0001
UpstreamTemp	0.13	0.05	35	2.65	0.0119
TreatmentProximity	0.43	0.10	35	4.42	0.0001

Random Effects

Groups	SD
Site	0.018
Residual	0.228

Summer Degree Days - Tectah

Summer Degree Days ~ Effective Shade + UpstreamTemp + TreatmentProximity with Random Effect of Site fit by Restricted Maximum Likelihood that includes weights argument that allows Reach and Year to vary.

Fixed Effects

	Value	SE	DF	t-value	p-value
Intercept	1329.03	48.79	35	27.24	<0.0001
EffectiveShade	-3.22	0.27	35	-11.73	<0.0001
UpstreamTemp	8.21	2.84	35	2.89	0.0066
TreatmentProximity	17.40	7.01	35	2.48	0.0180

Random Effects

Groups	SD
Site	5.493
Residual	18.755

Summer Daily Range - Tectah

Summer Daily Range ~ Effective Shade + UpstreamTemp with Random Effect of Site fit by Restricted Maximum Likelihood that includes weights argument that allows Reach and Year to vary.

Fixed Effects

	Value	SE	DF	t-value	p-value
Intercept	8.26	1.77	36	4.77	<0.0001
EffectiveShade	-0.10	0.01	36	-7.55	<0.0001
UpstreamTemp	0.17	0.07	36	2.58	0.0142

Random Effects

Groups	SD
Site	0.357
Residual	0.390

Summer Variance - Tectah

Summer Variance ~ EffectiveShade + UpstreamTemp + TreatmentProximity + Gradient with Random Effect of Site fit by Restricted Maximum Likelihood that includes weights argument that allows Reach and Year to vary.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	-0.07	0.42	34	-0.16	0.8771
EffectiveShade	-0.02	0.00	34	-4.61	0.0001
UpstreamTemp	0.13	0.01	34	11.73	<0.0001
TreatmentProximity	-0.14	0.02	34	-6.65	<0.0001
Gradient	0.05	0.01	34	7.91	<0.0001

<u>Random Effects</u>

Groups	SD
Site	0.239
Residual	0.181

Summer MWMT – Lost Man

Summer MWMT ~ Intercept with Random Effect of Site fit by Restricted Maximum Likelihood.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	13.58	0.16	10	83.41	<0.0001

<u>Random Effects</u>

Groups	SD
Intercept	0.226
Residual	0.103

Summer MWAT – Lost Man

Summer MWMT ~ Gradient with Random Effect of Site fit by Restricted Maximum Likelihood.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	12.56	0.16	9	78.52	<0.0001
Gradient	0.10	0.03	9	3.21	0.0107

<u>Random Effects</u>

Groups	SD
Intercept	0.005
Residual	0.086

Summer Degree Days – Lost Man

Summer MWMT ~ UpstreamTemp with Random Effect of Site fit by Restricted Maximum Likelihood.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	836.74	112.74	9	7.42	<0.0001
UpstreamTemp	21.11	8.29	9	2.55	0.0314

<u>Random Effects</u>

Groups	SD
Intercept	0.552
Residual	11.178

Summer Daily Range – Lost Man

Summer MWMT ~ Intercept with Random Effect of Site fit by Restricted Maximum Likelihood.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	0.72	0.02	10	39.76	<0.0001

<u>Random Effects</u>

Groups	SD
Intercept	0.001
Residual	0.062

Summer Variance – Lost Man

Summer MWMT ~ Intercept with Random Effect of Site fit by Restricted Maximum Likelihood.

<u>Fixed Effects</u>

	Value	SE	DF	t-value	p-value
Intercept	0.07	0.01	10	7.99	<0.0001

<u>Random Effects</u>

Groups	SD
Intercept	0.012
Residual	0.007

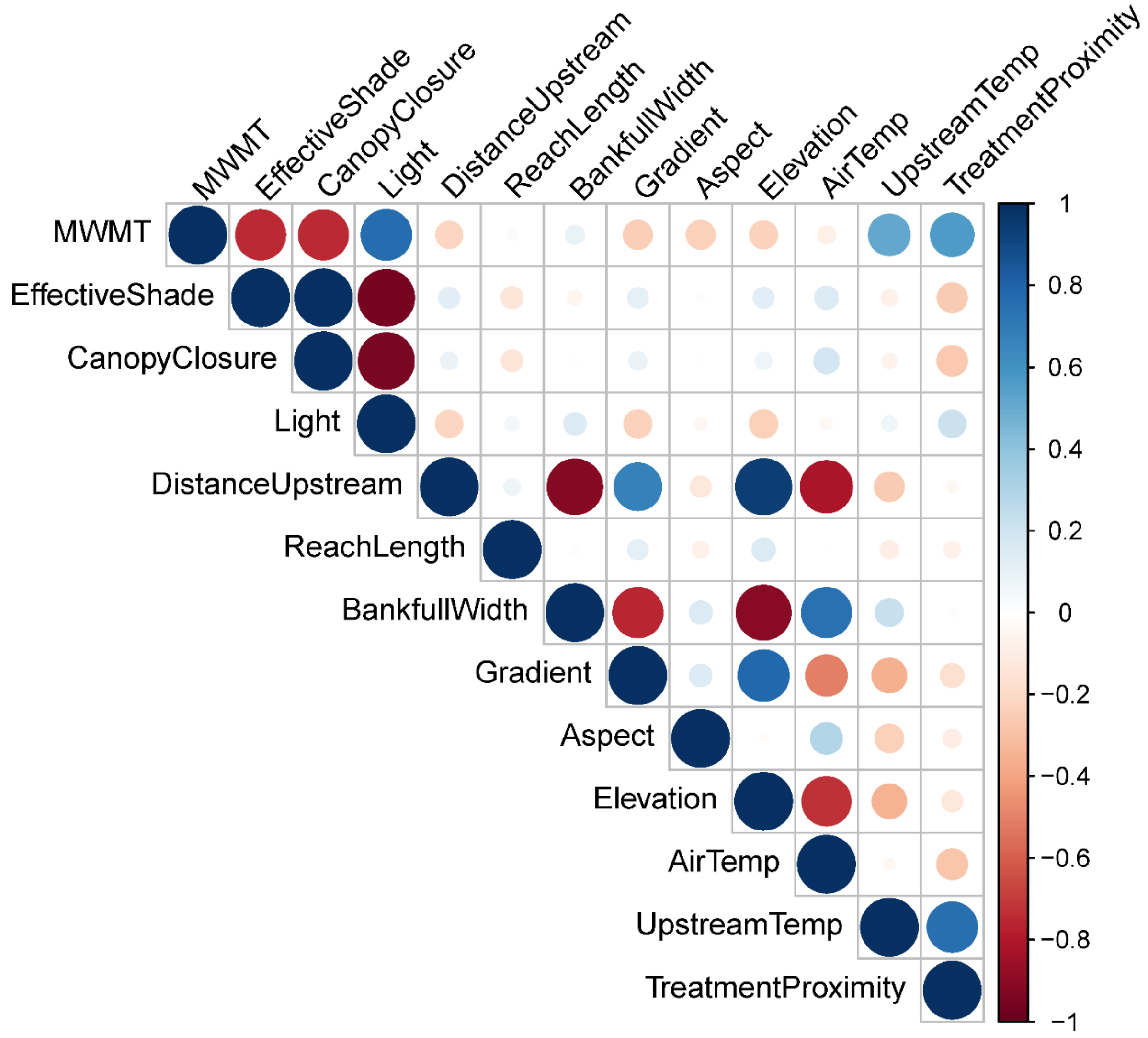

Figure A2.1.a. Correlation matrix for sites in Tectah watersheds. Environmental drivers of temperature responses for upstream reference, thinned, and downstream reaches using pre-treatment and post-treatment data. Correlation matrix between response in summer MWMT, shade and light responses associated with riparian thinning treatments, and study site characteristics for sites in the Tectah watersheds. Site characteristics included: distance upstream, reach length, bankfull width, aspect, gradient, elevation, air temperature, incoming upstream temperature, landownership, and proximity to upstream treatments.

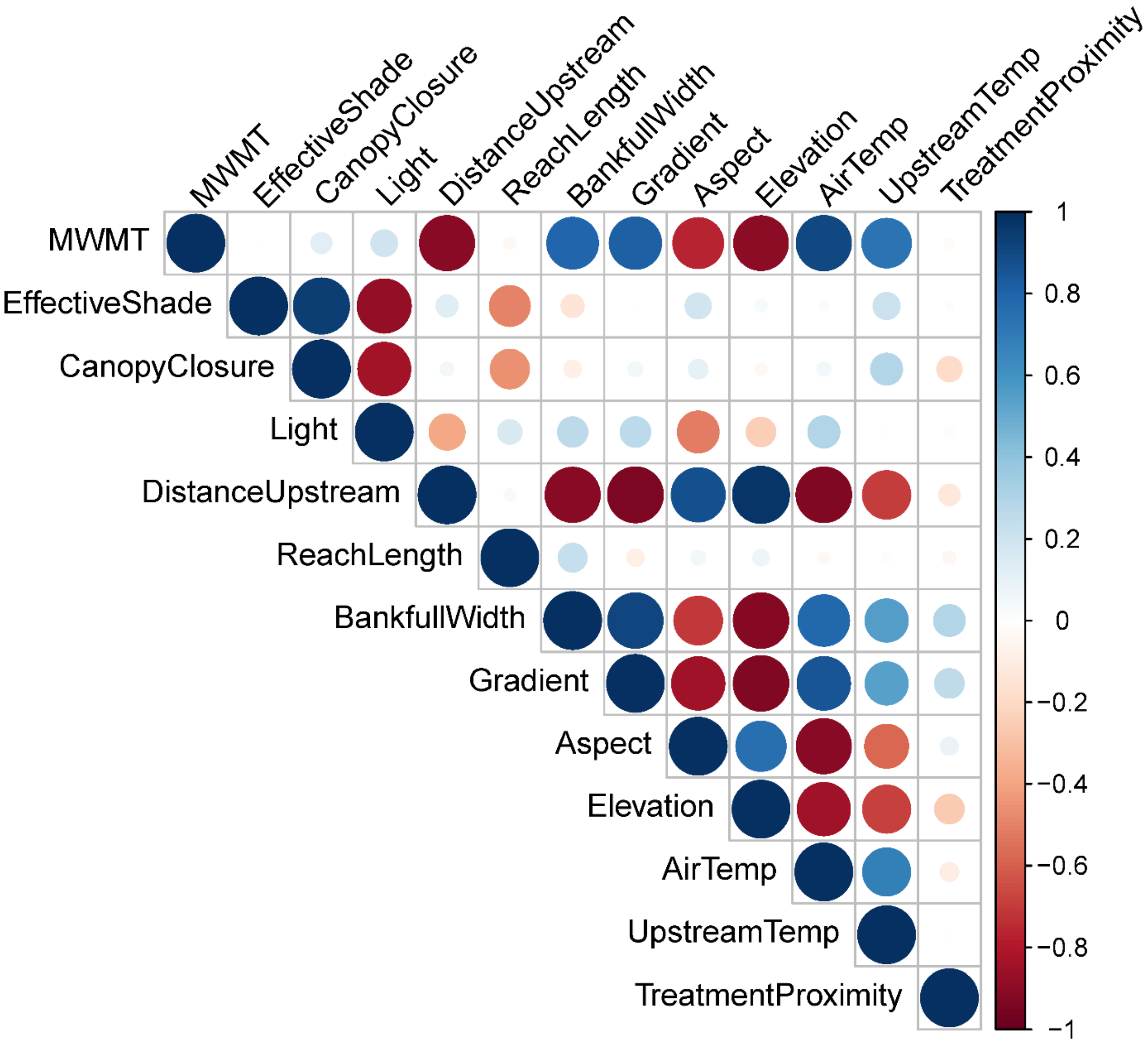

Figure A2.1.b. Correlation matrix for sites in Lost Man watershed. Environmental drivers of temperature responses for upstream reference, thinned, and downstream reaches using pre-treatment and post-treatment data. Correlation matrix between response in summer MWMT, shade and light responses associated with riparian thinning treatments, and study site characteristics for sites in the Lost Man watersheds. Site characteristics included: distance upstream, reach length, bankfull width, aspect, gradient, elevation, air temperature, incoming upstream temperature, landownership, and proximity to upstream treatments.

File A2.1. Reference sites analysis.

Evaluating the effectiveness of riparian buffer prescriptions relative to reference conditions for riparian shade, light, and stream temperature in small streams in coastal Northern California

Introduction

In this analysis we evaluated the effectiveness of experimental riparian buffer protections that follow the prescriptions described by the Aquatic Habitat Conservation Plan (AHCP) negotiated between Green Diamond Resource Company and the National Marine Fisheries Service and United States Fish and Wildlife Service (Green Diamond Resource Company 2006). We compared how these AHCP buffers influenced riparian shade, light, and stream temperature relative to intact forest conditions. AHCP buffer prescriptions included a single-sided 150 foot (~45 m) wide buffer zone that consisted of a 22.5 m wide inner zone of 85% canopy retention and a 22.5 m wide outer zone of 70% canopy retention (Green Diamond Resource Company 2006). Because the buffer treatment was only applied to one side and the other side was intact forest, we hypothesized that the AHCP buffer would result in minimal changes in shade, light, and stream temperature and would not differ relative to intact forest conditions.

Methods

We compared stream reaches lined by AHCP riparian buffer conditions to reaches lined by intact forests. AHCP buffers occurred adjacent to upslope harvest units while intact forest reaches occurred outside of harvest units. Stream reaches were 150-200m in length.

We collected data following a Before-After-Control-Impact study design where pre-treatment data was collected in 2016, harvest occurred in 2017, and post-treatment data collection occurred in 2018. We examined before-after responses in AHCP buffer and intact forest reference reaches located in the West and East Forks of Tectah Creek Watersheds. AHCP buffered reaches and intact forest reference reaches occurred upstream and downstream of experimental thinning reaches inside and outside of harvest units for a total sample size of 16 (Table 1). We pooled upstream and downstream reaches for comparisons of riparian shade and light, but because downstream temperature responses could be influenced by upstream experimental thinning reaches we examined temperature responses in upstream and downstream reaches separately.

We measured riparian shade using hemispherical photography. We considered canopy closure and effective shade to evaluate differences in riparian shade. We measured below canopy light using pyranometers. We measured stream temperature with digital temperature sensors. We evaluated stream temperature as the summer Maximum Weekly Average of the Maximum (MWMT) as an indication of magnitude. See main paper for more details about data collection methods. We compared before-after differences of riparian shade, light, and stream temperature conditions between AHCP and intact forest reaches using mean estimates, non-parametric bootstrapped 95% confidence intervals computed using the boot package in R (Canty et al. 2020), and non-parametric Kolmogorov-Smirnov tests ($\alpha = 0.05$). All graphics and analyses were conducted in R (R Core Team 2020).

Table 1. Distribution of sample sizes of AHCP buffered reaches and intact forest reference reaches in upstream and downstream reaches.

Buffer Type	Upstream	Downstream	All Reaches
AHCP	5	3	8
Intact Forest	3	5	8
Total	8	8	16

Results

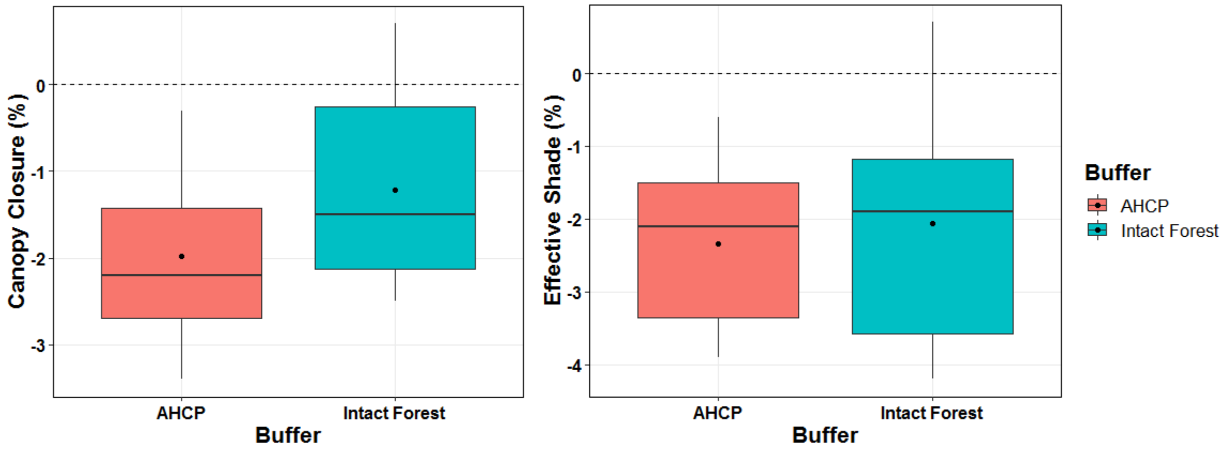

Fig 1. Boxplots of before-after differences in riparian shade in AHCP buffered and intact forest reaches as a) canopy closure (%), and b) effective shade (%). Black dots indicate mean values.

Analyses indicated that riparian shade did not statistically differ between AHCP buffered and intact forest reaches, and that differences overall were small. Canopy closure decreased in AHCP buffered reaches by a mean of 2.0% (95% CI: -2.7, -1.2) and intact forest reaches by a mean of 1.2% (95% CI: -2.0, -0.4) (Fig 1a), but did not differ between buffer types (K-S test: *p* = 0.627). Effective shade decreased in AHCP buffered reaches by a mean of 2.3% (95% CI: -3.1, -1.6) and intact forest reaches by a mean of 2.1% (95% CI: -3.2, -0.9) (Fig 1b), but also did not differ between buffer types (K-S test: *p* = 0.964).

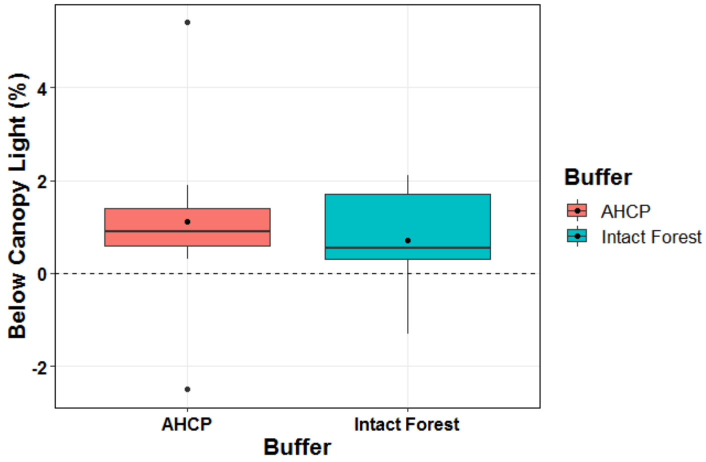

Fig 2. Boxplots of before-after differences in below canopy light (%) in AHCP buffered and intact forest reaches. Black dots within boxplots indicate mean values and black dots outside boxplots indicate outliers.

Below-canopy light increased in AHCP buffered reaches by a mean of 1.1% (95% CI: -0.4, 2.8) and intact forest reaches by a mean of 0.7% (95% CI: -0.2, 1.6) (Fig 2), but did not differ between buffer types (K-S test: *p* = 0.737).

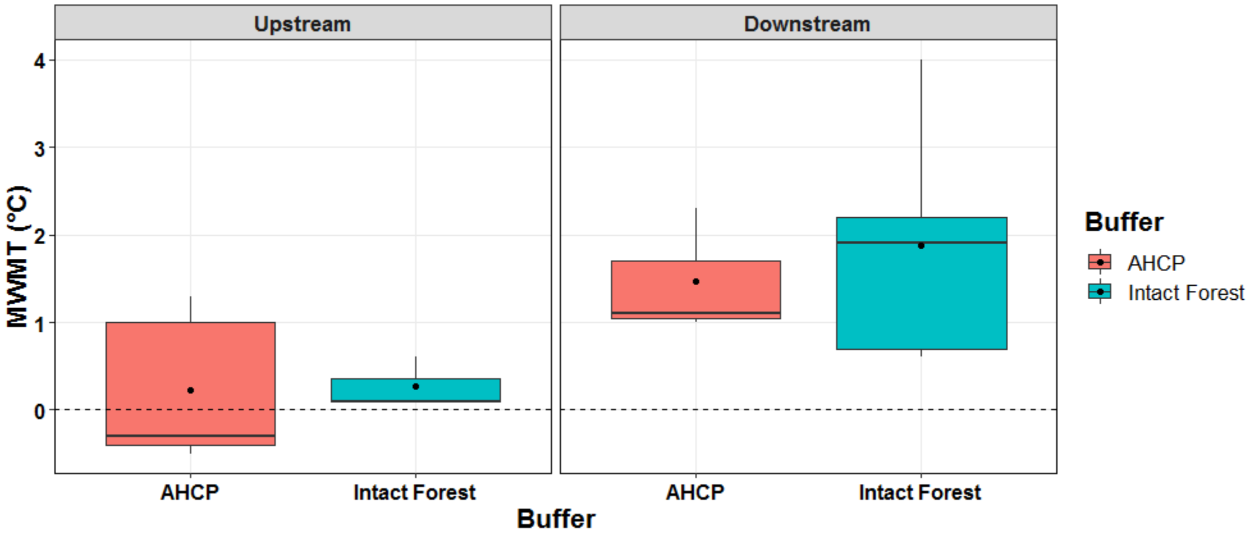

Fig 3. Boxplots of before-after differences in stream temperature as summer MWMT (°C) in AHCP buffered and intact forest reaches in a) upstream sites and b) downstream reaches. Black dots indicate mean values.

Stream temperature responses as summer MWMT increased in both upstream and downstream reaches but did not differ between buffer types (Fig 3). In upstream reaches, stream temperature in AHCP buffered reaches increased by a mean of 0.2°C (95% CI: -0.4, 0.9) and by a mean of 0.3°C (95% CI: 0.1, 0.6) in intact forest reaches (Fig 3a), but did not differ between buffer types (K-S test: *p* = 0.464). In downstream reaches, stream temperature increased in AHCP buffered reaches by a mean of 1.5°C (95% CI: 1.0, 2.3) and by a mean of 1.9°C (95% CI: 0.9, 3.0) in intact forest reaches (Fig 3b) and did not differ between buffer types (K-S test: *p* = 0.857).

Discussion

Recent research has shown that riparian buffers can be effective management strategies for protecting riparian forests and minimizing impacts to stream temperature (Moore et al. 2005). However, stream temperature responses to riparian buffers continue to vary depending on their implementation (Moore et al. 2005, Gomi et al. 2006, Groom et al. 2011, Janisch et al. 2012, Kibler et al. 2013, Bladon et al. 2016). In this analysis we evaluated the effectiveness of Green Diamond Resource Company's one-sided 45 m AHCP buffer prescriptions relative to intact forest conditions. We observed small reductions in shade, increases in light, and increases in stream temperature, but none of these responses differed between AHCP buffers and intact forest reaches, supporting our hypotheses and predictions.

Reductions in riparian shade were minor and did not differ between buffer treatments (intact forest vs. AHCP buffer). Measured differences in riparian shade were slightly greater as canopy closure than effective shade in AHCP buffered reaches relative to intact forest reaches. However, both of these differences were minor (all less than 1%) and did not differ significantly between buffer types. Reductions in shade measured in this study were substantially less than what has been documented with historical timber harvest practices (Moore et al. 2005) and were more consistent with what has been documented with recent contemporary buffer studies (Groom et al. 2011, Bladon et al. 2016), especially with wider buffer prescriptions (e.g. >15m). This is likely due to the width of the buffer prescriptions (~45m) and the fact that the buffer treatment was only applied to one side of the stream channel (the other side was lined by intact forest). The small reductions in shade we observed in both buffer types could be due to edge effects from adjacent thinning treatments. Alternatively, it could be due natural interannual variation such as storm events that caused individual trees to fall within the riparian zone of these forests.

Increases in light reflected the direction and magnitude of shade responses. Although percent light levels increased slightly more in AHCP buffered reaches than intact forest reaches, these differences were very small (<0.5%) and did not differ significantly between reach types. Few stream temperature studies directly measure solar radiation, but Kiffney et al. (2003) similarly did not observe differences between 30m buffers and control treatments. Similar to the riparian shade responses, increases in light observed in both reach types could be explained by edge effects of adjacent thinning treatments or natural interannual variation.

We observed distinct stream temperature responses in the upstream and downstream reaches. Maximum temperatures increased slightly in both reach types in upstream reaches, but the magnitude of these increases were small (<1.0°C), and were not affected by buffer treatments. Documented temperature responses were comparable to what has been observed with buffers of similar width (Groom et al. 2011, Bladon et al. 2016). The fact that we documented increases in temperature in both buffer types could suggest that 2018 was a warmer year than 2016. In addition because multiple thinning treatments occurred within these watersheds, increases in temperature in reference reaches could be due to the downstream transport of heat from upstream thinning treatments (Moore et al. 2005). Although we observed a wider range of values in AHCP reaches than in intact forest reaches, this is more likely due to the fact that more sites were influenced by downstream transport of heat rather than differences in buffer treatment.

Temperature responses in downstream reaches were larger than in upstream reaches (95% CI's ranged 1-3°C) but did not differ between buffer treatments. As a result, increases in temperature in downstream reaches were unlikely due to differences in riparian buffer prescriptions, but more likely to downstream transport of temperature increases observed in intensive experimental thinning reaches (Moore et al. 2005). Downstream temperature responses were slightly higher in intact forest reaches, but this is more likely due to the magnitude of upstream responses adjacent to intact forest reaches than due to differences in riparian forest conditions.

In conclusion, we observed that the AHCP buffer prescriptions resulted in minimal changes in riparian shade, light, and stream temperature and did not differ relative to intact forest conditions. These results suggest that the AHCP buffer prescriptions may offer similar protections to intact second-growth forests for the response variables we considered. These findings support previous research that has documented that riparian buffers can act as effective management strategies for riparian forests and instream conditions.

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Chapter 3

Table A3.1. Potential interacting factoring influencing local radiative and longitudinal advective energetic processes and implications for local and downstream thermal responses to riparian thinning.

Energy type	**Interacting factors**	**References**
Radiative	Shade/solar radiation - Vegetation density and cover - Topography - Aspect - Geographic location - Time of year - Channel morphology (water depth, volume, channel width, gradient) - Streamflow - Lithology	Johnson 2004 Caissie 2006 Moore et al. 2005 Dugdale et al. 2017
Advective	Streamflow Solar radiation Groundwater upwelling Hyporheic flow Tributary junctions Channel morphology (water depth, volume, channel width, gradient)	Story et al. 2003 Moore et al. 2005 Garner et al. 2014 Dugdale et al. 2017

Chapter 4

Table A4.1. Length-weight regressions used to estimate biomass of invertebrate and vertebrate prey items in diet. Length-Dry Mass Coefficients (y = ax^b)

Taxa	Source of Production	Lifestage	a	b	Source
Acanthasomatidae	Terrestrial	Adult	0.0341	2.688	Hodar 1996
Acari	Terrestrial	Any	0.053	2.494	Hodar 1996
Ameletidae	Aquatic	Larvae	0.0077	2.588	Benke et al. 1999
Amphipoda	Aquatic	Any	0.0058	3.015	Benke et al. 1999
Amphizoidae	Aquatic	Larvae	0.0077	2.91	Benke et al. 1999
Amphizoidae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Apataniidae	Aquatic	Larvae	0.0056	2.839	Benke et al. 1999
Aphididae	Terrestrial	Adult	0.005	3.33	Sabo et al. 2002
Arachnida	Terrestrial	Any	0.05	2.74	Sabo et al. 2002
Ariolimax	Terrestrial	Any	0.008738646	3.21	Baumgartner and Rothhaupt 2003
Ascaphus truei tadpole	Aquatic	Larvae	0.080509	1.9219903	Roon et al. (This study)
Asilidae	Terrestrial	Adult	0.006	3.05	Sabo et al. 2002
Athericidae	Aquatic	Larvae	0.004	2.586	Benke et al. 1999
Baetidae	Aquatic	Larvae	0.0053	2.875	Benke et al. 1999
Blephariceridae	Aquatic	Larvae	0.0067	3.292	Benke et al. 1999
Brachycentridae	Aquatic	Larvae	0.0083	2.818	Benke et al. 1999
Braconidae	Terrestrial	Adult	0.56	1.56	Sabo et al. 2002
Calamoceratidae	Aquatic	Larvae	0.004	2.933	Benke et al. 1999
Carabidae	Terrestrial	Adult	0.072	2.401	Sabo et al. 2002
Cecidomyiidae	Terrestrial	Larvae	0.0025	2.692	Benke et al. 1999
Cecidomyiidae	Terrestrial	Adult	0.1	1.57	Sabo et al. 2002
Cerambycidae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Ceratopogonidae	Aquatic	Larvae	0.025	2.469	Benke et al. 1999
Ceratopogonidae	Aquatic	Adult	0.1	1.57	Sabo et al. 2002
Chilopoda	Terrestrial	Any	0.0036	2.626	Hodar 1996
Chironomidae	Aquatic	Larvae	0.005097526	2.32	Smock 1980
Chironomidae	Aquatic	Pupae	0.005097526	2.32	Smock 1980
Chironomidae	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Chloroperlidae	Aquatic	Larvae	0.0065	2.724	Benke et al. 1999
Chrysomelidae	Terrestrial	Larvae	0.0077	2.91	Benke et al. 1999
Chrysomelidae	Terrestrial	Adult	0.0258	3.083	Hodar 1996
Cicadellidae	Terrestrial	Adult	0.079	2.229	Sabo et al. 2002
Cimbicidae	Terrestrial	Larvae	0.011265616	2.816	Sample et al. 1993
Cleridae	Terrestrial	Larvae	0.0338	2.162	Hodar 1996

Cleridae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Coccinellidae	Terrestrial	Larvae	0.0338	2.162	Hodar 1996
Coleoptera	Aquatic	Larvae	0.0077	2.91	Benke et al. 1999
Coleoptera	Aquatic	Adult	0.152895591	2.18	Smock 1980
Coleoptera	Terrestrial	Larvae	0.0338	2.162	Hodar 1996
Coleoptera	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Collembola	Terrestrial	Any	0.0056	2.809	Gruner 2003
Copepoda	Aquatic	Any	0.00817	2.55	Uye 1982
Corixidae	Aquatic	Adult	0.0031	2.904	Benke et al. 1999
Corydalidae	Aquatic	Larvae	0.0037	2.873	Benke et al. 1999
Crambidae	Terrestrial	Larvae	0.011	2.571	Hodar 1996
Curculionidae	Terrestrial	Larvae	0.0338	2.162	Hodar 1996
Curculionidae	Terrestrial	Adult	0.0607	2.315	Gruner 2003
Decapoda	Aquatic	Any	0.0147	3.626	Benke et al. 1999
Dicamptodon tenebrosus larvae	Aquatic	Larvae	0.0059123	2.6067147	Roon et al. (This study)
Diplopoda	Terrestrial	Any	0.00012	3.909	Hodar 1996
Diptera	Aquatic	Larvae	0.0025	2.692	Benke et al. 1999
Diptera	Aquatic	Pupae	0.0025	2.692	Benke et al. 1999
Diptera	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Diptera	Terrestrial	Larvae	0.0025	2.692	Benke et al. 1999
Diptera	Terrestrial	Adult	0.006	3.05	Sabo et al. 2002
Dixidae	Aquatic	Larvae	0.0025	2.692	Benke et al. 1999
Dixidae	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Dolichopodidae	Terrestrial	Adult	0.006	3.05	Sabo et al. 2002
Dytiscidae	Aquatic	Larvae	0.0077	2.91	Benke et al. 1999
Dytiscidae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Elateridae	Terrestrial	Larvae	0.0338	2.162	Hodar 1996
Elateridae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Elmidae	Aquatic	Larvae	0.0074	2.879	Benke et al. 1999
Elmidae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Empididae	Aquatic	Larvae	0.0054	2.546	Benke et al. 1999
Empididae	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Ephemerellidae	Aquatic	Larvae	0.0103	2.676	Benke et al. 1999
Ephemeroptera	Aquatic	Larvae	0.0071	2.832	Benke et al. 1999
Ephemeroptera	Aquatic	Adult	0.014	2.49	Sabo et al. 2002
Ephydridae	Aquatic	Larvae	0.0025	2.692	Benke et al. 1999
Formicidae	Terrestrial	Adult	0.56	1.56	Sabo et al. 2002
Gastropoda	Terrestrial	Any	0.008738646	3.21	Baumgartner and Rothhaupt 2003
Geometridae	Terrestrial	Larvae	0.011	2.571	Hodar 1996
Gerridae	Aquatic	Adult	0.015	2.596	Benke et al. 1999
Glossosomatidae	Aquatic	Larvae	0.0082	2.958	Benke et al. 1999

Goeridae	Aquatic	Larvae	0.0056	2.839	Benke et al. 1999
Haliplidae	Aquatic	Larvae	0.0074	2.879	Benke et al. 1999
Haliplidae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Hemiptera	Terrestrial	Adult	0.0341	2.688	Hodar 1996
Heptageniidae	Aquatic	Larvae	0.0108	2.754	Benke et al. 1999
Hydrachnidia	Aquatic	Any	0.132655465	1.66	Baumgartner and Rothhaupt 2003
Hydrophilidae	Aquatic	Larvae	0.0074	2.879	Benke et al. 1999
Hydrophilidae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Hydropsychidae	Aquatic	Larvae	0.0046	2.926	Benke et al. 1999
Hydroptilidae	Aquatic	Larvae	0.0056	2.839	Benke et al. 1999
Hymenoptera	Terrestrial	Adult	0.56	1.56	Sabo et al. 2002
Hymenoptera	Terrestrial	Larvae	0.011265616	2.816	Sample et al. 1993
Ichneumonidae	Terrestrial	Adult	0.56	1.56	Sabo et al. 2002
Insecta	Unknown	Adult	0.0064	2.788	Benke et al. 1999
Insecta	Unknown	Larvae	0.0064	2.788	Benke et al. 1999
Isopoda	Aquatic	Any	0.0101	2.844	Hodar 1996
Juga	Aquatic	Any	0.0182	2.6534	Preston et al. 2018
Lathridiidae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Lepidoptera	Terrestrial	Adult	0.012	2.69	Sabo et al. 2002
Lepidoptera	Terrestrial	Larvae	0.011	2.571	Hodar 1996
Lepidostomatidae	Aquatic	Larvae	0.0079	2.649	Benke et al. 1999
Leptoceridae	Aquatic	Larvae	0.0034	3.212	Benke et al. 1999
Leptophlebiidae	Aquatic	Larvae	0.0047	2.686	Benke et al. 1999
Leuctridae	Aquatic	Larvae	0.0028	2.719	Benke et al. 1999
Limnephilidae	Aquatic	Larvae	0.004	2.933	Benke et al. 1999
Megaloptera	Aquatic	Larvae	0.0037	2.838	Benke et al. 1999
Membracidae	Terrestrial	Adult	0.005	3.33	Sabo et al. 2002
Mycetophilidae	Terrestrial	Adult	0.1	1.57	Sabo et al. 2002
Nematoda	Aquatic	Any	0.0758	0.74	Miserendino 2001
Nematomorpha	Aquatic	Any	0.008	1.888	Miyasaka et al. 2008
Nemouridae	Aquatic	Larvae	0.0056	2.762	Benke et al. 1999
Neuroptera	Terrestrial	Any	0.007	2.739	Gruner 2003
Nitidulidae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Noctuidae	Terrestrial	Larvae	0.011	2.571	Hodar 1996
Noteridae	Aquatic	Larvae	0.0077	2.91	Benke et al. 1999
Noteridae	Aquatic	Adult	0.152895591	2.18	Smock 1980
Odonata	Aquatic	Any	0.0078	2.792	Benke et al. 1999
Oligochaeta	Aquatic	Any	0.008	1.888	Miyasaka et al. 2008
Oncorhynchus clarkii fry	Aquatic	Larvae	0.0002283	3.5857494	Roon et al. (This study)
Orthoptera	Terrestrial	Any	0.03	2.55	Sabo et al. 2002
Ostracoda	Aquatic	Any	0.00817	2.55	Uye 1982

Peltoperlidae	Aquatic	Larvae	0.017	2.737	Benke et al. 1999
Perlidae	Aquatic	Larvae	0.0099	2.879	Benke et al. 1999
Perlodidae	Aquatic	Larvae	0.0196	2.742	Benke et al. 1999
Philopotamidae	Aquatic	Larvae	0.005	2.511	Benke et al. 1999
Phoridae	Terrestrial	Adult	0.006	3.05	Sabo et al. 2002
Plecoptera	Aquatic	Adult	0.26	1.69	Sabo et al. 2002
Plecoptera	Aquatic	Larvae	0.0094	2.754	Benke et al. 1999
Polycentropodidae	Aquatic	Larvae	0.0047	2.705	Benke et al. 1999
Psephenidae	Aquatic	Larvae	0.0123	2.906	Benke et al. 1999
Pseudoscorpiones	Terrestrial	Any	0.0078	3.424	Hodar 1996
Psocoptera	Terrestrial	Any	0.0136	3.115	Gruner 2003
Psychodidae	Aquatic	Larvae	0.0025	2.692	Benke et al. 1999
Psyllidae	Terrestrial	Adult	0.0123	2.995	Gruner 2003
Pteronarcyidae	Aquatic	Larvae	0.0324	2.573	Benke et al. 1999
Ptychopteridae	Aquatic	Larvae	0.0029	2.681	Benke et al. 1999
Pyralidae	Aquatic	Larvae	0.011	2.571	Hodar 1996
Rhyacophilidae	Aquatic	Larvae	0.0099	2.48	Benke et al. 1999
Rodentia	Terrestrial	Adult	0.7464	1.0231	Zhu et al. 2012
Salpingidae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Sarcophagidae	Terrestrial	Adult	0.04	2.64	Sabo et al. 2002
Scarabaeidae	Terrestrial	Larvae	0.0112	2.776	Hodar 1996
Scarabaeidae	Terrestrial	Adult	0.0746	2.582	Hodar 1996
Scotylidae	Terrestrial	Adult	0.0313	2.531	Gruner 2003
Sialidae	Aquatic	Larvae	0.0037	2.753	Benke et al. 1999
Simuliidae	Aquatic	Larvae	0.002	3.011	Benke et al. 1999
Simuliidae	Aquatic	Pupae	0.002	3.011	Benke et al. 1999
Simuliidae	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Staphylinidae	Terrestrial	Larvae	0.0023	3.332	Hodar 1996
Staphylinidae	Terrestrial	Adult	0.001	4.026	Sabo et al. 2002
Syrphidae	Terrestrial	Larvae	0.0025	2.692	Benke et al. 1999
Tabanidae	Aquatic	Larvae	0.005	2.591	Benke et al. 1999
Tenebrionidae	Terrestrial	Adult	0.0513	2.669	Hodar 1996
Tenthredinidae	Terrestrial	Larvae	0.011265616	2.816	Sample et al. 1993
Thamnophis	Terrestrial	Larvae	0.0012	2.85767	Aleksiuk and Stewart 1971
Thysanoptera	Terrestrial	Any	0.0071	2.537	Hodar 1996
Tipulidae	Aquatic	Larvae	0.0029	2.681	Benke et al. 1999
Tipulidae	Aquatic	Pupae	0.0029	2.681	Benke et al. 1999
Tipulidae	Aquatic	Adult	0.006	3.05	Sabo et al. 2002
Trematoda	Aquatic	Any	0.0082	2.168	Benke et al. 1999
Trichoptera	Aquatic	Adult	0.01	2.9	Sabo et al. 2002
Trichoptera	Aquatic	Pupae	0.0056	2.839	Benke et al. 1999

Trichoptera	Aquatic	Larvae	0.0056	2.839	Benke et al. 1999
Uenoidae	Aquatic	Larvae	0.0056	2.839	Benke et al. 1999
Veliidae	Aquatic	Adult	0.0126	2.719	Benke et al. 1999
Vespidae	Terrestrial	Adult	0.56	1.56	Sabo et al. 2002

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Table A.4.2. Length-weight regression coefficients and percent dry mass estimates for estimating biomass of trout fry and larval amphibians. Length-Dry Mass Coefficients formula: (y = ax^b).

Species	**Sample Size**	**Mean Total Length (mm)**	**SD**	**Mean Wet Weight (g)**	**SD**	**a**	**b**	**R2**	**Percent Dry Mass**
Cutthroat Trout Fry (*Oncorhynchus clarkii*)	26	45.8	10.8	1.1	0.9	0.0002283	3.585749	0.96	0.25
Giant Salamander Larvae (*Dicamptodon tenbrosus*)	24	51.4	6.7	1	0.4	0.0059123	2.606715	0.77	0.18
Tailed Frog Tadpole (*Ascaphus truei*)	14	29.3	3.9	0.4	0.1	0.0805809	1.92199	0.69	0.2

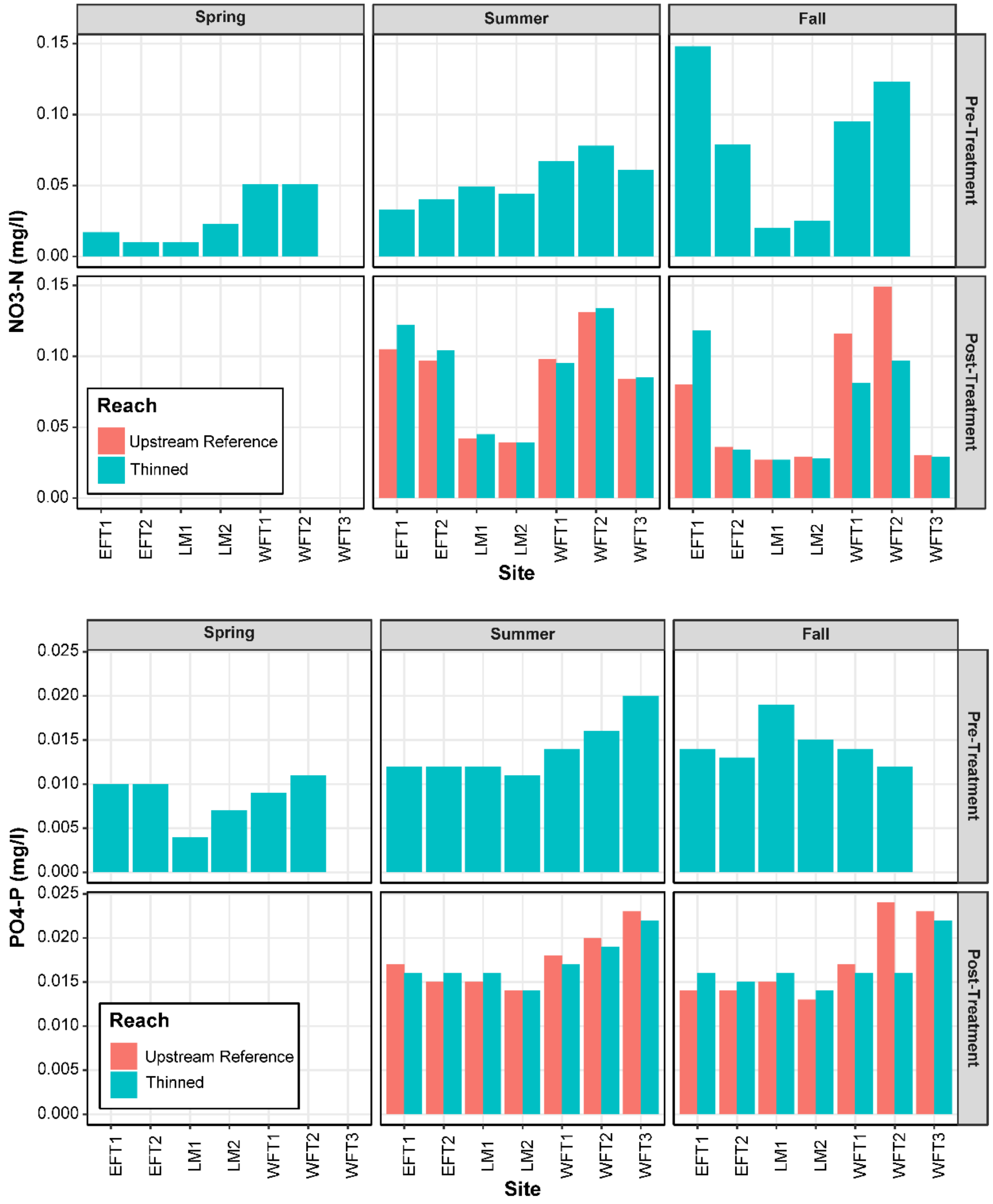

Figure A4.1. Seasonal nitrate and phosphate conditions in upstream reference and thinned reaches during pre and post-treatment years.

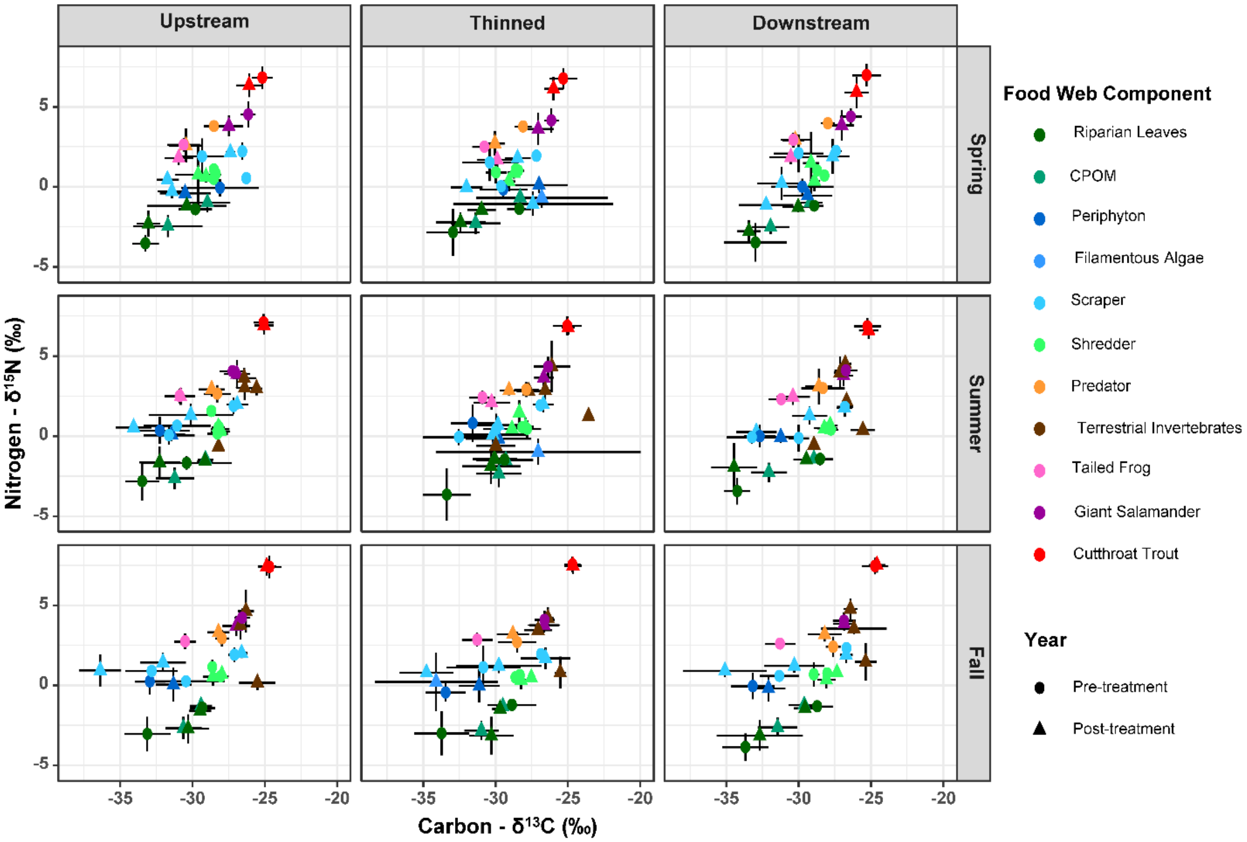

Figure A4.2. Bi-plot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of stream food webs in upstream reference, thinned, and downstream reaches during spring, summer, and fall. Points represent mean values and error bars indicate spatial variation across study sites (*n* = 5). Shape of points indicate pre-treatment and post-treatment conditions.