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Effects of Riparian Forest Thinning on Resident Salmonid Fishes in Coastal Northern California Catchments

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Received: 1 October 2024 | **Revised:** 7 April 2025 | **Accepted:** 12 April 2025

Funding: This research was supported by funding from the Green Diamond Resource Company, Save the Redwoods League, USDA Forest Service, U.S. Geological Survey, and OSU Department of Fisheries, Wildlife and Conservation Sciences.

Keywords: bioenergetics | coastal cutthroat trout | riparian forest restoration | stream-riparian linkages | trophic ecology

ABSTRACT

1. Resource managers are interested in whether thinning second-growth forests may be a viable restoration strategy for stream and riparian habitats, but may be concerned about the potential impacts that increases in stream temperature associated with riparian thinning treatments may have on cold-water salmonid fishes.
2. We evaluated the effects of riparian forest thinning on resident populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in coastal northern California catchments using a manipulative field experiment with a replicated before-after-control-impact design (pre-treatment data collected in 2016, thinning treatments occurred in 2017, and post-treatment data collected in 2018). Experimental thinning treatments reduced riparian shade by 20%–30% along five 150–200 m stream reaches. To provide a process-based evaluation of the implications of riparian thinning for coastal cutthroat trout, we combined seasonal observations of trout density, biomass, and growth with bioenergetics modelling.
3. Cutthroat trout density increased by 8%–31% and biomass increased by 27%–111% in thinned reaches 1 year post-treatment, but responses varied widely across sites and seasons so did not always differ statistically. Growth rates of cutthroat trout varied more among seasons than among reach types (upstream reference, thinned, and downstream), peaking in spring and overwinter relative to summer.
4. Bioenergetics modelling indicated that cutthroat trout responded to thinning-induced increases in stream temperature and shifts in prey energy density via higher consumption rates (i.e., fish fed more frequently) in thinned reaches. Additionally, reach-scale consumption estimates indicated that the energy intake of cutthroat trout increased at the population level in thinned reaches. However, thinned reaches exhibited relatively small changes in consumption, suggesting that riparian thinning was unlikely to enhance growth opportunities for cutthroat trout, supporting our empirical growth observations.
5. Collectively, our field experiment suggests that salmonid fishes may be resilient to thinning second-growth riparian forests when treatments do not substantially increase water temperatures. Moreover, our results highlight that pairing empirical data with bioenergetics modelling can provide valuable insights into the mechanisms driving fish responses to riparian forest restoration.

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1 | Introduction

After decades of timber harvest that clearcut riparian forests, current forest practices now largely protect riparian forests along fish-bearing streams in many regions including the Pacific Northwest, USA (Broadmeadow and Nisbet 2004; Boisjolie et al. 2019). These riparian protections seek to restore key functions disrupted by stream-adjacent timber harvest (Gregory et al. 1987; Broadmeadow and Nisbet 2004), including the provision of riparian shade to maintain cool stream temperatures for sensitive cold-water adapted fish species, particularly salmonid fishes (Moore et al. 2005). Recent evaluations have found that riparian buffers can effectively reduce water temperatures relative to historical timber harvest practices (Moore et al. 2005; Groom et al. 2011). However, forests within riparian buffer zones tend to differ substantially in composition and structure from the old-growth forests that preceded them and are often composed of dense, even-aged stands of second-growth forest that may limit instream aquatic productivity (Keyes and Teraoka 2014; Warren et al. 2016). As a result, riparian forest thinning has been proposed as a potential restoration strategy (Teraoka and Keyes 2011; Pollock and Beechie 2014; Benda et al. 2016), but there are concerns that increased solar radiation associated with thinning could have adverse effects on salmonid fishes by increasing water temperatures. In this study, we coupled a field experiment with bioenergetics modelling to evaluate how resident populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) may respond to riparian thinning.

Stream temperature is a primary driver of ecological processes in aquatic systems (Magnuson et al. 1979; Johnson et al. 2024), yet how cold-water fish respond to changes in stream thermal regimes depends on a variety of factors (Railsback 2022; Johnson et al. 2024). First, the effects of temperature on cold-water adapted fishes, like stream salmonids, are complex and vary among species, life stages, and populations (Huff et al. 2005; McCullough et al. 2009; Anlauf-Dunn et al. 2022; Jonsson 2023). Second, stream thermal regimes naturally fluctuate seasonally and spatially in catchments (Steel et al. 2017), so increases in stream temperature may not be problematic when temperatures are relatively cool, or if temperature changes occur at cooler times of year (Bear et al. 2007; Armstrong et al. 2021). Third, fish responses to changes in stream temperatures are not just a function of thermal conditions but also depend on the availability of prey resources to support their metabolism (Brett et al. 1969; Beauchamp 2009; Railsback 2022); fish can grow at warm temperatures if adequate food resources are available (Hughes and Grand 2000; Armstrong et al. 2021). As a result, it can be difficult to predict how fish will respond to changes in riparian forests based on water temperature conditions alone.

For example, despite widespread evidence that riparian canopy opening can increase stream temperatures (Moore et al. 2005; Groom et al. 2011), fish responses to forest harvest have varied extensively (Murphy and Hall 1981; Mellina and Hinch 2009). In fact, in the Pacific Northwest, historical timber harvest practices frequently led to increased fish density, biomass, and production (Murphy and Hall 1981; Hawkins et al. 1983; Bisson and Sedell 1984; Bilby and Bisson 1992; Mellina and Hinch 2009). Recent studies evaluating contemporary timber harvest have also documented increases in fish density and biomass, though fish responses tend to be more variable and smaller in magnitude (Wilzbach et al. 2005; Wootton 2012; Bateman et al. 2016, 2018; Jensen 2017). Moreover, recent studies by Kaylor and Warren (2017, 2018) have indicated that the long-term regrowth of second-growth riparian forests with dense riparian canopies can limit aquatic primary production that may even lead to reductions in trout biomass. The mechanisms driving fish responses to historical and contemporary forestry practices, however, remain poorly understood. Bisson and Sedell (1984) suggested that increased fish production following forest harvest could be either due to: (1) increased primary productivity owing to additional solar radiation leading to increases in prey resources for top predators or (2) increased stream temperatures that are closer to optimal growth of cold-water fish so long as temperatures did not exceed conditions that could lead to acute thermal stress. However, it remains unclear which of these explanations or some combination of the two may be responsible for driving fish responses to forest harvest.

Bioenergetics models, which integrate information on water temperature, prey resources, and fish physiology, may be well suited to address questions of how fish respond to changes in riparian forest conditions (Warren and Davis 1967; Railsback and Rose 1999; Beauchamp et al. 2007; Beauchamp 2009). As a result, bioenergetics modelling may provide unique insights not possible from empirical data alone. However, efforts to apply bioenergetics modelling to evaluate how fish respond to changes in riparian forest conditions have been limited. For example, bioenergetics simulations by Leach et al. (2012) suggested that increases in stream temperature associated with timber harvest in coastal British Columbia could negatively affect fish growth. Similarly, a bioenergetics study by Beakes et al. (2014) found that reductions in canopy cover from wildfire increased energetic costs for stream fish, leading to reductions in biomass in California catchments. One key takeaway from previous studies is that prey availability and consumption act as key limiting factors for fish, especially in summer months (Boss and Richardson 2002; Beauchamp et al. 2007; Ouellet et al. 2025), and can mediate fish responses to stream temperature alterations (Dineen et al. 2007; McCarthy et al. 2009; Leach et al. 2012; Jensen 2017). These studies highlight the utility of bioenergetics models to examine the interaction of thermal and trophic resources supporting stream fishes, thus providing relevant insights for evaluating the implications of riparian forest management.

In the Pacific Northwest, concerns associated with the legacy effects of past forest harvest activity are causing resource managers to explore whether thinning second-growth forests may be a viable restoration strategy for stream, riparian, and upland forest habitats (Teraoka and Keyes 2011; Pollock and Beechie 2014; Benda et al. 2016; Reeves et al. 2016; Yeung et al. 2017; Case et al. 2023). However, concerns have been raised about the potential ecological trade-offs riparian thinning may have on stream fishes and aquatic ecosystems (Pollock and Beechie 2014; Roon 2021). This has caused some managers to suggest that less-intensive opening of riparian canopies via thinning may be able to strike a balance—whereby increased solar inputs boost aquatic productivity without substantially increasing stream temperatures above levels that would be physiologically stressful for fish

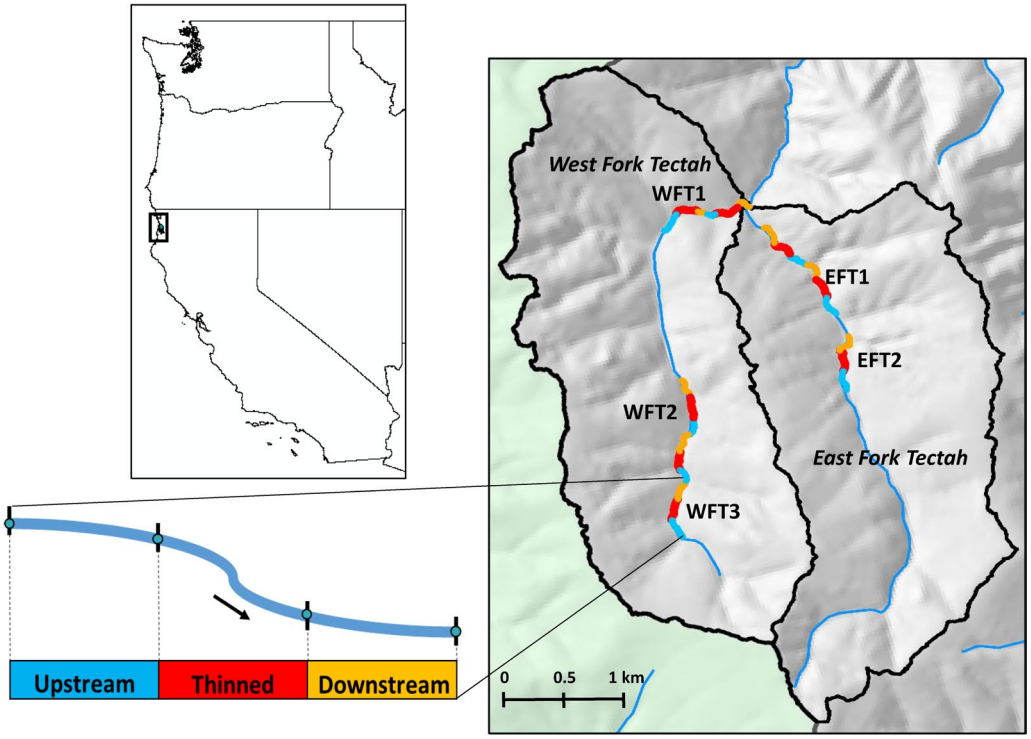

FIGURE 1 | Location of study catchments and experimental design in the west and east forks of Tectah Creek, northern California, USA. We collected data seasonally for this study following a replicated before-after-control-impact (BACI) study design where we measured stream temperature and collected data from resident coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) populations in upstream reference, thinned, and downstream reaches 1 year before and after experimental thinning treatments. The position of abbreviated names (WFT1, WFT2, WFT3, EFT1, and EFT2) on the map indicates sampling sites where we collected data ($n = 5$ sites, $n = 15$ total reaches). Map made by David 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://www/gis.data.ca.gov.

(Wilzbach et al. 2005; Wootton 2012; Warren et al. 2016). However, little is known about the effects of less-intensive thinning of riparian zones. Results from a recent field experiment in coastal northern California indicate that reductions in shade associated with riparian thinning treatments increased summer maximum stream temperatures by 2°C–4°C (Roon et al. 2021a), which propagated warm water downstream and increased thermal heterogeneity at a catchment scale (Roon et al. 2021b). At the same time, increases in light associated with riparian thinning treatments had little influence on trophic pathways supporting prey resources for top predators—coastal giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (Roon et al. 2022). However, thinning effects are likely context dependent, so questions remain about how potential shifts in thermal and trophic resources associated with riparian thinning may interact to ultimately affect stream fishes that inhabit study catchments.

Here, we combined empirical data collected from a manipulative field experiment with bioenergetics modelling to provide a process-based evaluation of the implications of riparian forest thinning for resident populations of coastal cutthroat trout. To do this, we studied experimentally thinned riparian canopies in two catchments located in coastal northern California, and collected fish data seasonally following a before-after-control-impact (BACI) design (Underwood 1994). We then used empirical data on stream temperature, diet, and measured seasonal growth rates of coastal cutthroat trout as inputs to run bioenergetics simulations (Deslauriers et al. 2017). The objectives of this study were to: (1) evaluate the effects of riparian thinning treatments on the density, biomass, and growth of adult and young-of-year (YOY) life stages of coastal cutthroat trout, and (2) explore the mechanisms of observed coastal cutthroat trout responses to thinning treatments with bioenergetics modelling. We applied bioenergetics modelling in two ways. First, we combined empirical data on stream temperature (Roon et al. 2021a), fish diet (Roon et al. 2022), and specific growth rates in the bioenergetics model to estimate seasonal consumption rates (Warren and Davis 1967; Railsback and Rose 1999). Second, we used seasonal consumption rates from the bioenergetics model to determine the range of temperatures at which growth could occur and how that may change with thinning treatments (Warren and Davis 1967; Railsback and Rose 1999; Jensen 2017). We focused this study on resident populations of coastal cutthroat trout, a widespread fish species along coastal catchments of western North America, with a relatively narrow thermal niche (Huff et al. 2005) and low growth typical during summer low flows (Boss and Richardson 2002; Sheldon and Richardson 2021; Sanders et al. 2024).

2 | Methods

2.1 | Study Catchments

This study took place in the west and east forks of Tectah Creek, a tributary of the lower Klamath River on private timberland owned by the Green Diamond Resource Company

TABLE 1 | Characteristics of thinned reaches where we sampled stream temperatures and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in the Tectah Creek study catchments in northern California, USA. Changes in riparian shade, light, and stream temperature in this table are expressed as the mean before-after-control-impact (BACI) differences estimated by ($Thinned_{post}$—$Thinned_{pre}$)—($Reference_{post}$—$Reference_{pre}$) across all study sites ($n = 5$). Maximum weekly maximum temperature; MWMT.

Catchment	Site	Catchment Position—Distance Upstream from Confluence (m)	Reach Length (m)	Bankfull Width (m)	Change in Riparian Shade (Δ%)	Change in Light (Δ%)	Change in Stream Temperature—summer MWMT (Δ°C)	Change in Stream Temperature—summer daily mean (Δ°C)
East Fork Tectah	EFT1	990	210	6.1	−19.2	19.9	1.8	0.5
	EFT2	1850	170	4.6	−30.5	29.3	3.8	1.5
West Fork Tectah	WFT1	535	175	6.0	−24.0	35.1	2.1	0.7
	WFT2	2750	205	4.7	−26.2	28.8	3.5	1.2
	WFT3	3840	220	3.2	−23.6	14.4	2.7	0.9

in coastal northern California (Figure 1). Study catchments were small (7–8 km^2) and densely forested, drained by small streams (bankfull width: 3–6 m). Study catchments 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 rain-driven hydrology in this region, with high flows persisting from autumn through spring 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 overall (summer daily mean temperatures generally < 16°C), with coolest temperatures occurring from autumn through spring and temperatures peaking during summer low flows (Roon et al. 2021a). Riparian forests consist of dense second-growth that heavily shade the stream channel (mean canopy closure: ~95%) with little longitudinal variation along streams. Riparian canopies include coast redwood (*Sequoia sempervirens*), red alder (*Alnus rubra*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), tanoak (*Notholithocarpus densiflorus*), and western red cedar (*Thuja plicata*). Resident populations of coastal cutthroat trout co-occur with coastal giant salamander and coastal tailed frogs (*Ascaphus truei*), as well as lower densities of southern torrent salamander (*Rhyacotriton variegatus*), northern red-legged frog (*Rana aurora*), and foothill yellow-legged frog (*Rana boylii*).

2.2 | Experimental Design

We collected data for this study following a replicated BACI study design (Underwood 1994) where riparian canopies were experimentally thinned. This study took place over the course of 3 years. We collected data 1 year before and 1 year after riparian thinning treatments in upstream reference, thinned, and downstream reaches replicated at 5 sites across the two catchments ($n = 15$ reaches total) (Table 1). We collected pre-treatment data in 2016, experimental thinning treatments took place in 2017, and we collected post-treatment data in 2018. We repeated sampling seasonally in spring, summer, and autumn.

Riparian thinning prescriptions targeted a reduction to 50% canopy closure within the riparian zone on both sides of the stream channel up to the stream edge along 150–200 m treatment reaches, which translated to mean reductions in riparian shade of 20%–30% and increases in solar radiation of 15%–35% over the stream channel relative to pre-treatment conditions (Table 1). Thinning treatments were part of a larger riparian canopy experiment included in a Habitat Conservation Plan involving Green Diamond Resource Company (GDRC) and two federal agencies, the National Marine Fisheries Service and the U.S. Fish and Wildlife Service (Green Diamond Resource Company 2006). Thinning treatments occurred next to upslope harvest units, and trees were removed from within the buffer zone on 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 20 m inner zone of 85% canopy retention and a 25 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. 2021a).

2.3 | Fish Sampling

We collected coastal cutthroat trout using a Smith-Root LR 24 backpack electrofisher (Smith-Root Inc., Vancouver, WA USA). We subsampled each reach in two or three 40-m sections isolated with fine-mesh block nets. Captured fish were briefly held before processing in 5-gal buckets filled with well-oxygenated stream water and an aerator or in temporary mesh enclosures placed in the stream channel. We anaesthetised fish using AQUI-S (AquaTactics Fish Health, Kirkland, WA USA) and allowed them to recover completely before returning them to the site of capture. We measured the length and mass of all fish captured to the nearest 1 mm and 0.1 g. We used single-pass electrofishing to minimise impacts on fish and amphibians, given its strong correlation with multi-pass methods (Kruse et al. 1998; Bateman et al. 2005). Single-pass estimates of density and biomass were divided by the area sampled. We estimated total trout

biomass and densities by multiplying single-pass electrofishing estimates by 2-pass mark-recapture abundance estimates ($n = 10$) which yielded capture probabilities of 0.6 in summer and 0.8 in autumn. Based on these estimates and channel characteristics during higher flow conditions, we assumed a capture probability of 0.4 in spring. Although this may introduce some bias in total density and biomass estimates (Rosenberger and Dunham 2005), any such bias would apply across sampling reaches.

We used different methods to estimate specific growth rates of YOY and adult life stages of coastal cutthroat trout. YOY and adult (age 1+) life stages were distinguished using length-frequency distributions (Figure S5a). To estimate summer cohort specific growth rates of YOY, which tended to be too small to tag, we calculated changes in site-specific mean weights between summer and autumn. Growth estimates using this approach could be biased by unequal patterns of movement (e.g., emigration or immigration), size-biased survival, recruitment, or other processes that we could not track without closely monitoring individuals. Accordingly, we interpreted our findings with these limitations in mind. To estimate seasonal individual growth rates of adult life stages, we measured changes in weight of recaptured individuals marked with 8- or 12-mm Passive Integrated Transponder (PIT) tags. We then estimated specific growth rates using the formula Specific Growth = $((\ln W_t - \ln W_0)/t) * 100$, where W_t is the final weight in grams, W_0 is the initial weight in grams, and t is time in days between captures. Of the 5948 total cutthroat trout we captured throughout the study (2807 adults, 3141 YOY), we tagged 1918 adult fish and recaptured 1058 individuals. Of those 1058 recaptures, we eliminated records of individuals that moved into adjacent reaches ($n = 13$ fish) and fish recaptured during nonconsecutive sampling dates ($n = 335$ fish), leaving a sample size of 710. Of those fish, we analysed individuals recaptured within either pre- or post-treatment years, for a final sample size of 586 individuals. We then separately estimated specific growth rates for: spring (April/May through July), summer (July through September/October), and overwinter (September/October through April/May).

2.4 | Bioenergetics Modelling

We applied bioenergetics modelling to explore how adult coastal cutthroat trout responded to potential changes in stream temperature and prey resources associated with riparian thinning treatments. We focused model simulations on adult life stages of coastal cutthroat trout because we lacked the diet and individual growth data necessary to parameterise bioenergetics models for YOY. We ran model simulations using the *Fish Bioenergetics 4.0* package (Deslauriers et al. 2017) in R (R Core Team 2020), parameterised for adult cutthroat trout using coefficients from Beauchamp et al. (1995). We recognise that the parameter sets used in bioenergetics models come with uncertainty (Bartell et al. 1986; Chipps and Wahl 2008), so we focused the interpretation of our analysis on the relative differences that emerged with thinning treatments.

We measured the inputs needed for the bioenergetics model (Deslauriers et al. 2017) including stream temperature (Roon et al. 2021a) and prey composition and energy density in cutthroat trout diets (Roon et al. 2022). We measured stream temperature using digital temperature sensors (a combination of Onset HOBO Water Temp Pro v2 and TidbiT v2 data loggers, Onset Computer, Bourne, MA, USA) (Roon et al. 2021a). We deployed temperature sensors at the upstream and downstream extents of upstream reference, thinned, and downstream reaches at all sites ($n = 20$ sensors total). Temperature sensors recorded hourly temperatures from October 2015 through October 2018, and temperatures were summarised as daily mean values. We collected diet samples from adult cutthroat trout to quantify prey composition and energy density during the electrofishing surveys described above. To do this, we used 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 $n = 1260$) (Roon et al. 2022). No diet samples were collected from YOY life stages to prevent injury. We identified, enumerated, and measured the length of all prey items and estimated biomass using published length-weight regressions (Roon 2021). Mean prey biomass in diets was converted into diet proportions used in bioenergetics simulations. We then summarised prey energy density in units of joules per gram (J/g) wet weight, following the categories described by McCarthy et al. (2009) and Thompson and Beauchamp (2016) (Table 2). No estimates of energy density were available for cutthroat trout fry or larval amphibians found in diets, so for these prey species, we generated length-dry mass relationships following Utz and Hartman (2006) and used derived values of percent dry mass to estimate energy density in Joules per gram wet weight using the equation in Hartman and Brandt (1995).

We applied bioenergetics modelling in two different ways. First, we estimated consumption rates by combining seasonal empirical data on stream temperature (Roon et al. 2021a), total prey energy density in diets (Roon et al. 2022), and cutthroat trout specific growth rates. Bioenergetics simulations were run for all adult fish with individual growth data ($n = 586$). We estimated consumption as pCmax, which can provide an estimate of feeding rate relative to a theoretical maximum based on body size, prey energy density, and stream temperature (Railsback and Rose 1999; Deslauriers et al. 2017). We also summarised absolute consumption as individual-level (per individual fish) and reach-level consumption rates (all adult fish within a reach). Given that consumption can vary with body size (Warren and Davis 1967; Deslauriers et al. 2017), we accounted for variation in body size distribution at each site by standardising individual consumption rates as J/g fish/day. To estimate the total energy flow supporting adult fish, we estimated consumption at a reach scale. Reach-level consumption rates of adult cutthroat trout standardised by habitat area (J/m^2/day) were then estimated by multiplying individual consumption rates (J/g fish/day) by mean biomass (g/m^2) at each site. Second, we conducted a scope-for-growth analysis which used seasonal pCmax estimates to separately estimate energy intake and energetic costs to determine the range of temperatures at which growth could occur, given seasonal consumption rates (Warren and Davis 1967; Jensen 2017). To assess thinning effects, we repeated bioenergetics modelling simulations for different reach types (upstream reference, thinned, and downstream reaches) across the different seasons (spring, summer, overwinter) and pre- and post-treatment years.

TABLE 2 | Prey categories, prey and predatory energy densities, and proportion of prey that is indigestible used for bioenergetics modelling. J/g; joules per gram.

	Energy density (J/g)	Indigestibility	References
Prey taxa			
Aquatic larvae and nymphs	3072	0.15	Thompson and Beauchamp (2016)
Aquatic adults	4225	0.15	Thompson and Beauchamp (2016)
Terrestrial larvae	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 (2021)
Amphibian larvae	3957	0.05	Roon (2021)
Predator Taxa			
Cutthroat trout	5763		Railsback and Rose (1999), Jensen (2017)

2.5 | Data Analysis

We evaluated the effects of riparian thinning on cutthroat trout using linear mixed-effects models in the *nlme* package in R (Pinheiro et al. 2020). Treatment effects were determined using a BACI model: Response Variable = Reach Type + Year +Reach Type*Year. We assessed statistical differences of thinning treatments if the BACI effect of Reach*Year was statistically significant ($\alpha = 0.05$) and by estimating BACI differences with 95% confidence intervals. BACI models were run separately for each season. We then applied this BACI model to evaluate the effects of thinning on cutthroat trout density, biomass, and specific growth rates. We also used the BACI model to evaluate the effects of thinning on outputs from the bioenergetics model including pCmax, individual-level (J/g fish/day) and reach-level consumption rates (individual consumption rates multiplied by fish biomass per reach). To see how cutthroat trout responses varied with increases in light associated with thinning treatments, we plotted before-after changes in fish responses against before-after changes in light. To estimate before-after differences, we subtracted mean values in upstream reference, thinned, and downstream reaches during post-treatment and pre-treatment years for each site. We used non-parametric Kolmogorov–Smirnov tests to assess differences in scope-for-growth curves between upstream reference, thinned, and downstream reaches during each season and between pre- and post-treatment years ($\alpha = 0.05$).

3 | Results

3.1 | Empirical Responses of Cutthroat Trout to Thinning

Cutthroat trout density showed slight increases in thinned reaches during the post-treatment year for both adult and YOY life stages, but responses varied widely across sites and so results did not differ statistically (Figures 2 and 3). Adult cutthroat trout density tended to increase in thinned reaches during the post-treatment year by a mean of 31% in spring, 8% in summer, and 19% in autumn (+0.03–0.05 fish/m^2) (Figure 2a), but did not differ statistically among reach types (BACI effect: $p > 0.05$) (Figure 2a) or correlate with increases in light during any season (Figure S1a). Similarly, YOY density tended to increase in thinned reaches by a mean of 33% in summer and 66% in autumn (+0.07–0.10 fish/m^2) (Figure 3a), but did not differ among reach types (BACI effect: $p > 0.05$) (Figure 3a) or correlate with increases in light (Figure S1a). Cutthroat trout density did not change in downstream reaches relative to upstream reference reaches during any season for either life stage (Figures 2 and 3).

Cutthroat trout biomass increased more in thinned reaches relative to trout density for both life stages (Figures 2 and 3). Adult cutthroat trout biomass increased in thinned reaches during the post-treatment year during all three seasons by a mean of 111% in spring, 27% in summer, and 54% in autumn (+1.7–2.2 g/m^2), but due to high levels of variation among sites only differed statistically among reach types in autumn (BACI effect: $p < 0.05$) (Figure 2b). Adult cutthroat trout biomass showed a weak positive association with increases in light during all seasons, but this relationship was only considered statistically significant in spring ($R^2 = 0.37$, $p = 0.037$) and marginally significant in autumn ($R^2 = 0.31$, $p = 0.062$) (Figure S1b). Relative to upstream reference reaches, YOY biomass increased in thinned reaches during the post-treatment year by a mean of 74% in summer and 157% in autumn (+0.30–0.33 g/m^2) and increased biomass in thinned reaches was considered marginally statistically significant in summer and autumn (BACI effect: $p = 0.08$) (Figure 3b). However, due to extensive variation across sites, YOY biomass responses did not correlate with increases in light during either season (Figure 1b). Cutthroat trout biomass did not differ statistically in downstream reaches relative to other reach types during any season for either life stage (BACI effect: $p > 0.05$), but YOY biomass tended to be slightly higher in downstream reaches during summer and autumn in the post-treatment year (Figures 2 and 3).

Cutthroat trout specific growth rates did not differ in thinned reaches from those in upstream or downstream reaches

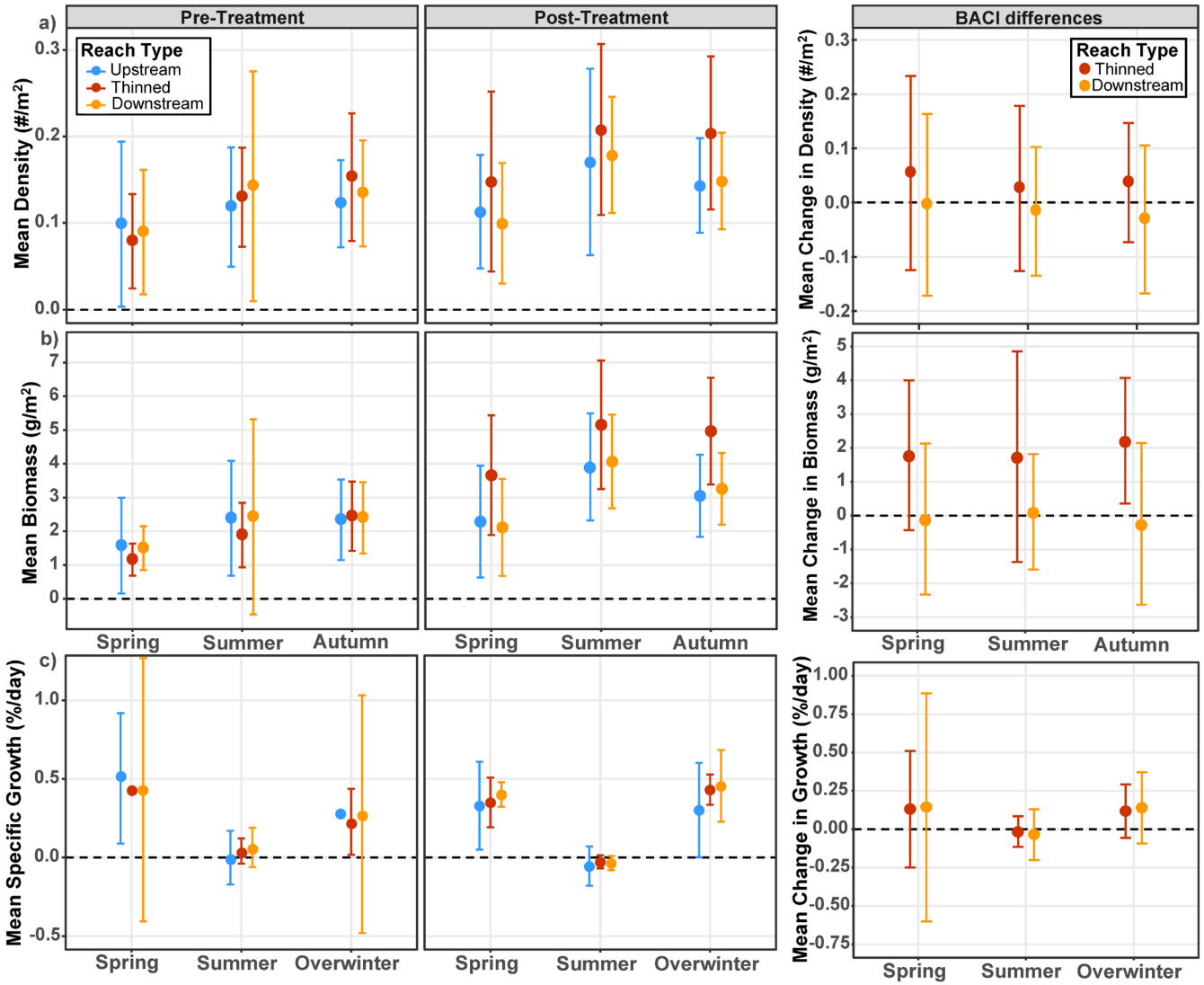

FIGURE 2 | Seasonal reach-scale estimates of adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). (a) Density (number per square meter; #/m^2), (b) biomass (grams per square meter; g/m^2), and (c) specific growth rates (percent per day; %/day) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah Creek study catchments in northern California, USA. Adult density and biomass estimates were conducted during seasonal fish sampling events in spring, summer, and autumn whereas specific growth rate estimates occurred between sampling periods. Before-after-control-impact (BACI) differences for all response variables in thinned and downstream reaches were estimated using the formula: (Treatment$_{post}$—Treatment$_{pre}$)—(Reference$_{post}$—Reference$_{pre}$). In all plots, points represent means across all sampling sites ($n = 5$) and error bars indicate 95% confidence intervals.

(Figures 2 and 3). Instead, adult cutthroat trout specific growth rates varied more among seasons than among reach types (upstream reference, thinned, and downstream) (BACI effect: $p > 0.05$) (Figure 2c). Adult cutthroat trout showed higher growth rates in spring (0.3%–0.7%/day) and overwinter (0.2%–0.5%/day) than in summer (−0.1% to 0.1%/day) (Figure 2c). Adult cutthroat trout growth rates did not statistically differ in thinned or downstream reaches between pre- and post-treatment years (Figure 2c). In general, YOY had higher growth rates in summer than adult life stages (0.7%–1.5%/day), but YOY summer growth rates did not vary among reach types in either pre- or post-treatment years (BACI effect: $p > 0.05$; Figure 3c). Neither adult nor YOY summer growth rates correlated with increases in light associated with thinning treatments (Figure S2).

3.2 | Thermal and Trophic Resource Responses to Thinning and Inputs to Bioenergetics Model

Mean daily stream temperatures during the pre-treatment year were warmest in summer (12.5°C–13.2°C), followed by spring (10.4°C–10.8°C) and overwinter (8.8°C–9.2°C) (Figure 4). Post-treatment stream temperatures increased in thinned reaches relative to pre-treatment conditions, but the magnitude of change varied among seasons, increasing by +0.5°C–1.5°C in summer, +0.0°C–0.6°C in spring, and by +0.0°C–0.2°C in overwinter (Figure 4). Mean stream temperatures increased in downstream reaches to a lesser extent than in thinned reaches, increasing by +0.2°C–1.1°C in summer, but showed minimal changes in spring and overwinter (Figure 4).

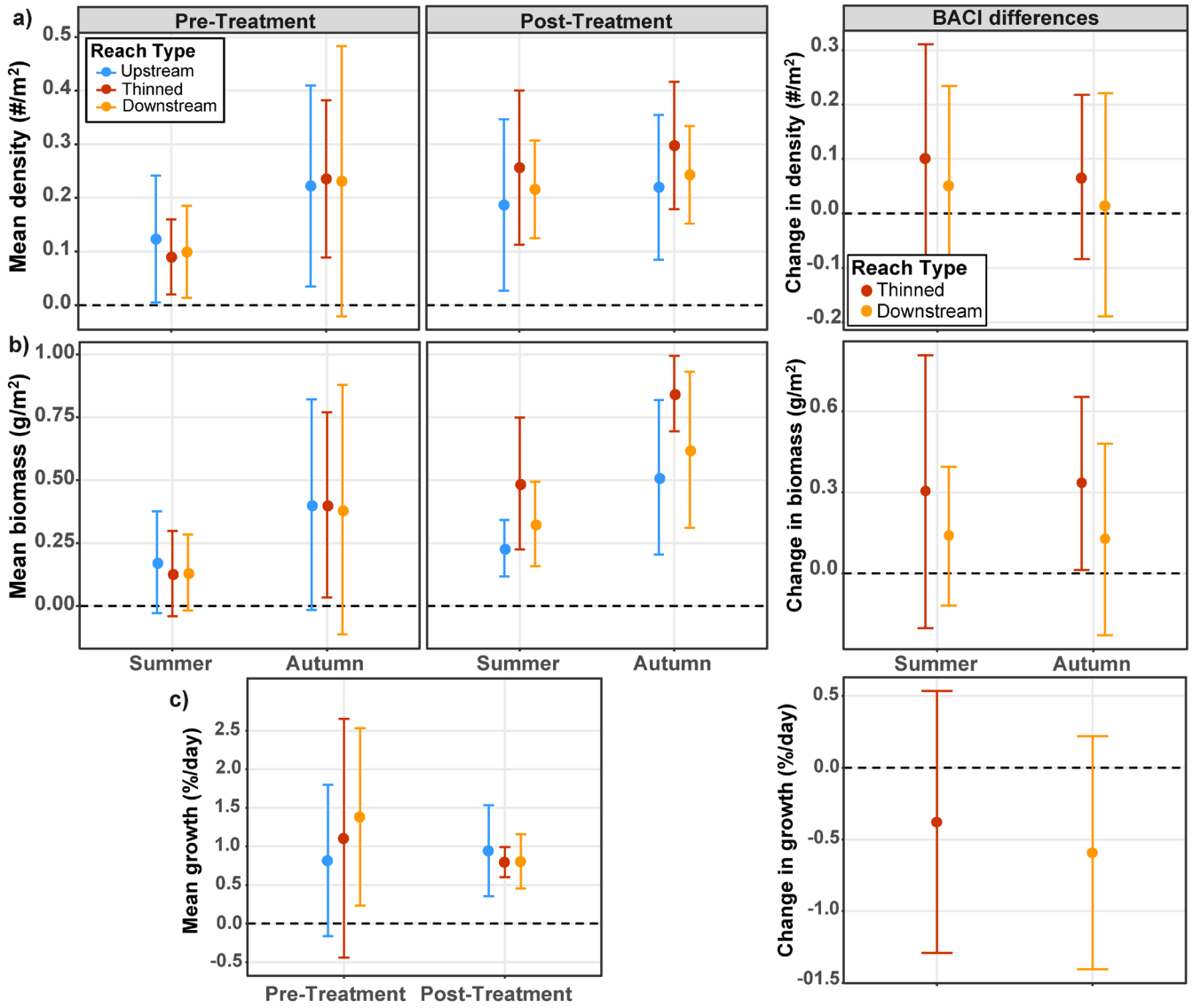

FIGURE 3 | Seasonal reach-scale estimates of young-of-year (YOY) coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). (a) Density (number per square meter; #/m^2), (b) biomass (grams per square meter; g/m^2), and (c) summer growth rates (percent per day; %/day) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah Creek study catchments in northern California, USA. YOY density and biomass estimates were conducted during seasonal fish sampling events in summer and autumn whereas summer growth rate estimates occurred between sampling periods. Before-after-control-impact (BACI) differences for all response variables in thinned and downstream reaches were estimated using the formula: (Treatment$_{post}$—Treatment$_{pre}$)—(Reference$_{post}$—Reference$_{pre}$). In all plots, points represent means across all sampling sites ($n = 5$) and error bars indicate 95% confidence intervals.

Prey energy density in cutthroat trout diets varied more among seasons than among reach types (Figure 5). Seasonal fluctuations in prey energy density were driven more by shifts in composition than by total energy density, which stayed relatively stable across seasons, with mean values ranging between 4400 and 5000 J/g (Figure 5). Cutthroat trout fed primarily on aquatic invertebrate larvae and adult beetles in spring, a mix of aquatic and terrestrial invertebrate taxa in summer, and primarily terrestrial invertebrates in autumn (Figure 5). Shifts in diet toward lower energy density prey taxa led to slight reductions in total prey energy density in thinned reaches compared to upstream reference reaches in the post-treatment year, decreasing by a mean of 3.5% or 160 J/g in spring, by 2% or 100 J/g in summer, and by 5% or 270 J/g in overwinter (Figure 5).

3.3 | Bioenergetics Modelling

Bioenergetics modelling simulations indicated that pCmax estimates of adult cutthroat trout in study catchments were low overall (pCmax range = 0.15–0.35) and varied both among seasons and among reach types (Figure 6a). Estimates of pCmax tended to be higher in spring (pCmax = 0.25–0.32) and overwinter (pCmax = 0.22–0.30) than in summer (pCmax = 0.18–0.24) in both the pre- and post-treatment years (Figure 6a). PCmax estimates increased in thinned reaches relative to upstream reference reaches in the post-treatment year by a mean of 20% overwinter and 17% in summer (BACI effect: $p < 0.05$), and tended to increase in thinned reaches by a mean of 11% in spring but did not differ statistically among reach types (Figure 6a). PCmax estimates correlated positively with increases in light associated

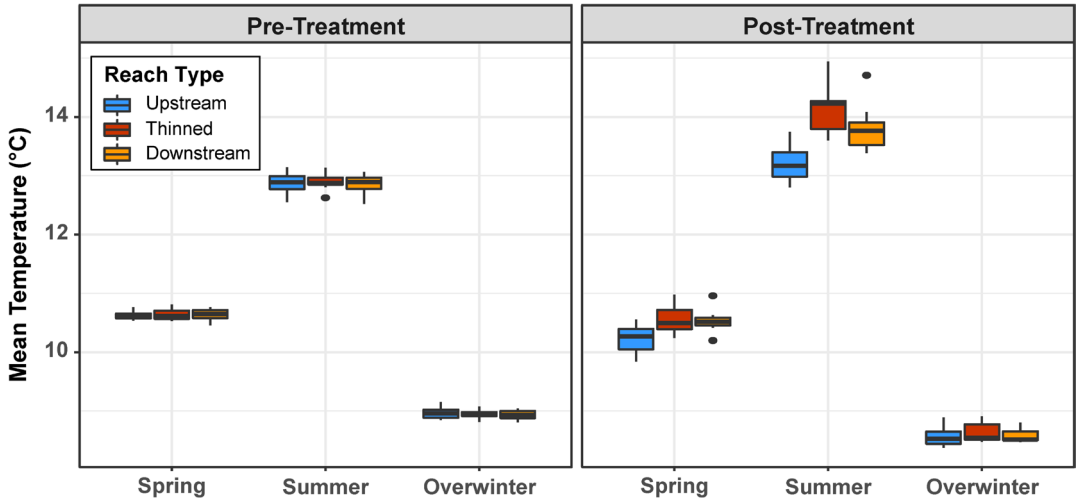

FIGURE 4 | Seasonal variation in stream temperatures (in degrees Celsius) in upstream reference, thinned, and downstream reaches during pre-treatment and post-treatment years in the Tectah Creek study catchments in northern California, USA. Boxplots show distribution of mean daily stream temperatures during spring, summer, and overwinter. All data represent mean estimates across all reach-scale sampling sites ($n = 5$).

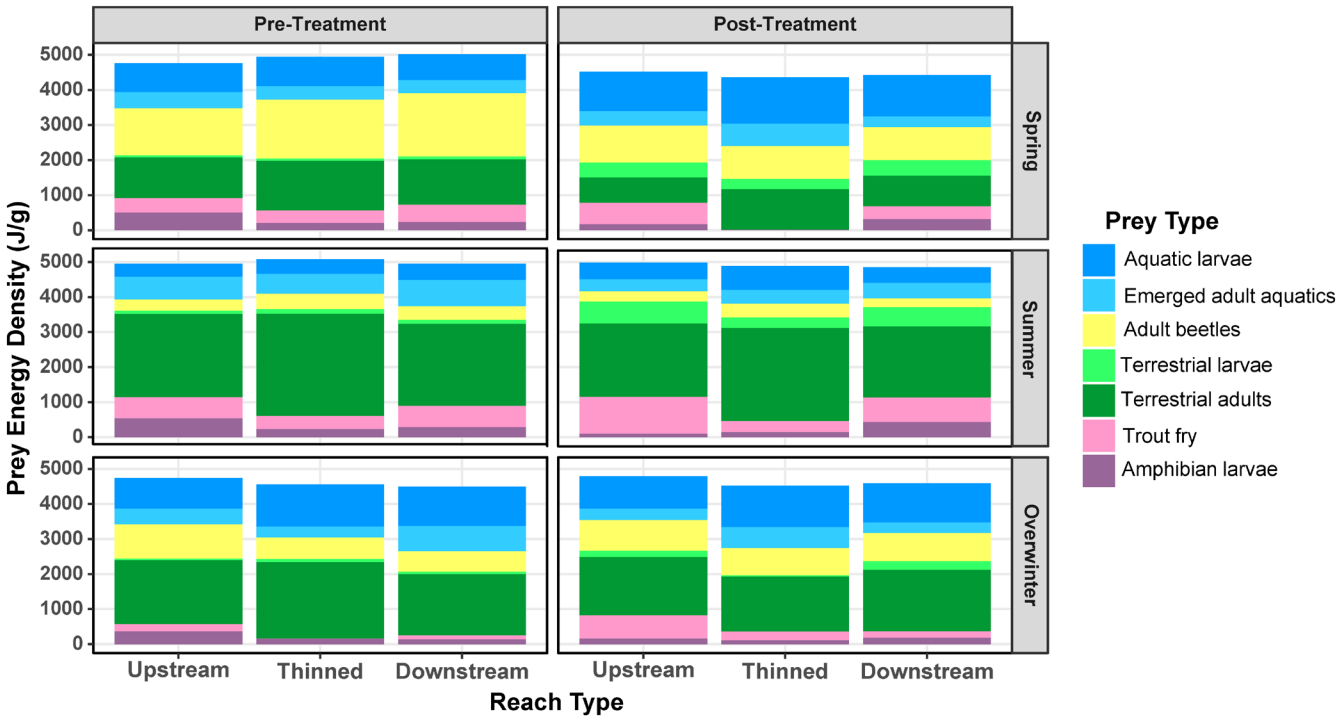

FIGURE 5 | Seasonal variation in prey energy density (in joules per gram; J/g) in diets of adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in upstream reference, thinned, and downstream reaches during pre-treatment and post-treatment years in the Tectah Creek study catchments in northern California, USA. Stacked bar graphs show the relative contribution of each prey type to the total energy density of prey in cutthroat trout diets. All data represent mean estimates across all reach-scale sampling sites ($n = 5$).

with thinning treatments, especially during summer and overwinter seasons (Figure S3a). PCmax estimates in downstream reaches also increased relative to upstream reference reaches during the post-treatment year but to a lesser extent than in thinned reaches (mean pCmax—spring: 7%, summer: 11%, and overwinter: 12%), but responses in downstream reaches did not differ statistically during any season (Figure 6a).

Individual consumption rates (in units of J/g fish per day) of adult cutthroat trout reflected the seasonal variation observed in pCmax, which tended to be highest in spring and overwinter than in summer (Figure 6b). BACI models indicated that individual consumption rates did not vary among reach types during any season (BACI effect: $p > 0.05$), although individual consumption rates tended to be higher in thinned reaches relative to upstream reference reaches by a mean of 39% in overwinter, 13% in spring, and 24% in summer, and differences in 95% confidence intervals suggested an increase in individual consumption rates in thinned reaches in summer (Figure 6b). Individual consumption rates also tended to be higher in downstream reaches relative to upstream

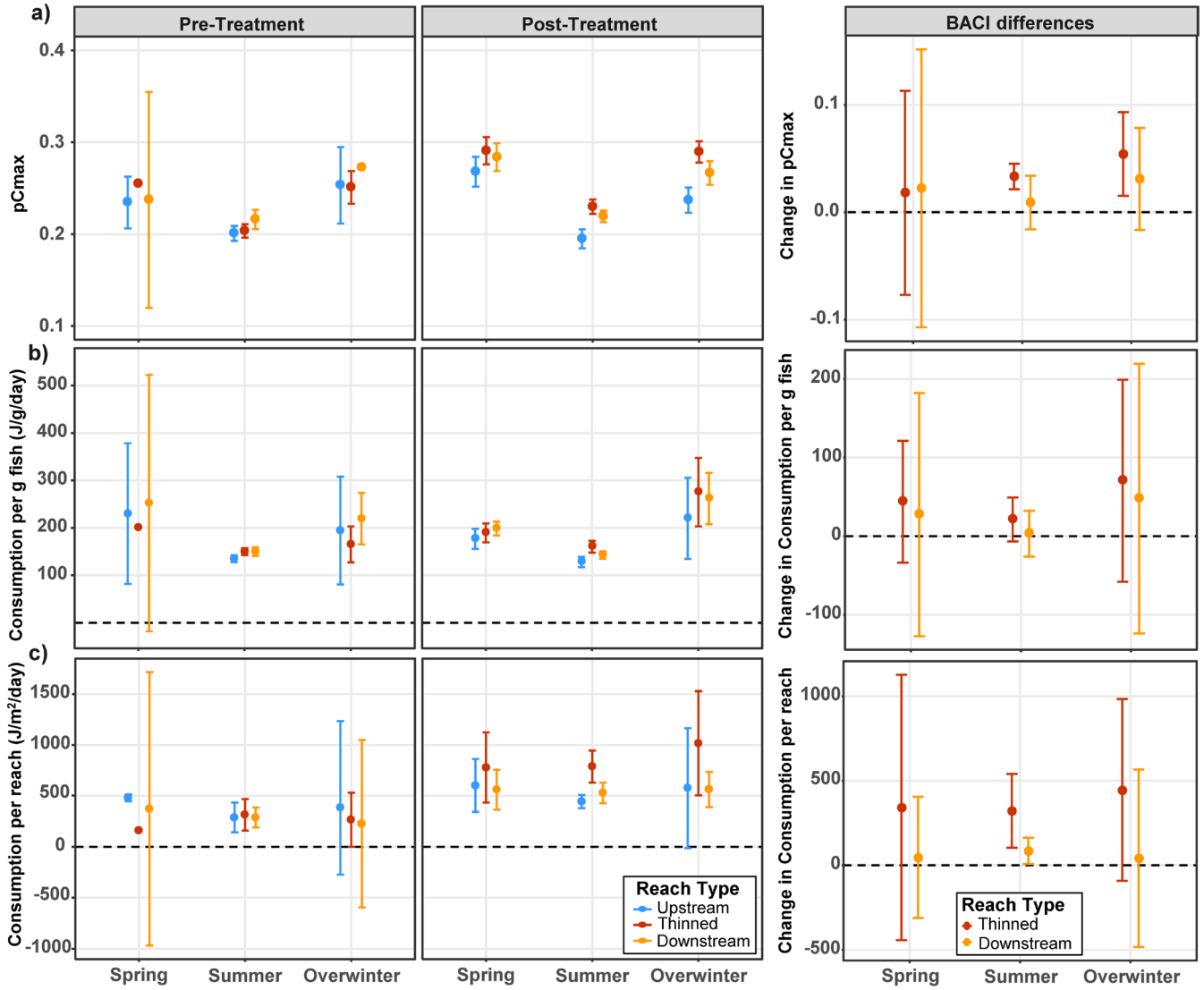

FIGURE 6 | Seasonal consumption estimates of adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) as (a) proportion of Cmax (pCmax), (b) individual-level consumption rates per fish (joules per gram fish per day; J/g/day) and (c) reach-level consumption rates for all fish (joules for all fish per m^2 per day; J/m^2/day) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah Creek study catchments in northern California, USA. Before-after-control-impact (BACI) differences for all response variables in thinned and downstream reaches were estimated using the formula: ($Treatment_{post}$—$Treatment_{pre}$)—($Reference_{post}$ – $Reference_{pre}$). In all plots, points represent means across all sampling sites ($n = 5$) and error bars indicate 95% confidence intervals.

reference reaches but to a lesser extent than in thinned reaches, especially in overwinter (mean increase of 32%), but did not differ statistically during any season (Figure 6b).

In contrast, reach-scale consumption rates of adult cutthroat trout increased significantly in thinned reaches by a mean of 79% in summer and by a mean of 107% in overwinter (BACI effect: $p < 0.05$), and by a mean of 45% in spring, but this response did not differ statistically (Figure 6c). Reach-scale consumption responses correlated positively with changes in light during all seasons (Figure S3b). Reach-scale consumption rates in downstream reaches did not differ statistically during any season, but increased by a mean of 28% in overwinter and 20% in summer (Figure 6c).

Scope-for-growth analyses indicated that at the observed consumption rates in the pre-treatment year, cutthroat trout growth potential occurred across a narrow range of temperatures during each season (temperature range for positive growth to occur: spring: 6°C–13°C, summer: 7°C–12°C, overwinter: 7°C–13°C) (Figure 7). At observed consumption levels, cutthroat trout growth potential peaked at mean stream temperatures of 9°C–10°C during all seasons for both the pre- and post-treatment years (Figure 7). Due to small increases in consumption associated with thinning treatments, thinning expanded the range of temperatures suitable for growth in thinned and downstream reaches during the post-treatment year by 1°C–2°C, especially in summer (6°C–14°C) and winter (5°C–15°C) (Figure 7). However, due to the increased energetic costs associated with warmer temperatures, scope-for-growth curves indicated that thinning was unlikely to significantly enhance cutthroat trout growth potential during any season of the post-treatment year (Figure 7). As a result, Kolmogorov–Smirnov tests indicated that scope-for-growth curves did not differ statistically among reach types

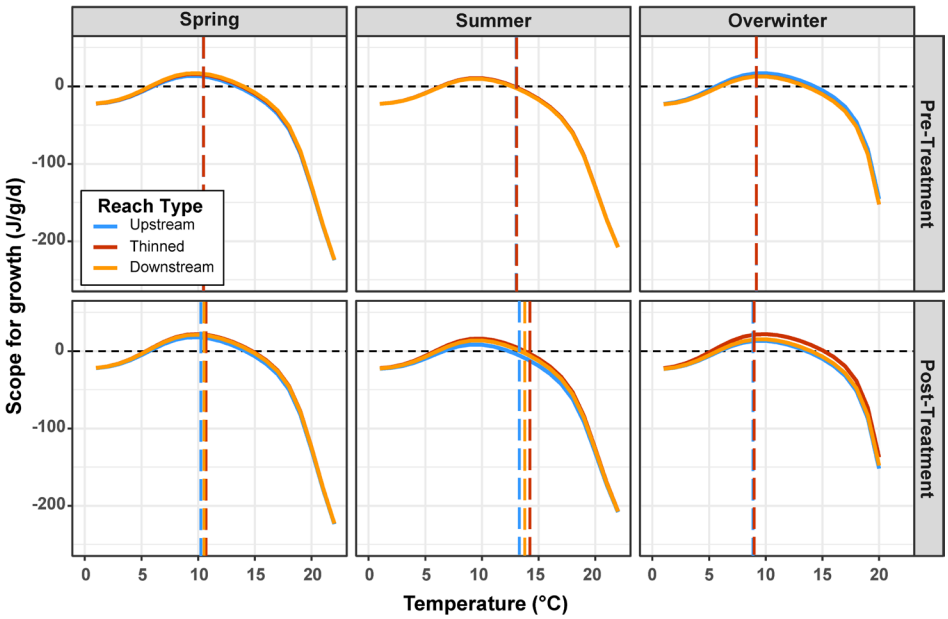

FIGURE 7 | Seasonal scope-for-growth curves for adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in upstream reference, thinned, and downstream reaches during pre- and post-treatment years in the Tectah Creek study catchments in northern California, USA. Scope-for-growth (in joules per gram per day; J/g/day) curves estimate the range of temperatures (degrees Celsius) growth could occur given the difference between energy intake (consumption) and energetic costs (egestion, excretion, respiration, and specific dynamic action) as estimated by the bioenergetics model for a 20 g adult cutthroat trout. Vertical dashed lines indicate mean temperatures in each reach type during each of the studied seasons and years.

during any season in the pre- or post-treatment years ($p > 0.05$) (Figure 7).

4 | Discussion

In this study, we provide a process-based evaluation of the implications of riparian forest thinning for resident populations of coastal cutthroat trout by combining a manipulative field experiment with empirical data and bioenergetics modelling. We observed that coastal cutthroat trout displayed mixed responses to riparian thinning 1 year post-treatment: trout density and biomass tended to increase in response to thinning treatments, yet seasonal growth rates remained unchanged. Bioenergetics modelling provided insights into the mechanisms driving these responses, revealing that cutthroat trout achieved similar seasonal growth rates in the face of thinning-induced increases in stream temperature or shifts in prey energy density via elevated individual- and reach-level consumption rates (i.e., cutthroat trout fed more frequently). However, scope-for-growth analyses indicated that thinning was unlikely to enhance growth opportunities for cutthroat trout due to higher energetic costs and warmer stream temperatures. These results help explain observed patterns in empirical growth, which varied more among seasons than with thinning treatments.

4.1 | Empirical Responses of Cutthroat Trout

Cutthroat trout density and biomass frequently increased in response to riparian thinning treatments, but responses varied widely across sites and did not always differ statistically. In general, responses of cutthroat trout to riparian thinning were modest relative to those measured in previous experiments that evaluated greater reductions of riparian canopy cover (Mellina and Hinch 2009), suggesting fish responses are likely to depend on the intensity of riparian canopy treatments. Whereas previous research has shown historical timber harvest practices that clearcut riparian canopies frequently led to substantial increases in salmonid fish density, biomass, and production (Murphy and Hall 1981; Hawkins et al. 1983; Bilby and Bisson 1992), current forest practices that include riparian buffers tend to have weaker influences on instream habitat conditions (Studinski et al. 2012; Cunningham et al. 2023) and produce smaller and more variable salmonid fish responses (De Groot et al. 2007; Wootton 2012; Bateman et al. 2016, 2018, 2021; Swartz and Warren 2023). Our results support these findings. For example, previous research conducted in the same study region by Wilzbach et al. (2005) documented that opening riparian canopies by 50% along a 100-m reach led to increased trout density by 0.3 fish/m^2 (+94%) and biomass by 1.4 g/m^2 (+34%). In our field experiment that reduced riparian shade by 19%–30%, we observed similar to greater increases in biomass of cutthroat trout (27%–111%), yet smaller changes in trout density (8%–31%).

Few other studies have evaluated the effects of riparian thinning to date, but results so far indicate mixed responses that tend to vary with thinning intensity: a finding consistent with our results (Hemstad et al. 2008; Chizinski et al. 2010; Studinski et al. 2017; Niles and Hartman 2021). For example, Hemstad et al. (2008) and Chizinski et al. (2010) observed that thinning treatments in Minnesota streams that reduced canopy cover by 6%–10% had no effect on aquatic habitat, macroinvertebrate, or stream fish assemblages. However, studies by Studinski et al. (2017) and Niles and Hartman (2021) in Appalachian catchments documented strong positive responses in brook trout (*Salvelinus fontinalis*) diets to more intensive thinning treatments of 50% and 90% reductions in basal area, which reduced canopy cover over

the stream channel by ~15% and ~50% respectively. Although we found that responses of cutthroat trout biomass to thinning treatments sometimes correlated with increased light availability, the density of cutthroat trout did not. Additional site-to-site variation in responses of trout to thinning treatments documented in our experiment could be a function of spatial heterogeneity in physical habitat conditions within and across the study catchments (Penaluna et al. 2015; Whitney et al. 2020; Hallbert and Keeley 2023).

Riparian thinning had no measurable effect on specific growth rates of cutthroat trout, which instead varied more among seasons than among thinned and un-thinned reaches (see also Morley et al. 2016). Growth can be used as an indication of favourable conditions supporting fish (Warren and Davis 1967; Armstrong et al. 2021; Railsback 2022; Kaylor et al. 2021). The fact that specific growth rates of cutthroat trout remained unchanged across multiple sites and seasons suggests that thinning had little influence on these stream fish. Although we observed minimal changes in seasonal growth rates, cutthroat trout may still have responded to thinning treatments via increased survival (Hughes and Grand 2000; Railsback and Harvey 2002). Moreover, increased cutthroat trout density and biomass in thinned reaches would likely heighten competition for prey resources, potentially resulting in density dependence and limiting individual-level growth responses (Grossman and Simon 2020; Matte et al. 2020). Our results contrast with Wilzbach et al. (2005), who documented higher specific growth rates of resident salmonid fishes under more intensive canopy reductions. Instead, we found cutthroat trout growth rates did not vary with changes in riparian canopy conditions, more similar to findings by Dineen et al. (2007) who evaluated brown trout (*Salmo trutta*) specific growth rate responses to varying types of riparian vegetation (open vs. closed canopy) in Ireland, and Jensen (2017) who assessed instantaneous summer growth rates of coastal cutthroat trout downstream of timber harvest in the Oregon Coast Range.

Seasonal variation in growth rates exceeded the effects of riparian thinning treatments. Cutthroat trout growth rates tended to be higher in spring and overwinter, rather than summer where growth rates averaged around 0. Low summer growth rates of resident salmonids have been documented by other studies around the region (Harvey et al. 2006; McCarthy et al. 2009; Raggon 2010; Jensen 2017; Sheldon and Richardson 2021; Swartz and Warren 2023; Sanders et al. 2024) and are likely due to low summer flow conditions that lead to greater exposure to predators that may make fish more risk averse, along with warmer stream temperatures, low drifting prey abundance, and higher fish densities (Harvey and White 2017; Rashidabadi et al. 2022). As a result, summer is typically considered a season of stress and lower survival for cutthroat trout in smaller streams in the Pacific Northwest (Berger and Gresswell 2009; Sheldon and Richardson 2021). Instead, growth rates tend to be higher in spring and overwinter when flows and concentrations, and fluxes of drifting invertebrates are higher (Li et al. 2016). High spring growth rates have been similarly documented in other studies of juvenile and adult salmonid fishes in northern California and Oregon (McCarthy et al. 2009; Kaylor et al. 2021; Rossi et al. 2022). These results highlight the value of year-round studies that can distinguish seasonal variation in fish responses (Brady et al. 2020) and aid in contextualising effect sizes of thinning treatments.

Although we documented no change in seasonal growth rates among reach types, shifts in cutthroat trout size distributions suggest that annual growth may have changed in thinned reaches (Figures S4 and S5). Such shifts in cutthroat trout size distributions can help explain the increases in cutthroat trout density and biomass and could be due to a combination of (1) earlier emergence, (2) increased recruitment, and (3) higher YOY and adult survival. For example, shifts in stream temperature during the treatment and post-treatments years may have resulted in earlier emergence of YOY, which would have had more time to grow during our study window (Campbell et al. 2020). In turn, increased annual growth could have positive effects on YOY survival, potentially resulting in more and larger individuals to recruit into adult life stages. These patterns are consistent with Bisson and Sedell (1984)'s "increased temperature hypothesis" and are supported by post-treatment increases in stream temperature and shifts in size distribution of YOY and adult life stages in thinned reaches relative to upstream reference or downstream reaches (Figures S4 and S5). Similar shifts in YOY size distributions were observed after increased temperatures associated with wildfire disturbance by Swartz and Warren (2022) in western Oregon, Rosenberger et al. (2015) in Idaho, and Silins et al. (2014) in the Canadian Rockies. Alternative hypotheses that may explain higher cutthroat trout biomass in thinned reaches include the increased food hypothesis, which suggests that opening riparian canopies can increase instream primary production, which could provide more aquatic invertebrate prey resources supporting top predators (Bisson and Sedell 1984). However, in a previous food web analysis (Roon et al. 2022), we found little empirical evidence that thinning treatments increased prey biomass in the diets of individuals fishes. However, this does not mean that prey abundance did not increase. Our findings suggest that any increase in prey abundance may have been spread across the fish population, resulting in higher population-level food consumption, but with negligible effects on individuals. Another alternative explanation is that increased fish biomass could also be due to fish moving into treatment reaches from adjacent reaches (Gowan and Fausch 1996; Roni 2019). However, our observations of movements of individually tagged adult fish provided no evidence of movement into thinned reaches.

4.2 | Cutthroat Trout Bioenergetics

Bioenergetics modelling provided key insights into cutthroat trout responses to thinning treatments that supported empirical observations. For example, cutthroat trout likely achieved similar seasonal growth rates in thinned reaches via increased consumption rates (i.e., fish fed more frequently). Factors driving consumption increases in thinned reaches varied seasonally. We saw the greatest increase in consumption rates in summer when stream temperatures were at their warmest. We observed similar patterns to a lesser degree in spring, where smaller increases in stream temperature due to thinning combined with cooler background temperatures led to smaller subsequent increases in consumption. However, increased consumption rates in overwinter, when we observed

no treatment-related changes in stream temperature, were more likely due to shifts in diet toward lower energy density prey taxa compared to other seasons. Bioenergetics models can be extremely sensitive to changes in prey energy density (Railsback and Rose 1999; Jensen 2017; Sanders et al. 2024). Although we found no evidence that thinning affected prey composition or biomass in cutthroat trout diets in a previous food web analysis (Roon et al. 2022), higher consumption rates could have masked changes in prey biomass in diets due to warmer temperatures leading to higher metabolic and digestion rates. Furthermore, Wilzbach and Hall (1985) speculated that increased light reaching the stream channel after riparian harvest could lead to increased foraging efficiency for cutthroat trout, potentially contributing to higher consumption rates observed in this study. Collectively, these results suggest that increased consumption rates may have allowed cutthroat trout to compensate for increased stream temperatures in spring and summer and shifts in prey energy density overwinter.

Few studies have applied bioenergetics modelling to evaluate the effects of forest harvest or other riparian disturbances on stream fishes. A study by Leach et al. (2012) applied bioenergetics modelling to evaluate how potential changes in stream temperature associated with forest harvest would affect cutthroat trout in southwestern British Columbia, finding that increases in stream temperature of ~5°C due to forest harvest would likely negatively affect cutthroat trout via lower summer growth rates. Beakes et al. (2014) also found that small increases in stream temperature of 0.6°C and a reduction in prey after wildfire led to an increase in energetic costs and decreases in biomass for *O. mykiss* in California streams. In contrast, Sanders et al. (2024) found no change in summer consumption rates of coastal cutthroat trout following timber harvest with a range of riparian buffer protections in the Oregon Coast Range. Similarly, Dineen et al. (2007) observed no effect of riparian canopy type (including grasslands, open canopies, and closed deciduous canopies) on brown trout consumption rates in streams in Ireland. Our results differ from these studies, thereby reaffirming that fish responses to changes in riparian forests depend not only on changes in stream temperature alone (Railsback 2022) but on the interaction of temperature conditions and prey resources.

Rates of consumption at a reach-scale, which combined estimates of individual consumption rates and biomass for adult life stages of cutthroat trout, suggested that thinning not only increased the energy intake rates of individual fish but also increased the cumulative population-level energy intake. Although we did not include YOY life stages in this analysis which accounted for 52%–53% of the population, YOY only accounted for 9%–10% of the overall biomass, suggesting that adult life stages represented the majority of consumptive energy flows in our study reaches. We did not measure prey availability in this study, but the increases in reach-scale consumption we observed provide key supporting evidence for the "increased food hypothesis" and help explain the density and biomass empirical responses of cutthroat trout (Bisson and Sedell 1984). Although we documented no change in prey biomass in cutthroat diets in an earlier food web analysis (Roon et al. 2022), the increase in individual- and reach-scale consumption rates documented in this study suggests that increased energy intake in response to thinning was likely spread across more and larger individual fish. These results highlight the complementary insights gained by pairing empirical data with process-based modelling approaches (e.g., Harvey et al. 2024). Collectively, these observations suggest that riparian thinning can have population-level implications for cutthroat trout in forested catchments.

Scope-for-growth analyses provided mechanistic insights into empirical growth responses, indicating that even though cutthroat trout consumption rates increased in response to thinning treatments, such changes in consumption were relatively small in magnitude, and thus unlikely to meaningfully enhance growth. This is likely due to the combination of low overall consumption rates and increased energetic costs associated with increased stream temperatures and reductions in prey energy density (Petty et al. 2014). Bioenergetics modelling suggested that due to low consumption rates cutthroat trout could only grow within a narrow range of stream temperatures under pre-treatment conditions, and the range of temperatures under which growth could occur only expanded slightly after thinning. Across all simulations cutthroat trout growth potential peaked at ~9°C–10°C, which coincides with temperatures typically experienced in spring and overwinter and the timing of higher seasonal empirical growth rates. Our results contrast with Leach et al. (2012) who suggested that increases in stream temperature associated with forest harvest in southwestern British Columbia were likely to decrease growth opportunities for cutthroat trout. However, their results were based on assumed levels of prey energy density that did not change after harvest. Instead, our results were more moderate, showing that increases in consumption were enough to offset the increased energetic costs associated with increased stream temperature, but not enough to enhance growth. Although bioenergetics simulations suggested minimal changes in growth, changes in prey availability and temperature associated with thinning treatments may still have influenced individual cutthroat trout via increased survival (Hughes and Grand 2000; Railsback and Harvey 2002). As a result, our data highlight that fish responses to riparian thinning may depend on background thermal and trophic conditions and how those conditions react to management (Railsback 2022).

4.3 | Future Directions

Our findings in this study point to several directions to potentially consider in future research addressing salmonid fish responses to riparian thinning or other riparian restoration efforts. Here, we only considered the immediate effects of thinning 1 year post-treatment. Given that changes in riparian forests can affect physical instream conditions and fish populations for decades, consideration of longer-term effects could be valuable (Connolly and Hall 1999; Young et al. 1999; Yeung et al. 2017). Moreover, food web dynamics, demographic processes, and resulting population responses of fish may take multiple years to manifest and could benefit from investments in intensive multi-year studies (Yodzis 1988). Such evaluations are rare in practice, but model-based approaches may provide an alternative (Harvey et al. 2024). For example, food web models (e.g., Bellmore et al. 2017) have been previously applied to evaluate forest practices and could be used to explore long-term implications of

riparian thinning treatments (Benjamin et al. 2022). In addition to a limited timeframe, we were limited to considering only local, reach-scale thinning responses. Given that previous research has documented that stream temperature responses to thinning can extend 100–1000 m downstream (Roon et al. 2021b), follow-up studies at broader extents could provide additional insight into the ecological consequences of these changes (e.g., Falke et al. 2019; Kaylor et al. 2021; Spanjer et al. 2022; Rossi et al. 2024). Finally, we only evaluated one specific intensity of thinning treatment: a 50% canopy reduction along both sides of the stream channel that led to reductions in riparian shade of 19%–30% along 100–200 m stream reaches. Evaluation of a broader range of thinning treatments could provide a more comprehensive understanding of thinning effects. Riparian thinning could have other benefits for stream and riparian forest habitats that we did not consider in this study such as accelerating the recovery of old-growth forest structure and composition (O'Hara et al. 2010; Teraoka and Keyes 2011; Keyes and Teraoka 2014; Case et al. 2023) and the recruitment of large wood (Pollock and Beechie 2014; Benda et al. 2016); future studies could potentially track the recovery rate of riparian vegetation and large wood and consider the potential synergistic effects of riparian thinning treatments combined with large wood additions for fish populations (Opperman and Merenlender 2004).

4.4 | Management Implications

Resource managers are interested in whether thinning second-growth riparian forests can strike a balance between causing small changes in stream temperature while still boosting productivity for aquatic ecosystems and fish (Wilzbach et al. 2005; Newton and Ice 2015; Roon 2021). However, stream-riparian linkages may be complex, so responses to changes in riparian forest conditions, such as thinning, can be difficult to predict (Gregory et al. 1991; Nash et al. 2021; Benjamin et al. 2022). Here we discuss the potential implications of our results for managers interested in riparian thinning and other types of active management in riparian zones (Berg 1995; Carey 2003; Swartz and Warren 2023). Our study results:

1. Highlight the value of controlled ecological experiments. Rather than assuming that riparian thinning or other understudied riparian restoration strategies may have certain effects on stream temperature or aquatic productivity (Newton and Ice 2015), field experiments can provide direct information that can guide natural resource decisions. It is important, however, to acknowledge that large-scale, field-based experiments also come with limitations. For example, such field experiments are often limited by small sample sizes, which, combined with extensive background temporal and spatial variation, can make it difficult to determine the statistical significance of treatment effects. As a result, variability in results can lead to discrepancies between statistical and biological significance, as evidenced here (Underwood 1994; Johnson 1999). Nevertheless, field experiments can provide important real-world observations that can improve decision making.
2. Demonstrate the importance of understanding processes. By combining empirical data with bioenergetics modelling, we gained unique insights into the processes driving empirical fish responses to riparian thinning treatments (Harvey et al. 2024). This in turn resulted in a better understanding of the mechanisms behind our empirical responses. Integrating complementary approaches can provide valuable insights into the mechanisms that help understand not just *how* fish responded, but also *why* fish responded to thinning treatments.
3. Suggest the importance of context. We documented moderate positive effects of thinning on coastal cutthroat trout in our study catchments, but it is important to keep in mind the study context and how responses are likely to vary in other locations. Our study took place in small, forested catchments in coastal northern California. Although thinning increased stream temperatures (Roon et al. 2021a), background temperatures were cool, and responses were small and did not approach levels that may lead to acute thermal stress. Moreover, as typical of low-order forested streams, study catchments tended to be low productivity (Vannote et al. 1980). As a result, we observed mixed responses of cutthroat trout to thinning treatments. However, the application of thinning in other contexts with other background conditions could affect the magnitude and direction of responses. Our results highlight that fish responses to riparian thinning may depend on a whole host of factors including the background thermal and trophic conditions as well as the thermal niches and energetic demands of the fish species that inhabit the study catchments (Anlauf-Dunn et al. 2022).

4.5 | Conclusions

Riparian thinning had mixed effects on resident coastal cutthroat trout populations that were generally smaller than the effects observed after more intensive reductions in riparian canopy (e.g., Wilzbach et al. 2005). Experimental thinning treatments supported increased reach-scale density and biomass of YOY and adult cutthroat trout, especially in later seasons. However, these responses varied widely across sites and were not supported by specific growth rates, which varied more among seasons than with thinning treatments. Shifts in size distributions suggest that local increases in cutthroat trout density and biomass could be due to increases in water temperature that allowed YOY fish to emerge earlier and recruit larger individuals into adult populations. Insights from bioenergetics modelling revealed that thinning increased consumption rates at individual- and reach-levels, which may have acted as a mechanism of resilience allowing fish to maintain similar growth rates despite increases in water temperature and shifts in prey energy density. However, bioenergetics modelling also suggested that thinning was unlikely to enhance growth opportunities for resident coastal cutthroat trout in forested catchments due to low overall consumption rates and higher energetic costs which may limit realised benefits for stream fishes. Collectively, these findings suggest that thinning in certain contexts (e.g., mild stream temperatures and sufficient prey resources) may enhance conditions for salmonid fishes. This study demonstrates that an understanding of thermal and trophic resources in addition to empirical fish

data may provide important contextual clues and improved insights to inform the potential implications of riparian management for resident fish species in forested catchments.

Author Contributions

Conceptualization: D.A.R., J.B.D., B.C.H., J.R.B., and J.R.B. Developing methods: D.A.R., J.B.D., B.C.H., J.R.B., and J.R.B. Conducting the research: D.A.R. Data analysis: D.A.R. and J.R.B. Data interpretation: D.A.R., J.B.D., B.C.H., J.R.B., and J.R.B. Preparation figures and tables: D.A.R. Writing: D.A.R., J.B.D., B.C.H., J.R.B., and J.R.B.

Acknowledgements

We thank Oregon State University technicians Kyle Smith, Jerika Wallace, Thomas Starkey-Owens, Mary Carlquist, Ashley Sanders, Morgan Turner, Alex Scharfstein, Cedar Mackaness, and Laura Nepstad for their help collecting data in the field and the laboratory as well as the aquatic biologists at Green Diamond Resource Company Pat Righter, Teal Richards-Dimitre, Matt Kluber, Will Devenport, Matt Nannizzi, Sean Studer, Mike Zontos, Jon Pini, and Jonathan O'Connell who helped with field sampling. Thanks to the USDA Forest Service PNW Research Station and Ivan Arismendi for providing space for processing macroinvertebrate samples. Thanks to David Beauchamp for providing guidance with the bioenergetics simulations. Thanks to Shelley Johnson, Ashley Sanders, Allison Swartz, and two anonymous reviewers for reviewing previous versions of the manuscript. This study was conducted according to protocols approved by OSU Animal Care and Use Permit Number 5037 and California Department of Fish and Wildlife Scientific Collection Permit Numbers 13298 and 6348. This research was supported by funding from the Green Diamond Resource Company, Save the Redwoods League, USDA Forest Service, U.S. Geological Survey, and OSU Department of Fisheries, Wildlife and Conservation Sciences. Publication of this paper was supported, in part, by the Neil Armantrout Graduate Fellowship. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Ethics Statement

This study was conducted according to protocols approved by OSU Animal Care and Use Permit Number 5037 and California Department of Fish and Wildlife Scientific Collection Permit Numbers 13,298 and 6348.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the Open Science Framework: https://doi.org/10.17605/OSF.IO/F57DK.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.