Wildfire in western Oregon increases stream temperatures, benthic biofilms, and juvenile coastal cutthroat trout size and densities with mixed effects on adult trout and coastal giant salamanders

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Abstract

Wildfire has become increasingly common and severe across forested landscapes. Shortly after wildfire, loss of riparian cover along streams and subsequent increases in light can elevate stream temperatures, a key control on metabolic rates of biota. Increased light can also increase autotrophic basal resource availability with potential bottom-up effects. We evaluated wildfire impacts on aquatic ecosystems in a replicated Before-After Control-Impact study 1 year after a severe wildfire in western Oregon, U.S. Stream temperature, chlorophyll *a* accrual, and age-0 coastal cutthroat trout size, density, and biomass increased in all three burned streams relative to changes in three unburned references. When streams were evaluated collectively, fire did not have an effect on larger vertebrate density or biomass. However, considering streams individually, two severely burned sites had substantial temperature increases and declines in larger vertebrate density and biomass, but the moderately burned site had modest temperature increases and adult cutthroat trout and Pacific giant salamanders increased. The loss of riparian canopies post-fire increased temperature and algae, but fish responses varied with age class and larger vertebrate responses were inconsistent.

Key words: wildfire, stream temperature, benthic chlorophyll α, Pacific giant salamander (*Dicamptodon tenebrosus*), coastal cutthroat trout (*Oncorhynchus clarkii clarkii*)

Introduction

Understanding the response of coldwater fish to forest disturbances driven by wildfire is increasingly important as climate change leads to greater wildfire severity, frequency, and season length across forested landscapes (Moriondo et al. 2006; Flannigan et al. 2009; Burke et al. 2021). Wildfire is a landscape disturbance with the potential to fundamentally alter the structure and function of stream and riparian ecosystems (Minshall et al. 1989; Pettit and Naiman 2007; Vaz et al. 2015). The loss of riparian cover exposes streams to greater solar radiation, which can lead to substantially elevated stream temperature conditions for coldwater-adapted aquatic vertebrates (Gresswell 1999; Bixby et al. 2015).

The effects of wildfire on aquatic systems and biota depend on burn severity and post-fire weather events and can fluctuate over time (Reeves et al. 1995; Gresswell 1999; Verkaik et al. 2013; Bixby et al. 2015). Short-term (0–3 years) effects of particular concern to aquatic vertebrates (fish and salamanders) are increases in stream temperature (Isaak and Hubert 2001; Hitt 2003) and high sediment and organic matter fluxes (Benda et al. 2003; Wondzell and King 2003; Verkaik et al.

2013), which, when decompose can lead to declines in dissolved oxygen (Hauer and Spencer 1991; Spencer et al. 2003; Bladon et al. 2014) and subsequent fish mortality (Bozek and Young 1994). Elevated stream temperature conditions are of most concern in systems with native coldwater-adapted organisms but may affect different species and life stages of aquatic biota differently.

Stream temperature is a fundamental driver of aquatic ecosystem processes and control on metabolic rates of aquatic biota. The removal of riparian canopies due to fire, especially in streamside forests with previously dense cover and shading, can lead to shifts in thermal regimes (Dunham et al. 2007; Mahlum et al. 2011; Rieman et al. 2012). Increased temperatures are generally greatest in the first few summers after a large fire if shade is reduced in a large portion of the stream network (Gresswell 1999; Dunham et al. 2007; Isaak et al. 2010; Rieman et al. 2012) and can have lethal effects or important sublethal effects on coldwater-adapted biota (Meeuwig et al. 2004). Studies have found that even moderate warming after fire (temperature increase of 0.6 °C, Beakes et al. 2014) can create stressful conditions for fish and cause decreased

coastal cutthroat trout density (in response to temperature increases of 2 °C–6 °C, Sestrich et al. 2011), with declines linked to increased metabolic demand and greater competition (Rosenberger et al. 2015). Although elevated stream temperatures have been linked to negative impacts to coldwater salmonids (Sestrich et al. 2011; Rosenberger et al. 2015), a number of post-fire studies have documented unchanged fish densities (Jones et al. 1981; Gresswell 1999; Jakober 2002; Rieman et al. 2012, Warren et al. 2022), increased fish densities (Rieman and Lee 1997), or higher growth rates (Heck 2006) associated with elevated stream temperature after fire, highlighting the need for more research quantifying fish responses to wildfire. Beyond fish, the effects of fire and associated increased stream temperatures on other dominant predators in headwater streams including stream salamanders is also equivocal (Hossack and Pilliod 2011).

Although the loss of riparian cover following wildfire can increase temperatures and create stressful conditions for coldwater-adapted species in streams, increased light to the stream can also stimulate stream periphyton growth, which can increase resources at the base of stream food webs and thereby potentially enhance conditions for apex predators (Hill et al. 1995; Hetrick et al. 1998; Sabater et al. 2000; Kiffney et al. 2003). In forested headwater ecosystems food availability, which is dominated by allochthonous inputs, can limit production of higher trophic levels (Bilby and Bisson 1992). However, removal of the canopy from fire and subsequent increases in light can increase autochthonous basal resources (Cooper et al. 2015; Klose et al. 2015) and shift stream food webs towards greater production through autotrophic energy pathways (Gresswell 1999; Spencer et al. 2003; Mihuc and Minshall 2005). The interaction of food availability and stream temperature is also important because studies have demonstrated that optimal temperature for fish growth shifts with consumption, so increases in temperature may be less stressful under conditions with greater food availability (Wurtsbaugh and Davis 1977; Railsback and Rose 1999; Beauchamp 2009). Therefore, simultaneous increases in both temperature and food resources together may be key when assessing potential effects of wildfire on fish and other apex predators.

Due to the unpredictable nature of wildfire, most research assessing responses of stream biota to wildfire lack either spatial or temporal (pre-treatment) replication to infer causal effects of fire. This study evaluates aquatic ecosystem and vertebrate responses to wildfire using a replicated Before-After Control-Impact (BACI) study design that takes advantage of fortuitous pre-treatment data from six forested streams in western Oregon, three that burned in a severe wildfire in 2020 and three reference streams just outside the fire boundary. We assessed stream temperature, chlorophyll *a* accrual, and the density, biomass, and condition of adult and juvenile coastal cutthroat trout and Pacific giant salamanders before and 1 year after a severe wildfire in western Oregon using a BACI study design. Here, we hypothesized that the removal of the riparian canopy after wildfire leads to declines in coastal cutthroat trout and Pacific giant salamander biomass, population size, or condition as a result of increased thermal stress. Or, conversely, that the increases in light post-fire drive increases in basal resource availability allowing metabolic rates to be met by increased consumption. The latter hypothesis resulting in either no clear fire effect on apex predators or even potential increases in stream vertebrate abundance and biomass in response to greater food availability.

Methods

Site description

Research was conducted in six replicate streams located within the McKenzie River Basin in the western Cascade Mountains of Oregon (Fig. 1). This region is characterized by a Mediterranean climate with high precipitation during cool winter months and little to no precipitation during summer months. The warm, dry summers of the Pacific Northwest region combined with changing climate and a history of fire suppression (Weisberg and Swanson 2003) are resulting in increased wildfires in this area (Littell et al. 2011; Stavros et al. 2014; Westerling 2016). In early September 2020, three of the six study streams were within the boundary of a large wildfire, the Holiday Farm Fire, which burned 702 km^2 of the McKenzie River basin over a mix of private and public land (Fig. 1).

The six study catchments are all mid-elevation (393–867 m) second- and third-order fish-bearing streams with cobble and boulder substrates. Stream reaches (90 m) ranged from 2.2 to 6.4 m in bankfull width and were shaded by 40–60 year old riparian forests (Table 1). Before the fire, all riparian areas consisted of dense, closed canopies comprised predominantly of red alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*) with sporadic western red cedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyllum*). The unburned streams (McTE, Loon Creek, and Chucksney Mountain Creek) are in the Willamette National Forest; McTE is located within the H.J. Andrews Experimental Forest, a long-term ecological research site. The three burned streams (W-113, W-100, and W-122) are on private land owned by Weyerhaeuser Company. All streams support coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and Pacific giant salamanders (*Dicamptodon tenebrosus*), and two (W-100 and W-122) contain sculpin (*Cottus* spp.).

Study design

The Holiday Farm Fire provided a large-scale natural experiment. Due to fortuitous pre-fire data collection in reference reaches of a previous study (Swartz et al. 2020), stream temperature, baseflow stream nutrient concentrations, benthic biofilms, and stream vertebrate abundance, biomass, and condition data were available in 90 m reaches at three study sites within the burn perimeter and three sites just outside the perimeter. Reaches in the present study are the unmanipulated reference reaches from the previous study (Swartz et al. 2020). Pre-treatment data were collected in summer 2018 for stream temperature, baseflow stream nutrient concentrations, benthic biofilms, and stream vertebrates, and an additional year of abundance, biomass, and condition data on stream vertebrates was collected in 2019 in all sites except

Fig. 1. Map of the Holiday Farm Fire in western Oregon USA (Albers Conical Equal Area, NAD83). The inset shows the location of the fire within Oregon, USA. The colored polygons depict the fire boundary and burn severity, which is indicated by the percent basal area mortality (%). Three of the streams in this study are within the fire boundary (W-113, W-100, and W-122) and three reference streams are outside the fire boundary (McTE, Loon, and Chucksney). Fire boundary and percent basal area mortality were provided by the US Department of Agriculture Forest Service Geospatial Technology and Applications Center (GTAC) (burnseverity.cr.usgs.gov/ravg/).
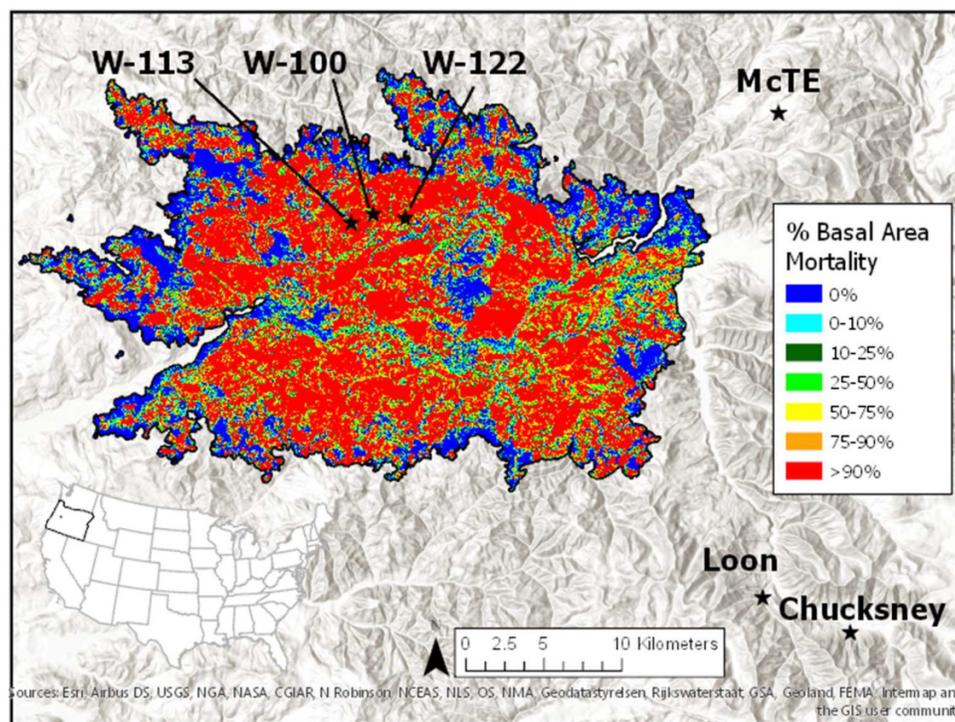
Table 1. Location, riparian burn status and severity, and site details for each of the six study streams in the central Cascade Mountains of western Oregon.

Stream	Fire impact	Basal area removed (%)	Elevation (m)	Latitude	Longitude	Bankfull width (m)	Wetted width (m)	Azimuth and aspect	Gradient (%)
McTE	Unburned	–	867	44.254544	−122.166720	2.2	1.23 (0.3)	SW - 221.6°	14
Loon	Unburned	–	721	43.953624	−122.183330	4.1	1.93 (0.8)	NE - 58.5°	10
Chucksney	Unburned	–	833	43.953624	−122.113550	5.2	2.34 (0.7)	NE - 29.1°	18
W-113	Burned	54.6 (34.4)	537	44.192892	−122.510742	3.3	1.62 (0.5)	SE - 118.2°	11
W-100	Burned	79.0 (24.0)	441	44.198130	−122.492983	5.4	3.61 (0.9)	SE - 136.9°	3
W-122	Burned	93.9 (13.1)	393	44.195514	−122.467184	6.4	4.65 (1.4)	SW - 220.7°	2

Note: Bracketed values represent one standard deviation.

W-122. We returned to all of the sites in the first summer after the wildfire (2021) to create a replicated BACI study. The BACI study design allows us to reduce inherent stream-to-stream environmental variability (e.g., gradient, geology, and substrate) and annual variability to elucidate effects from wildfire.

Burn severity

To evaluate fire severity at the three sites in the fire boundary, we used burn severity data from the Rapid Assessment of Vegetation Condition after Wildfire (RAVG) program managed by the U.S. Department of Agriculture Forest Service Geospatial Technology and Applications Center (burnseverity .cr.usgs.gov/ravg/), which provides a rapid initial assessment of post-fire vegetation following wildfires on national forests (which included area of the Holiday Farm Fire as it spanned both national forest area and private land). From the RAVG data set, we calculated impacts within 100 m along each stream reach using the Zonal Statistics tool in ArcGIS Pro. We chose to focus on local burn severity rather than impacts in the whole catchment or subcatchment because we were explicitly interested in local changes in shade and light, and because an earlier study found that this riparian metric was a better explanatory factor for local acute stream temperature responses than watershed burn severity for this fire (Sanders et al. 2022).

Temperature

In both pre-fire (2018) and post-fire (2021) assessments of stream temperature, we deployed temperature data loggers (Onset HOBO model UTBI-001, ± 0.2 °C accuracy, ± 0.16 °C resolution) at the downstream end of each 90 m study reach. Stream temperature data are available for all sites in each year for a 3 week period in mid-summer (12–30 July). Loggers recorded temperature every 15 min and were housed in white PVC piping with holes and placed parallel to flow to prevent warming from direct solar radiation. Prior to deployment, loggers were validated against one another in a well-mixed ice bath for 1 h recording every 15 s while allowing ice to melt and temperatures to warm. Loggers out of the range of accuracy specified by the manufacturer (±0.2 °C) were not used.

Macronutrients

Nitrate–N (NO_3^-–N) and phosphate–P (PO_4^-–P) concentrations were measured in early August on vertebrate sampling days (before fish sampling started) at the downstream end of each study reach. Three replicate samples were collected and filtered on-site (25 mm Whatman GF/F). Samples were kept on ice in the field and then frozen within 6 h of collection. Samples were analyzed within 2 months of collection using a Dionex 1500 Ion Chromatograph for nitrate–N, phosphate–P (detection limit = 2 $\mu g \cdot L^{-1}$). Standards were run with samples to ensure analytical accuracy and reproducibility.

Chlorophyll *a*

Chlorophyll *a* accrual in summer was quantified by deploying three ceramic tiles (15 × 15 cm) every 10 m (starting at 0 m) along each 90 m reach (30 tiles total per reach) on the stream substrate. Values were averaged per 10 m location (3 tiles) and then averaged over 10 locations along the 90 m reach. Tiles were deployed mid-July allowing biofilms to colonize for approximately 4 weeks, and tiles were spaced at regular intervals and positioned within riffle sections of the stream at a depth of 10–25 cm. In situ chlorophyll *a* measurements were conducted using a BenthoTorch (BBE Moldaenke GmbH). The BenthoTorch is a portable field instrument used for the quantification of chlorophyll *a* fluorescence on different substrates and provides a real-time measurement of benthic algae concentrations and has been shown to accurately quantify periphyton biomass expressed as chlorophyll *a* ($\mu g \cdot cm^{-2}$) (Kahlert and McKie 2014). However, BenthoTorch measurements can be erroneous if tiles are assessed in direct sunlight (Kaylor et al. 2018), therefore, tiles were shaded with black buckets for a minimum of 20 min before measurement.

Stream vertebrate biomass and density

In early August each sampling year (2018, 2019, and 2021) we conducted multiple-pass depletion electrofishing surveys in which we collected fish and salamanders in each of three successive passes through the study reach. The upper and lower ends of the reach were netted to prevent movement of individuals in or out of the reach. All surveys in 2021 were conducted within 3 weeks of when that site was surveyed in 2018 and 2019. Population estimates and 95% confidence intervals were determined using maximum likelihood estimation (Carle and Strub 1978) in the Fisheries Stock Analysis package (Ogle 2022) in R (R Core Team 2021) separately for (1) age 1 + coastal cutthroat trout (hereafter "adult cutthroat"), (2) young-of-year coastal cutthroat trout (hereafter "juvenile cutthroat"), (3) coastal giant salamanders, and (4) sculpin (when present). Density (abundance per square meter) of each species or age class was calculated as the population estimate divided by mean wetted area of the study reach. Biomass per area ($g \cdot m^{-2}$) was calculated by multiplying population estimates by mean weight of the species or age class and dividing by the mean wetted area of the study reach. Estimates of total reach-scale vertebrate densities and biomass were calculated by adding the population estimates and 95% confidence intervals from all species and age groups in a reach. All individuals captured in the multiple pass depletion surveys were measured (total length to the nearest millimeter) and weighed (to nearest 0.01 g). Relative condition was calculated by analyzing the residuals from the regression equation of ln length versus ln weight of all individuals during each year. Separate regression equations were used for different species groups. Large neotenic salamanders (defined as vent length > 190 mm) were not included for calculations of weight, length, and condition of salamanders. The relative condition analysis and the juvenile cutthroat trout size analysis only included data from 2018 and 2021 because of the importance of date on juvenile size and surveys in 2018 and 2021 were at most 9 days apart for individual sites. Surveys from 2019 were conducted approximately 7 days later in the year, and data from W-122 were not collected in 2019.

Statistical analysis

To determine the effects of fire on summer stream temperatures, nutrient concentrations, chlorophyll *a* accrual, and abundance, biomass, size each vertebrate species or age group, we used a linear mixed-effects model fit by restricted maximum likelihood in the nlme package (Pinheiro et al. 2016) in R. The following statistical model was used to describe the responses.

(1) $\quad T_t = Year + Location + Year : Location + (1|Stream) + \varepsilon_t$

where ε_t is the random error term for the *t*th group, where $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$ and ε_t and $\varepsilon_{t'}$ are independent. For all response variables, the model included the fixed effects of Year (pre or post), Location (burned or reference), and the interaction term Year:Location which identifies the BACI effect of the fire. Additionally, a random effect for stream was included to account for repeated measures and inherent variation between streams. We relaxed the assumption of constant variance in the model using a weights argument for response variables that required accounting for nonconstant variance. The effect of the fire was evaluated using model estimates of the Year:Location term, and the level of statistical significance was set at $\alpha < 0.05$.

Although linear models were used for the statistical analysis, to visualize the changes before and after the fire at each stream and the magnitude of responses for reference versus burned streams for each metric, we calculated response

Fig. 2. Stream temperature before (Pre) and after (Post) the fire during the 12–30 July period at the unburned sites (McTE, Loon, and Chucksney) and the burned sites (W-113, W-100, W-122). Dotted line indicates 16 °C.
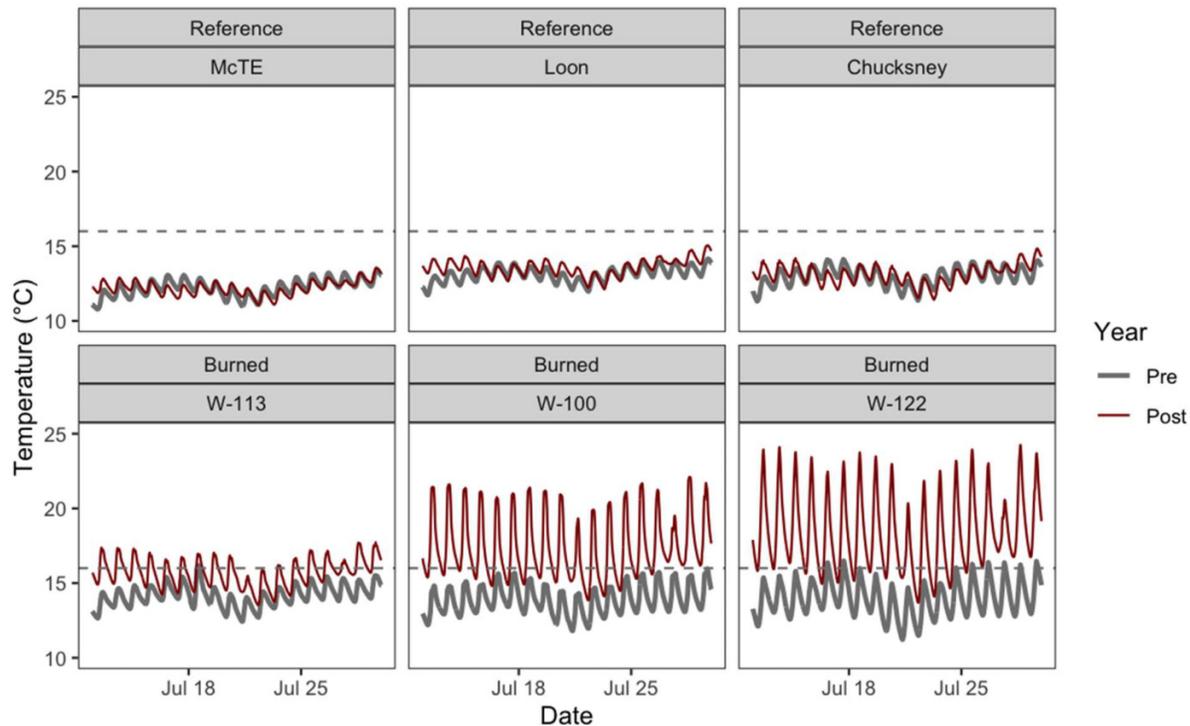
ratios. Response ratios are calculated as the value for a given metric in the year after the fire (always 2021) divided by the pre-fire value (either from 2018 or 2019) at that stream. In assessing overall ratio responses in stream temperature, chlorophyll *a*, nutrient concentrations, and juvenile length and weight values, we averaged the three response ratios for the burned and reference streams to summarize fire responses. For visualization of relative condition for each species group, we used response differences between post-fire and pre-fire because the mean residuals included negative values.

Results

Temperature, chlorophyll *a*, and nutrients

Before the fire, stream temperature at all six streams remained below 16.1 °C during the summer. After the fire, stream temperatures at the burned sites increased, whereas the unburned reference stream temperatures remained similar to pre-fire conditions (Fig. 2), resulting in a statistically significant effect of fire on daily mean, maximum, and daily range stream temperature metrics (Table 2). The average daily maximum stream temperature increased by 1.9 °C ($\pm$0.24), 5.7 °C ($\pm$0.23), and 7.3 °C ($\pm$0.26) at W-113, W-100, and W-122, respectively, with no change in daily maximum stream temperatures at the unburned sites. Similarly, the average daily mean stream temperature increased by 1.5 °C ($\pm$0.25), 3.5 °C ($\pm$0.26), and 4.5 °C ($\pm$0.30) at W-113, W-100, and W-122, respectively, with no change in mean daily temperature at the unburned sites. In addition to mean and maximum temperature increases, the daily range in temperature also

increased in the three burned sites relative to their pre-fire ranges (Fig. 2).

The temperature response was greater in the sites with higher burn severity (W-100 and W-122) than at W-113. Maximum daily temperatures in July 2021 reached 22.1 °C and 24.2 °C at W-100 and W-122, respectively, but only 17.5 °C at W-113 which was less severely burned (Table 1). Water temperatures in W-100 and W-122 only briefly exceeded 16 °C in 2018 (only 0.6% and 4.6% of the sampling period in W-100 and W-122, respectively). After the fire, W-113 exceeded 16 °C for 36.4% of this sampling period, W-100 for 70.2%, and W-122 for 82.1% of sampling period (Fig. 2). Stream temperatures exceeded 20 °C on 16 of the available 18 days in W-100 and on all 18 days in W-122. W-100 and W-122 also exceeded daytime temperatures of 22 °C and 24 °C, respectively. Stream temperatures at W-113 post-fire never exceeded 18 °C.

Before the fire (summer 2018), chlorophyll *a* accrual was largely comparable and overall consistently low across all streams (Fig. 3). However, in summer 2021, after the fire, chlorophyll *a* accrual at the burned sites increased substantially—by an average of 415% ($\pm$129%) relative to pre-fire accrual rates. In contrast, chlorophyll *a* in the unburned sites also increased slightly after the fire, but by only 28% ($\pm$5%) after the fire. Differences between chlorophyll *a* accrual between burned and unburned sites from the fire was statistically significant ($p < 0.001$, Table 2). Accrual varied among sites: W-113 increased by 320% after the fire, W-100 increased by 363%, and W-122 increased by 561%. The magnitude of the chlorophyll *a* response for the burned sites before and after the fire compared to the unburned sites was greater than any other metric evaluated here (Fig. 4). Chlorophyll *a* response

Table 2. Coefficients and effect sizes from the linear mixed-effects model for the response variables: average daily mean temperature, average daily max temperature, average daily range in temperature, mean N–NO$_3^-$ concentrations, mean P–PO$_4^-$ concentrations, and chlorophyll *a* accrual.

Response metrics		Effect	Model coefficient		Effect size	
			Estimate	S.E.	F	*p* value
Temperature	Average daily mean	Year	0.215	0.132	4.7	0.096
		Location	1.265	0.290	19.0	0.012
		Year:Location (Fire)	2.965	0.872	11.6	0.027
	Average daily max	Year	0.200	0.162	2.4	0.199
		Location	1.991	0.357	31.1	0.005
		Year:Location (Fire)	4.772	1.618	8.7	0.042
	Average daily range	Year	− 0.050	0.776	5.9	0.073
		Location	1.232	1.135	6.9	0.058
		Year:Location (Fire)	2.760	1.098	6.3	0.066
Concentrations	N–NO$_3$	Year	− 0.003	0.002	3.1	0.155
		Location	0.088	0.023	4.4	0.104
		Year:Location (Fire)	− 0.049	0.013	13.3	0.022
	P–PO$_4$	Year	0.002	0.001	1.1	0.362
		Location	− 0.002	0.009	0.1	0.756
		Year:Location (Fire)	− 0.001	0.002	0.6	0.498
Chlorophyll *a*	Chl*a*	Year	0.002	0.003	104.4	0.001
		Location	0.000	0.006	9.0	0.040
		Year:Location (Fire)	0.032	0.004	79.9	0.001

Note: Year (pre or post-fire), Location (inside or outside the fire boundary) Year:Location are fixed effects where Year:Location (post-fire and inside the fire boundary) represents the interaction term for the effect of the fire.

Fig. 3. Means and standard deviations of chlorophyll *a* accrual on tiles every 10 m along stream reaches in the summer before (Pre) and the summer after (Post) the fire at the unburned sites (McTE, Loon, and Chucksney) and the burned sites (W-113, W-100, W-122).
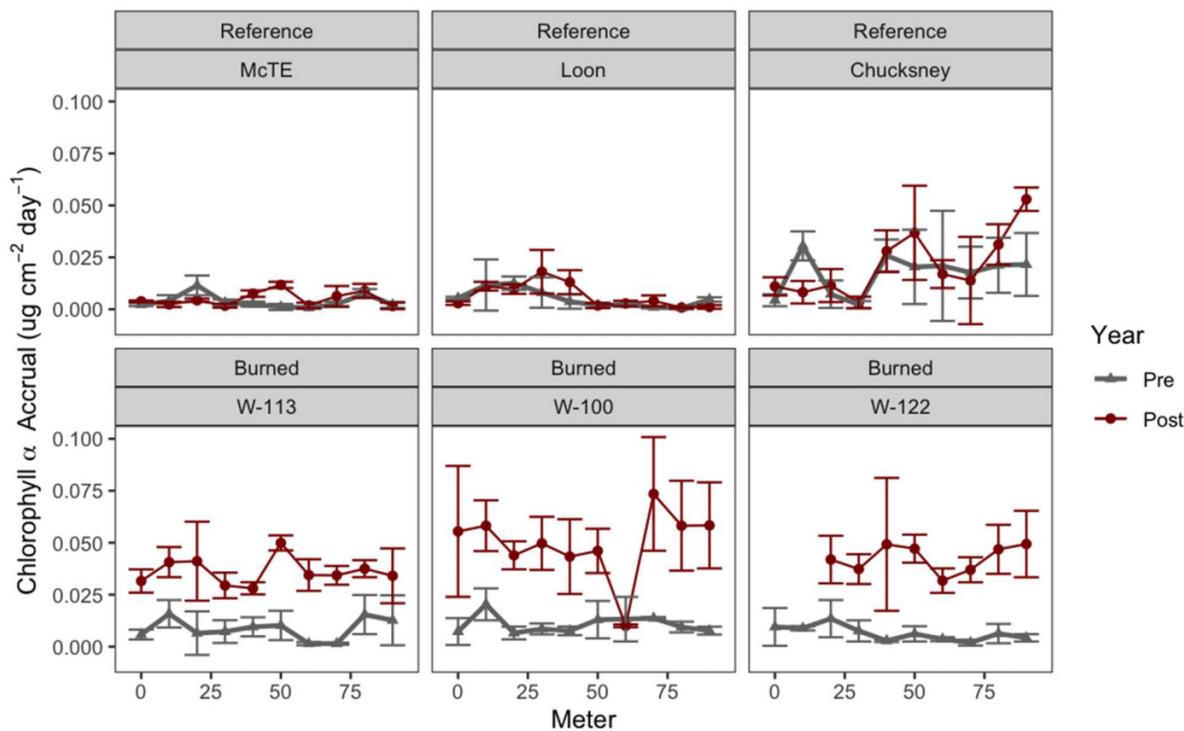
Fig. 4. Average response ratios (from 2021 to 2018) of the burned and unburned sites for averages of the daily maximum temperatures, mean temperatures, ranges in temperatures, nitrate–N, phosphate–P, and chlorophyll *a* accrual.
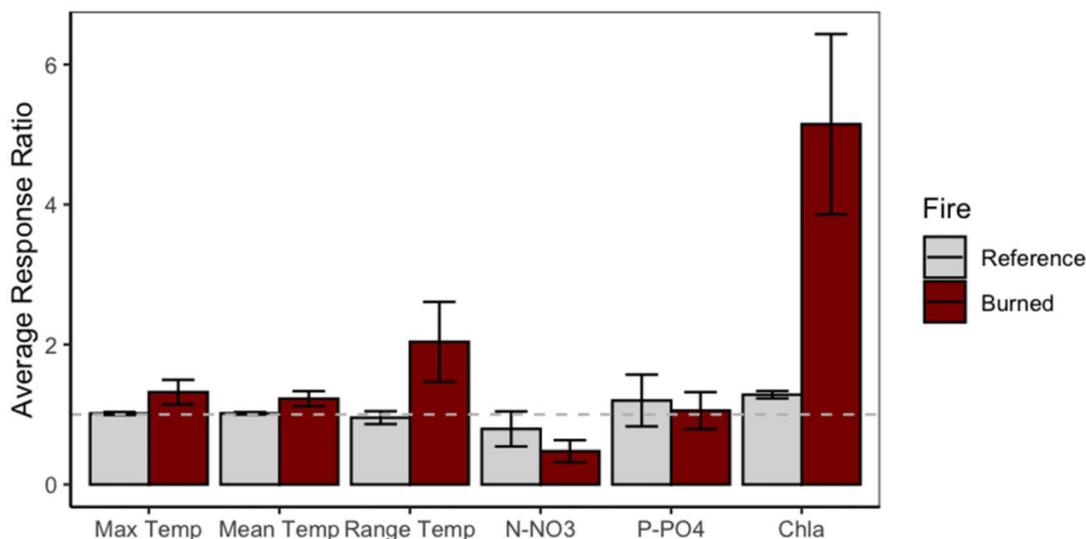
Fig. 5. Biomass (*a*, *b*) and density (*c*, *d*) response ratios comparing the post-fire year (2021) to each of the two pre-fire years 2018 (*a*, *c*) and 2019 (*b*, *d*) at each stream for separate species groups (CT, adult cutthroat trout; DC, salamanders; TV, total vertebrates; YOY, juvenile cutthroat trout).
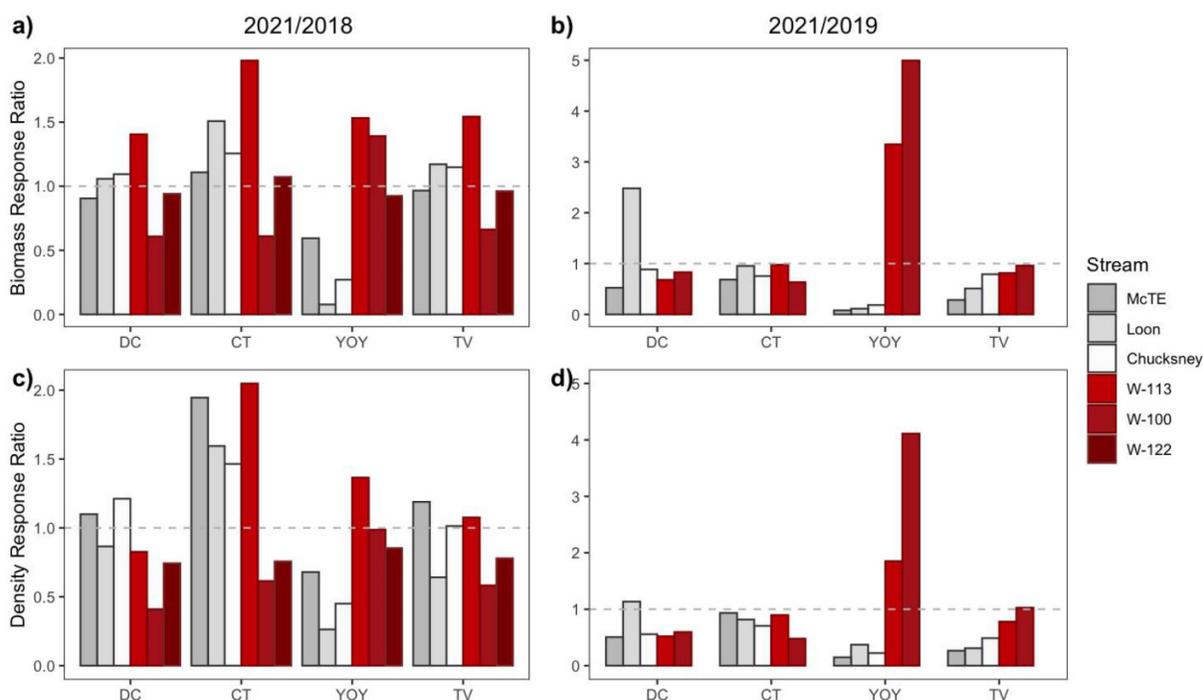
among the three burned sites corresponded to burn severity, with the greatest increase in chlorophyll *a* at the most severely burned site (W-122), and the smallest increase at the least severely burned site (W-113).

Stream nitrate–N concentrations decreased significantly at the burned streams after the fire (Table 2, Fig. 4); however, stream phosphate–P concentrations in burned sites relative to unburned sites within each year from a mid-summer low-flow sampling event did not change significantly as a result of the fire (Table 2).

Vertebrates

Collectively, aquatic vertebrates did not have a response to the fire in the year following the event. In the BACI linear model the Year:Location interaction term representing the effect of the fire was not statistically significant for biomass (g·m^{-2}) or density (abundance per square meter) estimates of adult coastal cutthroat trout, Pacific giant salamanders, and total vertebrates (Fig. 5, Table 3). Variability among years and among streams affected these metrics more than the effect of the fire (Table 3). However, juvenile cutthroat trout re-

Table 3. Coefficients and effect sizes from the linear mixed-effects model for the vertebrate response variables: biomass of adult cutthroat trout (CT), juvenile cutthroat trout (YOY), salamanders (DC), total vertebrates (TV) and mean length and weight of juvenile cutthroat trout (YOY).

Response metrics	Species Group	Effect	Model coefficient		Effect size	
			Estimate	S.E.	F value	*p* value
Biomass	CT	Year	0.001	0.007	<0.1	0.973
		Location	− 0.004	0.010	0.2	0.682
		Year:Location (Fire)	− 0.001	0.010	<0.1	0.933
	YOY	Year	− 0.003	0.001	16.3	0.003
		Location	0.005	0.002	93.5	0.001
		Year:Location (Fire)	0.009	0.003	10.9	0.009
	DC	Year	− 0.004	0.005	0.7	0.419
		Location	0.042	0.026	2.8	0.172
		Year:Location (Fire)	− 0.005	0.013	0.2	0.701
	TV	Year	− 0.029	0.019	8.4	0.018
		Location	0.036	0.027	6.5	0.063
		Year:Location (Fire)	0.020	0.037	0.3	0.604
Mean length	YOY	Year	− 6.533	2.889	0.2	0.673
		Location	16.335	5.071	22.3	0.009
		Year:Location (Fire)	11.207	4.086	7.5	0.051
Mean weight	YOY	Year	− 0.409	0.229	<0.1	0.994
		Location	1.225	0.359	25.9	0.007
		Year:Location (Fire)	0.816	0.324	6.3	0.065

Note: Year (pre or post-fire), Location (inside or outside the fire boundary), Year:Location are fixed effects where Year:Location (post-fire and inside the fire boundary) represents the interaction term for the effect of the fire.

Fig. 6. (*a*) Average differences of the post-fire year (2021) compared to the pre-fire year (2018) for mean relative condition (residuals of ln length versus ln weight relationship during each year) of adult cutthroat trout (CT), salamanders (DC), and juvenile cutthroat trout (YOY), and (*b*) average response ratios (post-fire/pre-fire) of mean length and weight of juvenile cutthroat trout.
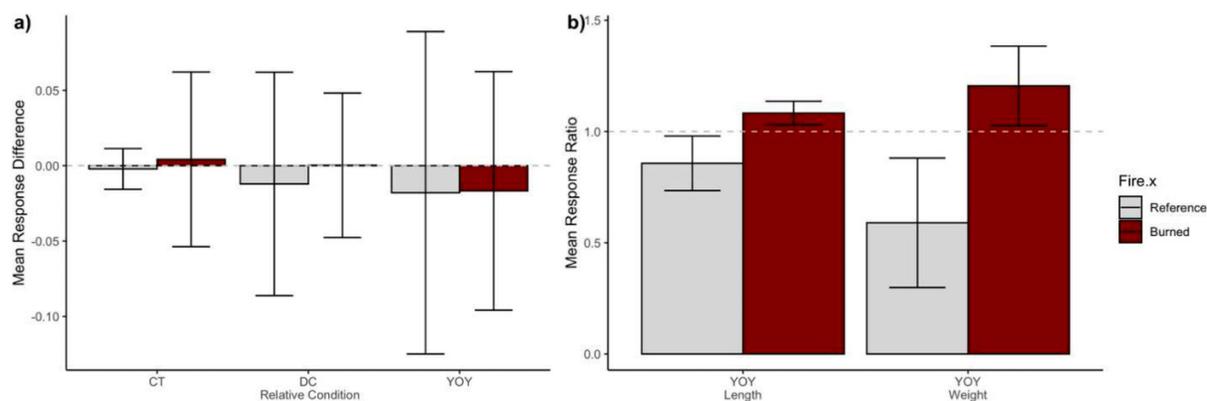
sponded post-fire with significant increases in both biomass and density (Table 3). Response ratios (post-fire year/pre-fire year) were 2–20 times larger for burned sites than unburned sites (Fig. 5).

Although the collective analysis indicated no statistically significant effect of wildfire on adult coastal cutthroat trout when all sites were combined, when assessed individually, results from two of the three impacted sites suggested a negative response to the fire. Adult coastal cutthroat and Pacific giant salamander density and biomass in 2021 decreased at both W-100 and W-122 relative to pre-treatment

data in 2018; however, when evaluating changes in 2021 to pre-treatment data in 2019, differences between burned and reference streams were not statistically significant. Conversely, at W-113 adult cutthroat and salamander density and biomass increased post-fire (Fig. 5).

Mean relative body condition was not affected by the fire for any of the species groups including juvenile cutthroat trout (Fig. 6). However, the size of juvenile coastal cutthroat trout were greater in burned sites following the fire as length increased (11.2 ± 4.1 mm, $p = 0.05$) and weight increased (0.8 ± 0.3 g, $p = 0.07$) (Table 3, Fig. 6).

Discussion

Pre-existing stream surveys and the serendipitous occurrence of wildfire provided the opportunity to conduct a study evaluating the effects of wildfire on multiple abiotic and biotic responses in forested headwater stream ecosystems using a BACI study design. In evaluating short-term (1 year) responses to wildfire at three burned streams, we found large increases in stream temperature, chlorophyll *a*, and juvenile coastal cutthroat trout biomass, density, mean weight, and mean length compared to three unburned reference streams (Table 2). There were no collective statistically significant effects of fire on adult coastal cutthroat trout, Pacific giant salamanders, or total vertebrate biomass, as these responses varied across the three burned streams (Fig. 5). Overall the increases in both chlorophyll *a* and juvenile coastal cutthroat trout abundance and biomass provide striking evidence to partially support the hypothesis that increased primary production resulting from reduced light limitation mitigates thermal stress or even has a positive effect on vertebrate populations and biomass via increased food availability through bottom-up drivers.

Temperature

The elevated stream temperatures in burned areas where canopy shading was reduced or lost were well above the thermal conditions that coastal cutthroat trout and salamanders commonly experience in this region (Huff et al. 2005). Large increases in average daily maximum and mean stream temperatures occurred in the burned study sites during our study period (maximum temperature increases of 1.9 °C–7.3 °C and mean temperature increases of 1.5 °C–4.5 °C) (Fig. 2). The increases observed in our study were greater than those documented in a number of other fire studies but were not unprecedented. In western regions including Montana, Colorado, Idaho, north-central Washington, and the Canadian Rocky Mountains, daily maximum stream temperatures between 1.3 °C and 6.0 °C were observed in the first few years post-fire (Helvey 1972; Burton 2005; Mahlum et al. 2011; Rhoades et al. 2011; Sestrich et al. 2011; Wagner et al. 2014). In Yellowstone National Park, post-fire temperatures at burned sites regularly exceeded 20 °C in the first 5 years after the fire (Minshall et al. 1997), consistent with post-fire temperatures in two of the three streams in the current study.

Burn severity corresponded to the increases in stream temperature amongst our three streams, which is consistent with other fire studies that have linked temperature increases to the amount of basin burned at moderate to high severity (Gresswell 1999; Sestrich et al. 2011; Rieman et al. 2012). Although the change in light availability is likely the strongest control on stream temperature responses, position in the watershed, and stream size may also be noteworthy (Dunham et al. 2003; Bixby et al. 2015; Koontz et al. 2018). In our analysis, the smallest burned stream had the smallest temperature response and the largest stream had the largest temperature response (Fig. 2). This pattern contrasts with an earlier study at these sites on temperature responses to canopy removal in which stream size was more important than canopy openness in evaluating the effects of canopy gaps on thermal regimes

(Swartz et al. 2020). We attribute this discrepancy primarily to both the amount of riparian canopy loss and the extent of the fire impact throughout the network. The amount of canopy removal by Swartz et al. (2020) was relatively consistent across sites, but in the present study, varying fire severity led to differences in the amount of remaining canopy cover and subsequent changes in solar radiation. Also, as temperature effects from riparian disturbances can often manifest more explicitly downstream (Roon et al. 2021), the temperature responses in the larger streams are likely reflecting a broader extent of effects from the loss of streamside shading upstream as well as locally within the reach.

Chlorophyll *a* and nutrients

Chlorophyll *a* accrual increased significantly in burned streams following the Holiday Farm Fire likely because of the release from light limitation and the increase in stream temperature from the burning of the riparian canopy. The results from this study are striking in the magnitude of the primary producer response, but generally consistent with experimental riparian forest canopy removal studies from this region (Kiffney et al. 2003; Ambrose et al. 2004; Wootton 2012) and with other studies quantifying benthic biofilm responses to fire (Minshall et al. 2001; Simpson and Cooper 2006; Verkaik et al. 2013; Cooper et al. 2015; Klose et al. 2015). Although a major driver of autotrophic responses to fire is linked to burn severity in the riparian zone (Cooper et al. 2015), other factors such as nutrient availability or scour associated with debris flow following fire provide strong controls on whether chlorophyll *a* increases or decreases post-fire and how long it takes for primary producers to recover (Minshall et al. 1997; Bêche et al. 2005; Tuckett and Koetsier 2016; Harris et al. 2018; Williams Subiza and Brand 2018). Low nutrient availability may limit development of benthic biofilms post-fire despite the persistence of open canopies (Malison and Baxter 2010). We did not see clear inhibition of a biofilm response due to nutrient availability, but the strong increase in primary producers may have interacted with the nutrient response. In our study, scour was not likely to have been an important factor, as winter in 2020–2021 in this region was abnormally dry. While the specific streams assessed here do not have long-term flow data, they are all within 25 km of a long-term USGS gage on Lookout Creek which is within the same western Cascades McKenzie River catchment and experiences similar precipitation patterns and events. The winter of 2020–2021 had the lowest peak discharge of the past 20 years at Lookout Creek, and since 1963, there have only been two other winters that had lower peak flow (Fig. S2). In the Mediterranean climate of western Oregon summers are very dry with no precipitation events large enough to create substantial scour (Fig. S2).

Many studies have reported increasing exports of both nitrogen and phosphorus after a fire (Hauer and Spencer 1991). In our study, wildfire resulted in minor but statistically significant declines in nitrate–N concentrations in burned streams (Fig. 4, Table 2). Unfortunately, we are restricted to data on stream concentrations and cannot calculate fluxes or total losses over time. Nitrogen is the dominant limiting nutri-

ent in these streams, and given the magnitude of the autotrophic response and the clear link between increasing light availability and increased nutrient demand (Hill et al. 2010; Matheson et al. 2012; Warren et al. 2017), we hypothesize that the decline we observed was due to increased demand by stream autotrophs. Phosphorus is not commonly a limiting nutrient in these systems and we saw no significant changes in phosphate–P concentrations.

Vertebrates

When considering our three replicate burned sites together in the collective BACI analysis, we found little support for the hypothesis that increased summer temperatures negatively affect coastal cutthroat trout and salamander density, biomass, or condition in the three study sites. However, when evaluating sites individually, we documented declines in adult cutthroat trout and Pacific giant salamander biomass and density in the two streams (W-100 and W-122) that regularly experienced temperatures above 21 °C (Fig. 5). It is noteworthy that despite these relative declines, adult coastal cutthroat trout population abundance and biomass were not severely depressed, and we found no evidence that coastal cutthroat trout or Pacific giant salamanders were extirpated from the sites that experienced substantial temperature increases during the first summer following the fire. These negative responses were apparently offset in the collective analysis by the less severely burned stream (W-113) where stream temperature increases were moderate (did not exceed 17.5 °C) and adult coastal cutthroat trout and Pacific giant salamanders increased after the fire.

Mixed responses to fire are not unprecedented, as the influence of multiple changes to aquatic habitat and fire severity has led to both positive and negative fish responses to fire ranging from extirpation and mortality (Bozek and Young 1994; Rinne 1996; Minshall et al. 1997; Cooper et al. 2015), to increases in density, biomass, or growth (Dunham et al. 2003; Heck 2006; Howell 2006; Rieman et al. 2012). Fish mortality after fire is often associated with debris flow events that occur in conjunction with high flows when a pulse of ash and sediment leads to decreased dissolved oxygen availability (Reale et al. 2015), but as previously mentioned, in western Oregon there is little to no rain in the summer and the 2020–2021 winter season between the time of the fire and our data collection period was very dry relative to most winters in the region (Fig. S2). Further, we did not observe major changes in channel reorganization or physical habitat, and although many standing-dead trees were located adjacent to the stream, few had been recruited to our reaches. With the lack of large geomorphic responses after the fire, we are able to focus here on 1 year responses that are predominately due to the removal of shade by riparian canopies.

Laboratory studies have found thermal tolerance upper limits for different strains of cutthroat trout to range from as low as 19.6 °C for west-slope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Colorado to 25.7 °C for coastal cutthroat trout (Golden 1978; Dickerson and Vinyard 1999; Wagner et al. 2001; Bear et al. 2007), and the persistence of fish post-fire is not uncommon (e.g., Gresswell 1999; Dunham et al. 2003;

Rieman et al. 2012). However, even if temperatures are below the lethal limit, substantial post-fire temperature increases can result in stressful conditions for coastal cutthroat trout and other coldwater salmonids (Dunham et al. 2007; Sestrich et al. 2011; Beakes et al. 2014; Rosenberger et al. 2015). Summer stream temperatures from the burns sites were well above the central realized thermal niche for coastal cutthroat trout in the Cascades ecoregion (which is a mean of 14.2 °C and an upper limit of 16.2 °C) (12.0 °C and 14.2 °C, respectively, for Pacific giant salamanders) (Huff et al. 2005). Therefore, although the post-fire temperatures in the current study did not reach lethal thresholds, they were potentially stressful, yet these species persisted after the fire across all of the burned locations.

The persistence of coastal cutthroat trout and Pacific giant salamanders in high temperature post-fire conditions may be to some extent due to thermal refuge from cold groundwater (Ebersole et al. 2001) and diel fluctuations with cooler temperatures at night that allow fish to recover physiologically (Dickerson and Vinyard 1999; Johnstone and Rahel 2003; Schrank et al. 2003). However, thermal refuges in our streams are likely too small to sustain the same densities seen in pre-fire conditions. And, while temperatures declined at night, in W-100 and W-122 the average night-time minima exceeded pre-fire maxima and generally remained above 15 °C. In addition to potential refugia, we suggest that the persistence of trout in these systems after fire was related to food availability and consumption. Food availability and consumption rate are key controls on fish growth and can have a more prominent impact than alteration of the thermal regime (Railsback and Rose 1999; Beauchamp 2009; Leach et al. 2012; Railsback 2022). We hypothesize that the increase in basal resource availability (chlorophyll *a* accrual) driven by high light (and possibly elevated watershed nutrients) and warmer temperatures led to increased invertebrate abundance, biomass, and growth, which led to greater consumption by coastal cutthroat trout and Pacific giant salamanders. Although we did not collect invertebrate data directly in this study, other researchers have found increased secondary production after wildfire with potential associated increases in fish production (Minshall 2003; Malison 2008; Malison and Baxter 2010; Rieman et al. 2012), and we note that potential connections between increased resource availability and thermal tolerances is an area for future research in understanding fish responses to fire and other disturbances.

When evaluating sites individually, adult cutthroat trout and salamanders increased at W-113 where temperatures never exceeded 17.5 °C (Fig. 5). We attribute this to a temperature regime that remained within the thermal optima for trout for the majority of the time such that increased consumption could compensate for elevated metabolic demand. This response aligns with previous work on rainbow trout (*Oncorhynchus mykiss*) in similar headwater systems which found that if food is abundant, growth increases with increasing temperature up to approximately 17 °C (Wurtsbaugh and Davis 1977). The response also aligns with riparian forest removal studies that also found increased vertebrate responses despite moderate temperature increases (Wilzbach et al. 2005).

Declines in fish and salamander biomass in the two streams that regularly exceeded 21 °C may be due to temperatures consistently exceeding optimal thermal ranges for growth (14 °C–16 °C) (Bear et al. 2007). W-100 and W-122 exceeded 16 °C (the coldwater criterion in these stream systems, ODEQ 2004), 70% and 82% of the study period after the fire, so the vertebrates in these streams experienced summer thermal conditions well above optimal temperatures even if food availability was adequate. W-100 and W-122 also contain sculpin, but at both sites the post-fire abundance and biomass estimates were within the 95% confidence interval of the most recent pre-fire estimate. Therefore, although we do not have reference data available, we did not observe fire effects on sculpin populations or biomass. We suggest that the variation in adult cutthroat trout and salamander responses among the burned sites after the fire was a result of the duration and magnitude of thermal stress that remained within a near optimal condition in one site but was consistently exceeded in others.

In contrast to adult fish, juvenile coastal cutthroat trout biomass, density, mean weight, and mean length increased post-fire (Fig. 6b). The increase in density is likely due to a number of factors including greater basal resource availability and earlier insect emergence (Malison and Baxter 2010; Harris et al. 2018). In addition the removal of most trees in a catchment (whether due to fire or forest management) can lead to greater summer baseflow discharge in the first few years after the loss of trees (Lavabre et al. 1993; Seibert et al. 2010; Niemeyer et al. 2020), and this could also potentially increase summer habitat availability for small fish by creating more interstitial spaces and lateral stream habitat (Bateman et al. 2018). The increase in the average size of juvenile individuals (11.2 ± 4.1 mm in length and 0.87 ± 0.25 g in weight, Table 1) may be related to earlier emergence and longer growing season as a result of increased light and water temperature in the spring after the fire, which is consistent with other studies showing larger juvenile sizes at age in systems with declines in riparian shading (Holtby 1888; Heck 2006; Armstrong et al. 2021). The 1 year post-fire increases in both size and density of juvenile coastal cutthroat may be an important source of population resilience to fire in systems that experience severe declines in adult fish, especially as greater juvenile size has been linked to greater rearing, and for anadromous species, greater emigration survival (Zabel and Achord 2004; Ebersole et al. 2006; Monzyk et al. 2009; Pess et al. 2011).

Conclusions

By evaluating responses across three replicate sites using a BACI study design, we explored a collective response to fire. While the temperature and primary production responses were clear and generally consistent across burned streams, we found that vertebrate responses were not consistent, likely due to local habitat dynamics, fire severity, and upstream effects of fire that were beyond our sampling frame. Neither coastal cutthroat trout nor Pacific giant salamanders were extirpated from any of the systems, but the winter post-fire was anomalously dry with few high flow events to mo-

bilize sediment. These findings expand our understanding of the thermal stream conditions in which coastal cutthroat trout and Pacific giant salamanders can persist while adding to the growing body of empirical data quantifying how different components of the stream ecosystems initially respond to fire. Our data support the suggestion that fish in these systems are resilient to this type of disturbance; however, temperature increases that are not accompanied by increased food availability may pose greater threats to aquatic vertebrate populations. The differential response of juvenile and adult fish seen here also suggests population-level resilience even if the adult fish are negatively affected in systems with large temperature increases. Further work following the 2021 cohort will help elucidate the degree to which population resilience may be supported by the response of juvenile fish.

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Article information

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Data availability

All portions of the data presented here will be made publicly available at the H.J. Andrews Experimental Forest Data Archive (https://andrewsforest.oregonstate.edu/data).

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