Wildfire and the effects of shifting stream temperature on salmonids

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Abstract.   The frequency and magnitude of wildfires in North America have increased by four-fold over the last two decades. However, the impacts of wildfires on the thermal environments of freshwaters, and potential effects on coldwater fishes are incompletely understood. We examined the short-term effects of a wildfire on temperatures and Steelhead/Rainbow Trout (*Oncorhynchus mykiss*) bioenergetics and distribution in a California coastal stream. One year after the wildfire, mean daily stream temperatures were elevated by up to 0.6°C in burned compared to unburned pools. Among burned pools, light flux explained over 85% of the variation in altered stream temperatures, and 76% of the variation in light flux was explained by an index of burn severity based on proximity of the pool to burned streamside. We estimated that salmonids of variable sizes inhabiting burned pools had to consume between 0.3–264.3 mg of additional prey over 48 days to offset the 0.01–6.04 kJ increase in metabolic demand during the first post-fire summer. However, stomach content analysis showed that fish in the burned region were consuming relatively little prey and significantly less than fish in the reference region. Presumably due to starvation, mortality, or emigration, we found a significant negative relationship between the change in total salmonid biomass over the post-fire summer and the average energy costs (kJ·g^{-1}·day^{-1}) within a burned pool. This study demonstrates that wildfire can generate thermal heterogeneity in aquatic ecosystems and drive short-term increases in stream temperature, exacerbating bioenergetically stressful seasons for coldwater fishes.

Key words: bioenergetics; climate change; disturbance; endangered species; fire; landscape ecology; riverscape; riparian.

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INTRODUCTION

The frequency and duration of large wildfires in Western North America has increased by nearly four times over the last two decades (Westerling et al. 2006). This dramatic increase could be driven by altered land-use, changes in patterns of precipitation, and increases in temperature (Westerling et al. 2006). Under current IPCC climate scenarios, the frequency and duration of wildfires in North America is expected to continue increasing (Running 2006, Meehl et al. 2007). For example, wildfire burn areas are predicted to increase by an additional 78–118% over the next century in Canada (Flannigan et al. 2005); thus, we need to better

understand how wildfire affects ecosystems and vulnerable species. In this warming world, how do wildfires contribute to warming temperatures for thermally sensitive species?

Wildfire can increase temperatures in aquatic ecosystems from 0° to 15°C on short and protracted time scales (Gresswell 1999, Isaak et al. 2010), via different putative mechanisms (Gresswell 1999, Dunham et al. 2007). For example, immediate temperature change in aquatic systems during a wildfire is controlled by convection, the fire's intensity, and the volume of water in the burned region (Rieman and Clayton 1997). The degree of protracted warming, in contrast, is hypothesized to depend on burn severity, stream channel reorganization, the volume of burned riparian vegetation, and the subsequent increase in solar radiation (Minshall et al. 1989, Rieman and Clayton 1997, Gresswell 1999, Dunham et al. 2007). However, the effects of wildfire across a burned landscape are often heterogeneous, leading to disparate local alterations in stream temperatures. For example, Dunham et al. (2007) analyzed a set of temperature data collected before and after wildfires in the Boise River Basin of central Idaho, USA and found that fire heterogeneously increased stream temperatures from 0.4° to 3.7°C. The authors hypothesized that the variation among sites was partly attributed to secondary disturbances such as channel reorganization and changes in channel morphology, as well as to spatial variability in burn severity and degree of recovery of streamside vegetation (Dunham et al. 2007). Studies similar to Dunham et al. (2007) that have temperature data from both before and after a wildfire are uncommon. As such, our understanding of the short- and long-term effects of wildfire are based on limited information, especially regarding the conservation and management of thermally-sensitive species (Minshall et al. 1989, Dunham et al. 2003).

Salmonids are ecologically important and thermally sensitive stream fishes (Baxter et al. 2004, Meissner and Muotka 2006, Isaak et al. 2010, Wenger et al. 2011). Populations of numerous salmonid species are declining throughout their historical range due partly to thermal exclusion from spawning and rearing habitat (Gustafson et al. 2007, Isaak et al. 2010, Wenger et al. 2011). Although wildfires usually do not cause direct mortality of salmonids, they can contribute significantly to warming waters well after the fire is over (Gresswell 1999, Dunham et al. 2007, Isaak et al. 2010). For example, Isaak et al. (2010) found that both large-scale climate forcing and wildfire were associated with warmer headwater streams in the Boise River basin Idaho, USA, and predicted that these temperature changes have resulted in the loss of 11–20% of spawning and rearing habitat for Bull Charr (Salvelinus confluentus) over the last two decades. In that study, wildfire contributed to approximately nine percent of the warming trend in burned regions (Isaak et al. 2010). Thus, climate warming and wildfire additively elevate temperatures in coldwater habitats, which will likely affect thermally sensitive species (Rieman et al. 2003, Isaak et al. 2010, Mahlum et al. 2011). Consequently, several species of trout and salmon in the USA are expected to lose between 11% and 77% of suitable coldwater habitat due to climatic warming by the 2080s; however, the role of wildfire in contributing to shifting thermal environments remains uncertain (Dunham et al. 2003, Isaak et al. 2010, Wenger et al. 2011).

Here we examine the short-term effects of wildfire on temperatures and Steelhead/Rainbow Trout (Oncorhynchus mykiss) bioenergetics and distribution in a California coastal stream. A wildfire in 2009 burned a major tributary of the Scott Creek watershed in central California that we were actively studying, thereby providing the opportunity to compare mean daily stream temperatures before, during, and after a wildfire at numerous locations in the burned region (Fig. 1). We asked three interrelated questions: How does wildfire alter stream temperatures? Does spatial variation in fire intensity drive spatial heterogeneity in stream temperatures and fish bioenergetics? How do coldwater fishes respond to fire-mediated temperature changes? This case study provides a close look at the effects of wildfire on local temperature dynamics and illuminates linkages between disturbance and abiotic and biotic responses.

METHODS

Study system

The Lockheed wildfire burned approximately 41% (32 km²) of the Scott Creek watershed from
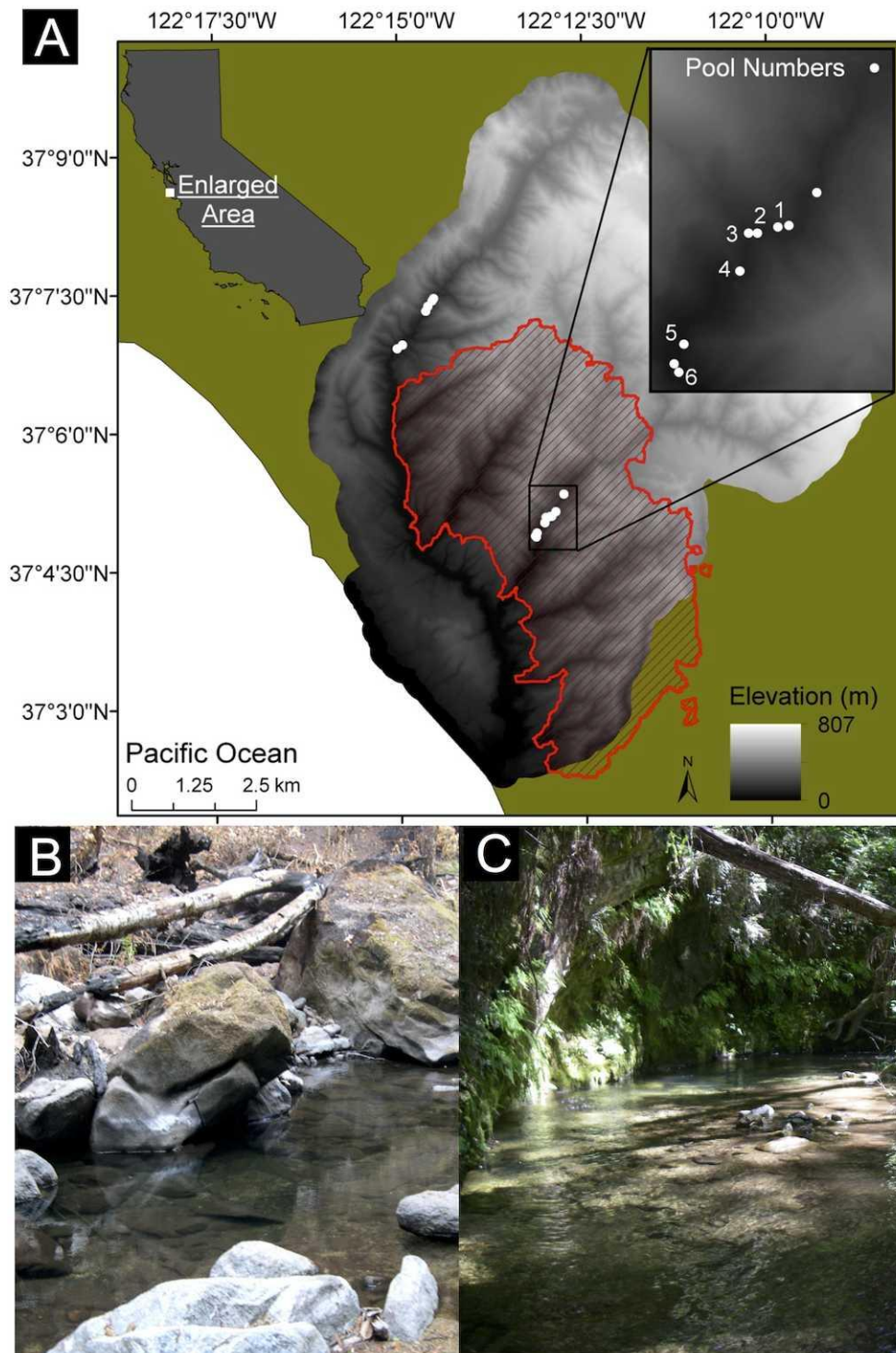
Fig. 1. Map of Scott Creek, California, and study pools labeled 1–6 in the burned region and unlabeled reference pools located outside the indicated burn region (A). Unlabeled pools in the burned area were added in summer of 2010. The burn extent of the Lockheed wildfire (2009) is outlined in a red-hatched polygon. Also depicted are images of a (B) burned pool and (C) representative reference pool.

August 12 to 23, 2009 (Fig. 1). Scott Creek is a precipitation-dominated central California coastal stream that drains 78 km² of the Santa Cruz Mountains into the Pacific Ocean and contains Endangered Species Act (ESA)–listed Steelhead/Rainbow Trout (*O. mykiss*, listed as threatened) and the southernmost population of Coho Salmon (*O. kisutch*, ESA listed as endangered). The drainage area, mean annual discharge, riparian vegetation, and fish communities of Scott Creek are similar to other small coastal streams in California (Sogard et al. 2012). We conducted our study over the summer, during which California coastal streams are considered stressful for salmonids due to low flow, low prey availability, and seasonally high water temperatures (Grantham et al. 2012, Sogard et al. 2012, Sloat and Osterback 2013). Previous studies have reported negative growth rates and low survival of young-of-the-year salmonids during California summers partly due to bioenergetic stress, highlighting that small temperature changes may have important consequences for growth and survival (Hayes et al. 2008, Sogard et al. 2009, Sloat and Osterback 2013). We focus on six stream pools within the burned area that we had been monitoring prior to the wildfire (Fig. 1B, Big Creek tributary; pool length 11.3 ± 1.4 m [mean ± SE]) and six pools that were at least 1 km from the wildfire burn perimeter (Fig. 1C, Upper Scott Creek; pool length 9.2 ± 1.8 m). Prior to the wildfire, the pools in the burned and reference regions had similar canopy cover and morphology, and they were located in tributaries with similar aspect and catchment areas (Fig. 1). Thus, this disturbance presented us with a natural "experiment" to examine the effects of wildfire on stream temperatures and salmonids in a representative California coastal stream.

Wildfire and abiotic responses

We collected hourly temperature (°C) and light (lumen·m⁻²) data before, during, and after the wildfire in burned and unburned pools with Onset corp. HOBO Pendant Temperature/Light Data Loggers. For analysis, we focus on three periods during the summer months, "pre-fire" (July 8–August 11, 2009), "during fire" (August 12–23, 2009), and "post-fire" (July 15–August 31, 2010). Within each time period we compared mean daily stream temperatures from each burned pool to the average of mean daily stream temperatures across all unburned pools. Hereafter, we refer to the unburned pools collectively as the "reference region". Using multiple linear regression in program R (R Development Core Team 2011), we regressed the daily temperatures in the burned region against the daily reference temperatures, with categorical factors for the discrete time periods (i.e., pre- vs. post-fire "Fire") and individual burned pools ("Pool ID"). In essence, this approach uses the reference region temperatures as a control. Using Akaike Information Criterion corrected for small sample sizes (AICc), we compared the performance of the most complex model, including all factors and interactions between them, to a candidate set of sub models (Table 1). We identified models of greater parsimony by assuming that a lower AICc score is indicative of a better balance between model fit and model complexity. We accepted a more complex model only if the AICc score was more than four units lower than a simpler model (Burnham and Anderson 2002) and used the most parsimonious model to estimate the degree of temperature change in burned pools relative to the reference region temperatures.

We compared changes in stream temperatures and light level to assess if changes in solar radiation were associated with changes in temperature, and we compared changes in light level with an index of burn severity to assess if the proximity of charring or burned vegetation to the stream was related to changes in solar radiation. Immediately after the wildfire (September 2009), we measured the minimum distance (meters, m) from the water's edge of each pool in the burned region to the nearest indication of charring or burned vegetation; as such, the proximity of burn evidence served as an index of burn severity. We used linear regression to estimate how much of the observed variation in temperature change was explained by light flux (the difference in median light level between the pre- and post-fire time periods), and how much of the observed variation in light flux was explained by our index of burn severity.

Salmonids and stream temperatures

In the summer after the wildfire we conducted single pass electrofishing in burned and reference

Table 1. The competing models, ranked in order of AICc, used for predicting pool-specific changes in temperature after the wildfire.

Rank	Model parameters	df	AICc	ΔAICc
1	RT+ F + PID + F:RT + F:PID + RT:PID	15	−479.1	0
2	RT+ F + PID + F:PID	14	−478.2	0.9
3	RT+ F + PID + F:RT + F:PID + RT:R + RT:F:PID	25	−463.6	15.5
4	RT+ F + PID	9	−314.0	165.1
5	RT+ F	4	−254.4	224.7
6	RT+ F + RT:F	5	−254.2	224.9
7	RT+ PID	8	−81.5	397.6
8	RT	3	−47.0	432.1
9	Null	2	1005.2	1484.3

Note: Parameters are defined as Reference Temperatures (RT), Time factor before vs. after the wildfire (F), Pool ID (PID).

pools during two periods (June 2010 and September 2010) to collect, measure, and tag salmonids. We added four pools to the original six burned pools (Fig. 1A inset) and two pools in the reference region to bolster our dataset. We blocked each pool with small mesh nets at the upstream and downstream ends, and electro fished upstream from the tail of each pool. All captured salmonids were lightly anesthetized (MS 222) and measured (fork-length, mm, and weight, g). Single-pass electrofishing can provide relatively accurate estimates of fish abundance when sampling short reaches on small streams (Sály et al. 2009), but due to unknown capture probabilities among sites and regions we could not precisely estimate pool-level or regional fish densities. Thus, we consider the difference in total salmonid biomass in each burned pool between sampling events as an index of change over the post-fire summer. We also evacuated the stomach contents of salmonids longer than 55 mm fork-length (FL) via gastric lavage to estimate prey consumption. Salmonids longer than 65 mm were tagged with full duplex Passive Integrated Transponder tags (Allflex corp.). Recaptures in September allowed us to estimate individual growth over the summer.

We used bioenergetics models to explore the energetic costs of fire to fish. With the algorithm and coefficients from Hanson et al. (1997), we estimated the specific rate of respiration (R, $kJ·g^{-1}·day^{-1}$) for *O. mykiss*, where R is a function of the allometric mass function intercept ($a = 0.00264$, $g·g^{-1}·d^{-1}$), fish mass (W, g), the slope of the allometric mass function ($b_1 = -0.217$), a temperature dependent coefficient of consumption ($b_2 = 0.06818$), water temperature (T, °C), and an oxycalorific coefficient (13.56, $kJ·g$ oxygen^{-1})

to convert from consumed oxygen to consumed energy (Hanson et al. 1997; Eq. 1).

$$R = aW^{b_1} \times e^{b_2 T} \times 13.56.$$

Using pool-specific estimates of temperature change from before and after the wildfire in the burned region, we calculated the change in energetic costs (kJ) for salmonids in each burned pool. Specifically, we calculated daily values of R ($kJ·g^{-1}·day^{-1}$) using mean daily stream temperatures from July 15 to August 31, 2010 for the mass of each fish observed during the June and September electrofishing samples. We multiplied R by each observed fish mass to estimate $kJ·day^{-1}$ for each fish, and we summed the daily energy cost ($kJ·day^{-1}$) from July 15 to August 31, 2010 to estimate kJ expended by each fish over those 48 summer days. We subtracted the degree of pool-specific temperature change from July 15 to August 31, 2010 mean daily stream temperatures and repeated these bioenergetic calculations for each burned pool. We thus could back-calculate the net change in energetic costs (kJ) for the fish we observed in the burned region. We calculated the kernel density (i.e., frequency distribution) of the net change in energetic costs to illustrate variability across individuals and pools; higher kernel density indicates more frequently observed energy costs. To contextualize our bioenergetic estimates, we calculated the minimum prey mass that must be consumed to offset increased energetic demands. We note that bioenergetics of salmonids depends on R and other factors such as population density, prey availability, and additional physiological functions. However, focusing on R avoids uncertain assumptions regarding fish activity levels, rates of prey consumption, and energy lost due to
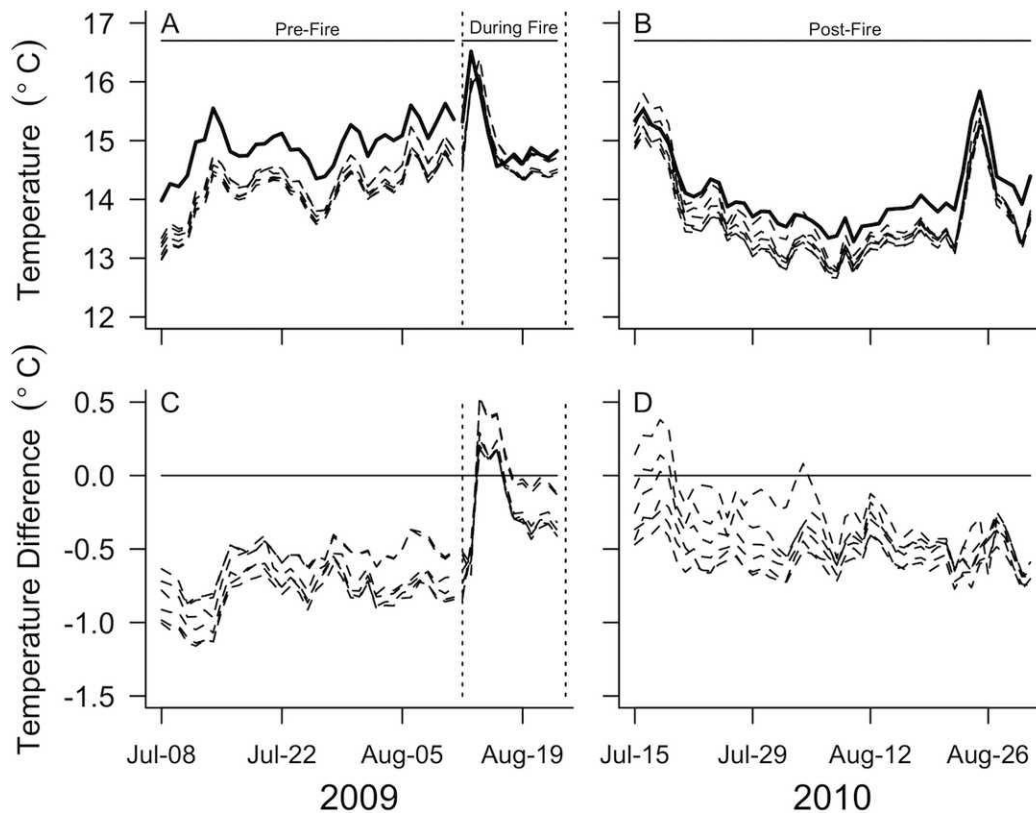
Fig. 2. Pre-fire, during, and post-fire (A and B) mean daily stream temperatures for the reference region (solid line), and the burned pools (dashed lines) and (C and D) temperature difference between the burned pools and reference region. The date range and corresponding water temperatures during the Lockheed wildfire are bound by vertical dotted lines. The left panels (A and C) show the summer of the fire (2009), while the right panels (B and D) show the summer after the fire (2010).

specific dynamic action, egestion, and excretion (Hanson et al. 1997). Our conservative analysis allows us to examine the minimum energy deficit fish accrued during the post-fire summer and provides insight into how much prey are needed to compensate for those costs. To examine the fish response to these energetic conditions, we used linear regression to estimate how much variation in the change in salmonid biomass between electrofishing surveys within each pool could be explained by the post-fire R for a salmonid of average mass.

RESULTS

Wildfire and abiotic responses

Stream temperatures were variable during the wildfire and among years in both regions (Fig. 2). Prior to the wildfire, mean daily stream temper-

atures were 14.2°C ± 0.4°C (mean ± SD) and 14.9°C ± 0.9°C in the burned and reference regions respectively. The Lockheed wildfire increased stream temperatures in both regions during the wildfire, and reached a maximum of 16.5°C to during the peak of the wildfire (Fig. 2A). Generally, stream temperatures were cooler in the burned (13.7°C ± 0.7°C) and reference (14.1°C ± 0.9°C) regions over the post-fire summer (Fig. 2B). However, the temperature difference between regions was narrower after the wildfire fire (Fig. 2).

Wildfire associated changes in mean daily stream temperatures in the burned region, relative to the reference region, were dissimilar during and after the fire (Fig. 2C, D). Compared to reference temperatures, mean daily stream temperatures among the burned pools increased

relatively homogenously by 0.56°C ± 0.03°C (mean ± SE) during the fire (Fig. 2C). During the post-fire summer, the difference in temperature between burned and reference pools indicated an average increase of 0.34°C ± 0.09°C in the burned region mean daily stream temperatures; however, there was a significant difference among burned pools (Figs. 2D and 3A, Table 2). For example, mean daily stream temperatures showed a relative increase of 0.6°C ± 0.03°C in pool 2 compared to 0.04°C ± 0.05°C in pool 6 (Fig. 3A). Mean daily stream temperatures in the burned region were best explained by a multiple linear regression model that included the reference temperatures and factors for "Time," "Pool ID," and an interaction between "Time" and "Pool ID" (adjusted $R^2 > 0.95$; Table 2). All factors were significant in the model ($P < 0.05$; Table 2). The top ranked model included two additional interaction terms (Table 1), but was more complex and only slightly more supported (ΔAICc < 1), with a negligible change in explained variance (Δ adjusted $R^2 < 0.001$); thus, we used the simpler model that excluded uninformative parameters (Arnold 2010). Lower ranked models were substantially less supported (ΔAICc > 15) and were not considered in further analysis.

We observed instream light levels (lumen·m^{-2}) increase during the post-fire summer (Fig. 4). During the wildfire our temperature and light data loggers were buried beneath debris, which likely impeded light penetration to the data loggers. As such, we could not accurately measure the change in light during the wildfire. Within a few months following the wildfire most of the instream debris was transported downstream. The summer following the wildfire we measured an increase in the median light levels in the burned region and in the reference region to a lesser degree (Fig. 4B). The observed increase in the reference region median light levels was likely driven by one pool, where a redwood tree (*Sequoia sempervirens*) fell and opened the canopy. The flux in median light levels between the pre- and post-fire summers among burned pools was variable, ranging from approximately −410 to 2150 lumen·m^{-2}, and was associated with elevated mean daily stream temperatures (Fig. 3B). Specifically, we found a strong positive relationship between increased stream temperatures and
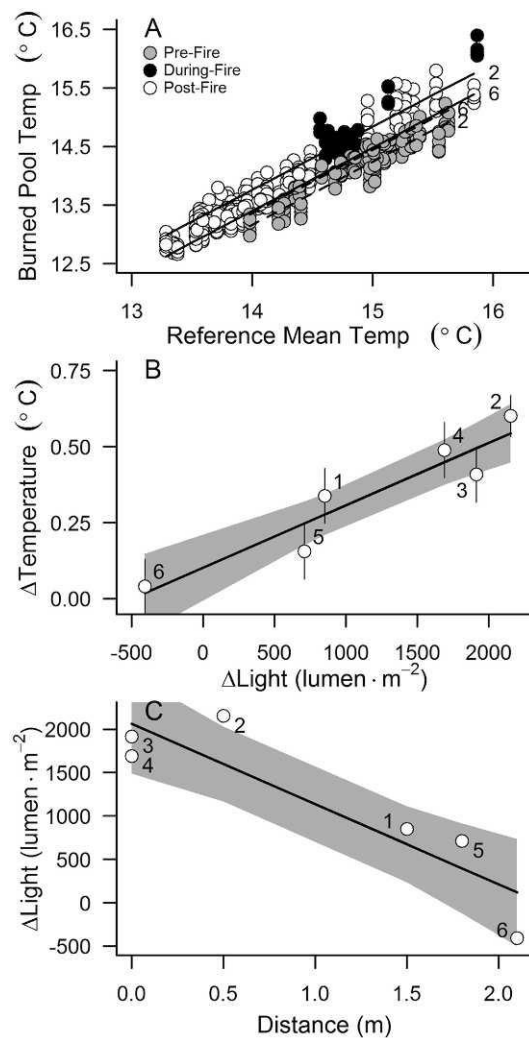

Fig. 3. Relationship between reference and burned pool (A) mean daily stream temperatures from the pre-fire (grey circles, July 8–August 11, 2009), during-fire (black circles, August 12–23, 2009) and the post-fire (white circles, July 15–August 31, 2010) time periods. Linear model fits (lines) are shown for the most (2) and least (6) burned pools. (B) The relationship between change in light flux and the estimated change in temperature for each burned pool. The line indicates the best linear model fit. (C) The relationship between proximity to burned vegetation or earth and change in light flux for each burned pool. We bound (B and C) the 95% CI of linear model fit with grey polygons and estimated (B) Δ degrees with error bars. Pool numbers (1–6) are next to each data point in the plot.

Table 2. Regression coefficients obtained from the most parsimonious linear regression fit to estimate stream temperature change.

Parameter	Coefficient	SE	t	P
Intercept	−1.37124	0.1755	−7.81	<0.001
Reference Temp	1.08065	0.01233	87.61	<0.001
Pre-Fire	−0.60075	0.03421	−17.56	<0.001
Pool 1	−0.31614	0.03008	−10.51	<0.001
Pool 3	−0.12946	0.03008	−4.30	<0.001
Pool 4	−0.18643	0.03008	−6.20	<0.001
Pool 5	−0.25026	0.03008	−8.32	<0.001
Pool 6	−0.35941	0.03008	−11.95	<0.001
Pre-Fire: Pool 1	0.26311	0.04632	5.68	<0.001
Pre-Fire: Pool 3	0.19271	0.04632	4.16	<0.001
Pre-Fire: Pool 4	0.11176	0.04632	2.41	0.0162
Pre-Fire: Pool 5	0.44549	0.04632	9.62	<0.001
Pre-Fire: Pool 6	0.56038	0.04632	12.10	<0.001

Note: All pool specific levels of significance are based on the model confidence intervals and fit relative to Pool 2.

light flux in burned pools ($P < 0.01$, adjusted R^2 = 0.86; Fig. 3B). We observed more burned vegetation and fallen trees around pools that had a larger positive flux in light and change in water temperature. As well, we found that the proximity of burned vegetation or earth to the water's edge in a burned pool was strongly and negatively related with light flux ($P = 0.02$, adjusted $R^2 = 0.76$; Fig. 3C).

Salmonids and stream temperatures

The number and size of salmonids (*O. mykiss*) captured among regions in June and September varied (Table 3). In June 2010, we captured approximately 7% more fish in the burned region than in the reference region, and these fish were 15% longer and 46% heavier on average. In September 2010, the difference in the number of captured fish between regions increased to 58%. The increased difference between regions in September compared to June was due to a 28% increase and 14% decrease in captured fish in the burned and reference regions respectively. Although we captured more individuals in the burned region in September, the average length and mass of fish between regions was more similar in September compared to the average length and mass of fish in June (Table 3). We
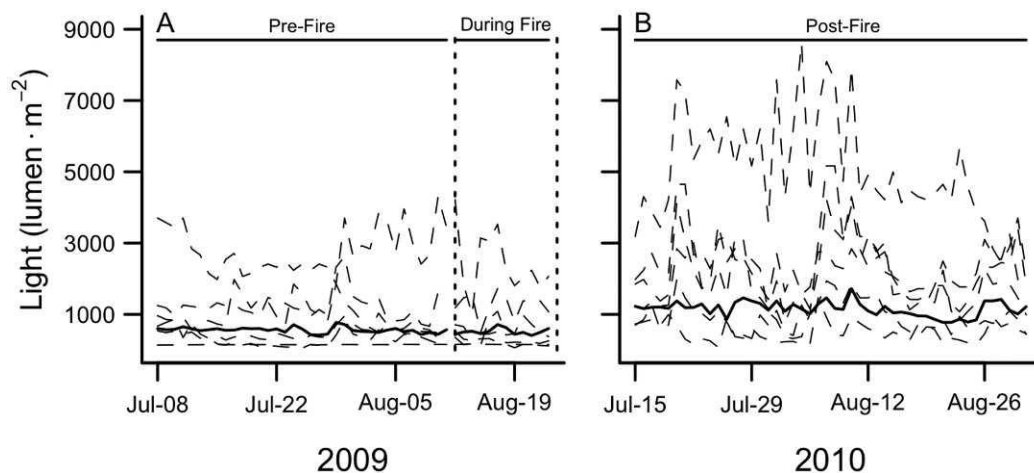

Fig. 4. Pre-fire, during, and post-fire instream light levels for the reference region (solid line), and the burned pools (broken lines). The date range and corresponding water temperatures during the Lockheed wildfire are bound by vertical dotted lines. The left panel (A) depicts the summer of the fire (2009), while the right panel (B) shows the summer after the fire (2010).

Table 3. Summary statistics for salmonids captured during the electrofishing surveys in June and September 2010. Where applicable the mean (± SD) across pools is reported.

Statistic	Burned region		Reference region	
	June	September	June	September
Fish captured	47	60	44	38
Fork length (mm)	92.8 ± 39.9	99.6 ± 38.0	80.9 ± 34.0	97.6 ± 33.0
Mass (g)	13.6 ± 17.8	15.5 ± 19.5	9.3 ± 10.2	14.5 ± 17.0
Fish tagged (N)	34	. . .	25	. . .
Recaptured fish (N)	. . .	8	. . .	3
Δ Individual mass (%)	. . .	−3.7 ± 8.8	. . .	9.9 ± 13.1
Mean prey (mg)	30.4 ± 114.8	13.6 ± 24.1	43.6 ± 136.6	27.6 ± 38.8
Median prey (mg)	6.7	4.6	10.6	13.1
Prey (mg) per fish (g)	0.99 ± 1.74	1.01 ± 2.09	2.03 ± 4.53	1.66 ± 1.94

Note: Mean and median prey masses are dry weights of both terrestrial and aquatic sources found in the stomach contents.

recaptured 8 of the 34 tagged fish from the burned region (mean individual mass change = −3.7% ± 8.8% [mean ± SD]; Table 3). The mass of 6 of these 8 recaptured fish decreased over the post-fire summer. In contrast to changes in individual fish mass, the mean fish mass in the burned region increased by approximately 14% between June and September. In the reference region, 2 of the 3 recaptured fish gained mass (mean individual mass change = 9.9% ± 13.1%; Table 3). Similarly, the mean fish mass in the reference region increased by approximately 56% between June and September.

The amount of prey found in *O. mykiss* stomachs differed between regions but not between survey months (Table 3). The average mass of stomach contents was influenced by individual *O. mykiss* with large prey items in their guts. For example, we found one fish in June with a 582 mg (dry mass) Pacific Giant Salamander (*Dicamptodon* spp.) in its stomach. After standardizing the mass of prey (mg) by fish mass (g), we found that both the mean and median amount of prey consumed per fish (prey (mg)·fish (g)$^{-1}$) were similar between June and September within each region (Table 3). We found that the amount of prey consumed per fish in the burned region was significantly less compared to fish from the reference region (log(prey (mg)·fish (g)$^{-1}$ + 1); GLM, $P = 0.011$; Fig. 5A).

On average, the post-fire energy cost (R) for salmonids was 2.34% higher than pre-fire energy cost in the burned pools relative to the reference pools. The maximum predicted change in energy costs was in pool 2 at 4.0% (CI, 4.67–3.71%) and the smallest was in pool 6, where confidence limits overlapped with 0. Pools with larger post-fire temperature differences had kernel density distributions that were shifted towards larger increases in energy costs (Fig. 5B). Given that fish of different sizes have different energetic expenditures, the observed size distribution of fish also influenced the distribution of predicted changes in energy costs. For example, energetic costs in pool 2 increased with fish size, estimated as an additional 0.19 kJ over the post-fire summer for a 1.1-g fish (5th percentile of fish size), 1.06 kJ for a 9.8-g fish (median fish mass), and 4.96 kJ for a 70.1-g fish (95th percentile of fish size). Due to variation in temperature change and fish size, the estimated energetic costs to individual fish among all the burned pools ranged between 0.01 and 6.04 kJ. As such, we estimated that fish in the burned region needed to consume approximately 0.3–264.3 mg (dry mass) of additional prey over 48 days to offset those added metabolic costs, with larger fish burning more energy than smaller fish in the same water temperature and thus requiring more prey. In terms of prey items, 0.3–264.3 mg of prey (dry mass) equates to approximately 10–2,250 average-sized mayflies (*Ephemeroptera* spp.; Cummins and Wuycheck 1971, Benke et al. 1999; M. Beakes, *unpublished data*).

Within the burned region, total salmonid biomass change between June and September was negatively associated with increased post-fire summer energetic demands. Overall, we observed an increase in fish abundance and size between the electrofishing surveys in the burned region over the summer. However, specific pools had different patterns of change in total salmonid biomass, ranging from an increase of 78.7 g in
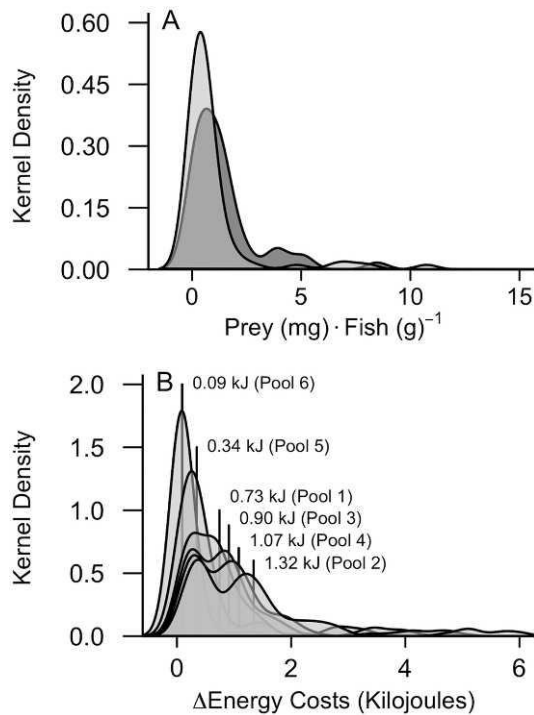
Fig. 5. Kernel density distribution of (A) salmonid gut contents combined between sampling months for the reference region (dark grey polygon, n = 48) and the burned region (light grey polygon, n = 72). This distribution shows variability across individuals; higher kernel density indicates more frequently observed stomach content measurements. (B) Kernel density distribution of estimated post-fire Δ energy for each burned pool derived from R, the measured temperature change, and range of fish masses in the burned region. Thus, the observed size range of fish in the different pools drives the distribution in change in energy costs. Mean post-fire Δ energy for each burned pool is marked by vertical lines and text.

pool 1, to a decrease of 41.9 g in pool 2 (Fig. 6). These post-fire changes in salmonid biomass were negatively correlated with the predicted metabolic cost of the pool ($P = 0.034$, adjusted R^2 = 0.43; Fig. 6). We removed a single outlier pool from this analysis that had high residual variance (Studentized residual = −3.1); deviation from the model fit in this pool was driven by a single O. mykiss that was not recaptured in the September electrofishing survey and was the largest fish we observed during the course of this study.
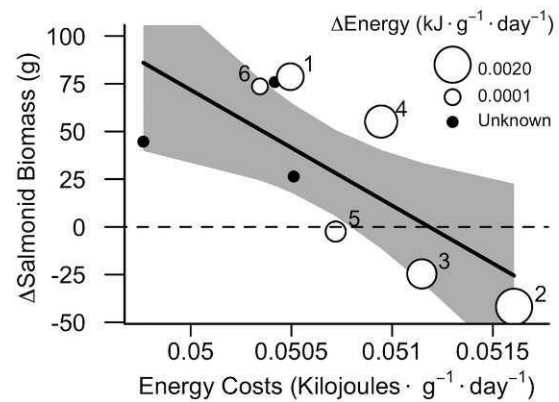

Fig. 6. Relationship between estimated energy cost of the pool and the observed change in salmonid biomass. Linear model fit and 95% CI (grey polygon) between energetic costs R for an average size fish (14.66 g) and over-summer change in salmonid biomass. Pool numbers (1–6) are next to each respective data point. The predicted change in energy costs scales with the size of each point except for pools added in 2010 summer (black), for which we could not estimate pre-fire costs.

DISCUSSION

In a central California coastal stream we found that wildfire altered stream temperatures, which in turn led to elevated energetic needs for thermally-sensitive O. mykiss. Daily stream temperatures were 0.6°C warmer on average one year after the fire in the most intensely burned pool, relative to unburned regions. While this does not sound like much change, it is worth noting that this is the equivalent of approximately two decades of directional climate warming (Stefan and Preud'homme 1993, Meehl et al. 2007). We estimated that these shifts in relative temperature also increased bioenergetic costs for coldwater salmonids, and over the post-fire summer we observed that total salmonid biomass decreased the most in pools that had the highest energetic costs. Together, these data suggest that fire, through removing riparian vegetation, leads to increased light, thereby warming temperatures, which in turn drives local decreases in bioenergetically stressed salmonids.

Our study illustrates how fine-scale heterogeneity in burn severity drives spatial variation in

abiotic conditions. More severely burned pools had increased light, and this increased light was associated with relatively increased stream temperatures. Our results corroborate observations from several other studies (e.g., Albin 1979, Amaranthus et al. 1989, Royer and Minshall 1997, Hitt 2003, Dunham et al. 2007). For example, Isaak et al. (2010) estimated that 50% of the stream temperature warming within burned regions in Idaho, USA, could be accounted for by increased solar radiation associated with canopy and vegetation loss. Often, burn severity is measured on a categorical scale (e.g., moderate, stand replacing, etc.), which necessities spatial averaging of fire intensity and implies a homogenous effect of the wildfire over large spatial scales. For example, based on the US Forest Service Burned Area Reflectance Classification (BARC) we would conclude that most, if not all, of our burned pools fell under the category of "moderate" burn severity, rendering the analysis presented in this study impossible. By integrating local measures of distance to burn in our analysis we have provided new empirical measures for how heterogeneity in burn intensity can generate a heterogeneous thermal environment even at small spatial scales.

Our study illustrates how fire contributes to the temporal dynamics in stream abiotic conditions, over short time periods. The fire itself led to a short-term increase in temperature, and then the removal of riparian vegetation apparently led to increases in stream temperature that lasted for at least one year. Our evidence suggests that temperature is linked to light flux controlled by riparian vegetation. As streamside vegetation regenerates, stream temperatures will likely return to their pre-perturbed state, as suggested in previous research (e.g., Gresswell 1999, Dunham et al. 2007, Verkaik et al. 2013).

We estimated that energy costs increased by up to 4.0% in some burned pools, equating up to 6.04 kJ of added energetic expense for the largest fish over the post-fire summer. To offset these costs, individual fish would have to increase their prey consumption rate, lose energy reserves, or seek less energetically costly habitat. In general, prey available in the drift appears limited in California coastal streams during the summer and fall partly due to low base flows (e.g., Sogard et al. 2012), and our diet data indicate that most fish in the burned region were eating relatively little compared to fish in the reference region.

Thermal heterogeneity caused by the wildfire was associated with shifts in *O. mykiss* biomass, perhaps due to individual mass loss, mortality, and potential emigration from more energetically costly pools (Fig. 6). We suspect that insufficient prey consumption during the post-fire summer resulted in lost energy reserves for some fish. Negative summer growth estimates have previously been observed in this and other coastal California watersheds, reflecting overall poor growth conditions in the summer for age-1 and larger fish (e.g., Hayes et al. 2008, Sogard et al. 2009, Grantham et al. 2012). As such, this pattern of weight loss is not unique to the burned region of Scott Creek, but rather highlights that these populations must delicately balance energetic costs and energetic intake during the food-poor and warmer summer months. Some of the shifts in *O. mykiss* biomass we observed over the summer within burned pools and at the aggregate region scale may have also been influenced by movement. *O. mykiss* have been shown to move between habitats in search of more thermally suitable habitat on small spatial scales (Ebersole et al. 2001). However, *O. mykiss* movement on large spatial scales can be limited in California coastal watersheds during the summer (Hayes et al. 2011). Resource limitation can lead to increased antagonistic behavior and territoriality (Grant and Kramer 1990, Keeley 2001, Harvey et al. 2005, Sloat and Osterback 2013), driving size-selective movement or mortality where smaller individuals perish or are forced to emigrate from resource limited habitats (e.g., Keeley 2001). Indeed, studies have shown that warm summer water temperatures can drive changes in the abundance and distribution of salmonids (e.g., Sestrich et al. 2011, Sloat and Osterback 2013). Although water temperatures throughout Scott Creek during and after the wildfire were well within the thermal limits of *O. mykiss*, our results do suggest that small-scale changes in temperature can influence these fish.

The effects of wildfire on water temperature and fish are likely seasonally dynamic. In contrast to the dry, food-poor summer months, food availability and growth of both age-1 and young-of-year California coastal salmonids generally increases in the winter and spring (Hayes

et al. 2008, Sogard et al. 2009, 2012). Historically, however, winter/spring water temperatures in the upper watershed and in the burned region of Scott Creek fall several degrees below the optimal temperatures for *O. mykiss* food consumption and growth (Myrick and Cech 2000, Hayes et al. 2008, Sogard et al. 2012). If wildfire increases stream temperatures throughout the year, we hypothesize that wildfire may improve growth conditions in the food-rich winter and spring (Hanson et al. 1997).

We focused on salmonids, their energetics, and their abiotic environment, but wildfire can also simultaneously affect other aspects of stream ecology. Generally, wildfire is considered to be among the most important forms of natural disturbance, with multiple direct and indirect affects on aquatic ecosystems (Gresswell 1999, Malison and Baxter 2010*a*, Verkaik et al. 2013). For instance, wildfire can act as a fertilizing agent in aquatic ecosystems. By burning vegetation in the riparian zone and surrounding areas, wildfires can increase nutrient availability and light, which subsequently stimulates primary production (Minshall et al. 1989, Gresswell 1999, Dunham et al. 2003, Verkaik et al. 2013). In some aquatic systems, wildfires lead to greater benthic invertebrate production (e.g., Malison and Baxter 2010*a*). Alternatively, many studies report that benthic macroinvertebrate production remains unchanged or declines initially and returns to pre-fire levels within a few years post-fire (reviewed by Minshall 2003, Verkaik et al. 2013). The production of invertebrate prey naturally fluctuates seasonally in burned and unburned watersheds, although peak production may become asynchronous relative to neighboring unburned systems (Malison and Baxter 2010*b*). As such, the long-term effects of the Lockheed wildfire on stream temperatures and fish in Scott Creek will likely be dependent on within season changes to the prey base and water temperature.

Wildfire and climate warming can act in concert to warm waters. Small or isolated populations of coldwater species will be disproportionately affected by warming temperatures, especially those near the limits of their distribution (Isaak et al. 2010, Wenger et al. 2011). The net effect of wildfire on stream temperatures and fish will likely be spatially variable. Stream temper-

atures will increase more in areas of a watershed more intensely burned relative to those less intensely burned. As well, warming waters during food-poor seasons will carry greater bioenergetic costs, whereas warming during food-rich seasons may produce bioenergetically favorable conditions for accelerated growth. Our study illustrates how wildfire can drive short-term, highly localized increases in stream temperature with associated effects on the bioenergetics and distribution of salmonids. More generally, our study highlights the importance of considering the fine-scale impacts of large-scale disturbances on the thermal environments of aquatic ecosystems.

ACKNOWLEDGMENTS

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