Received: 31 May 2022 | Accepted: 6 June 2022

DOI: 10.1002/ecs2.4233

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Ecosphere Naturalist

Loss of riparian forests from wildfire led to increased stream temperatures in summer, yet salmonid fish persisted

Dana R. Warren[1,2] | **David A. Roon**[2,3] | **Allison G. Swartz**[1] | **Kevin D. Bladon**[3]

[1]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

[2]Department of Fisheries and Wildlife Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[3]Department of Forest Engineering, Resources, and Management, Oregon State University, Corvallis, Oregon, USA

Correspondence
Dana R. Warren
Email: dana.warren@oregonstate.edu

Funding information
National Council for Air and Stream Improvement; Oregon Forest Industries Council

Handling Editor: Debra P. C. Peters

Abstract

Native salmonid fishes—cutthroat trout (*Oncorhynchus clarkii*) and steelhead/rainbow trout (*Oncorhynchus mykiss*)—are ecologically, culturally, and economically important species distributed across western North America. These fish are generally considered "cold-water" adapted species. As such, recent studies have speculated about the potential effects of climate change on these native salmonids if stream temperature thresholds exceed 16–20°C during the summer. However, the magnitude of stream thermal responses to the slow but steady increases in regional temperatures associated with climate change remains uncertain and hard to predict. Comparatively, abrupt disturbances, such as wildfire, may produce almost instantaneous and substantial increases in stream temperatures that may persist for multiple years until near-stream vegetation becomes re-established. In the first summer following a severe wildfire in western Oregon, we observed the initial persistence of populations of *O. clarkii clarkii* (coastal cutthroat trout) and *O. mykiss* (rainbow/steelhead trout). The fire burned the entire catchment, including the riparian area (~76% of the watershed area burned at moderate or high severity), resulting in stream temperature that regularly exceeded 20°C and represented increases of 6–7°C relative to prefire conditions. However, the mechanisms enabling the persistence of cold-water fishes despite the dramatic increases in stream temperature remain unclear and require further investigation. Nevertheless, wildfires represent acute natural disturbances that can substantially alter stream thermal regimes and provide unique insights that allow us to better understand how native fishes in natural systems cope with projected increases in stream temperatures.

KEYWORDS

cutthroat trout, *Oncorhynchus clarkii*, *Oncorhynchus mykiss*, rainbow trout, riparian forest, steelhead trout, thermal tolerance, wildfire

---

How do wildfires affect fish? This is a common question asked by scientists, resource managers, and the public, but it does not have a simple answer. Wildfires can have complex effects on aquatic ecosystems (Bixby et al., 2015; Jager et al., 2021; Silins et al., 2014), and the nature of fish responses to wildfires may depend on the time scale of the observations (Gresswell, 1999), severity of the fire, or on the ecological context of where the fire occurs, which collectively can lead to notably different and highly variable short- and long-term responses (Bixby et al., 2015; Gomez Isaza et al., 2022; Jager et al., 2021). The response of fish will also depend on the focal species, with some groups potentially responding positively while others may respond negatively (LeMoine et al., 2020). Therefore, to answer the general question of how wildfires affect fish, we need to draw from an extensive suite of studies that document species- and context-specific responses (Bixby et al., 2015; Gomez Isaza et al., 2022; Jager et al., 2021). With this in mind, our objective was to contribute to our understanding of fish responses to wildfire in forested landscapes by documenting how two cold-water adapted salmonid species responded to substantial increases in stream temperatures that occurred in the summer after a severe wildfire in a headwater ecosystem in the western Cascades of Oregon.

Cutthroat trout (*Oncorhynchus clarkii*) and steelhead/rainbow trout (*Oncorhynchus mykiss*) are native salmonid species distributed across western North America. These fish are generally considered to be "cold-water" adapted species, which may become stressed and experience reduced vigor if stream temperatures increase (Magnuson et al., 1979; McCullough et al., 2009; Sauter et al., 2001). In our study, we documented the initial persistence of coastal cutthroat trout (*O. clarkii clarkii*; Figure 1) and *O. mykiss* (using species name to encompass sympatric populations of both resident rainbow trout and anadromous steelhead trout) through the summer in a headwater stream system in western Oregon 1 year after a severe wildfire burned the catchment. The Hinkle Creek watershed, a tributary to the Umpqua River, was almost entirely burned by the Archie Creek Fire (~531 km^2) in September 2020. Approximately 44.0% of the catchment was burned at moderate severity and 32.9% was burned at high severity. The fire left few riparian trees alive along most of the stream network, severely reducing the shade over the stream (Figure 1). This loss of riparian forests led to thermal conditions in the stream that were notably warmer (6–7°C) than any temperatures previously recorded in the watershed over 6 years of measurements (Figure 2), with water temperatures after the fire regularly exceeding 22°C during summer months.

Wildfires can elicit a series of complex effects on aquatic ecosystems (Bixby et al., 2015; Robinne et al., 2020). However, increases in stream temperature are a primary concern, potentially resulting in negative consequences for salmonid fishes (Bixby et al., 2015; Gomez Isaza et al., 2022; Gresswell, 1999). In previous studies, loss of riparian canopies due to forest disturbance has resulted in

FIGURE 1 (a) Riparian zone along the South Fork of Hinkle Creek where stream temperature monitoring and fish sampling took place; (b) coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) captured from the middle reach of Southfork Hinkle Creek in mid-July 2021. Photograph credit: David Roon.

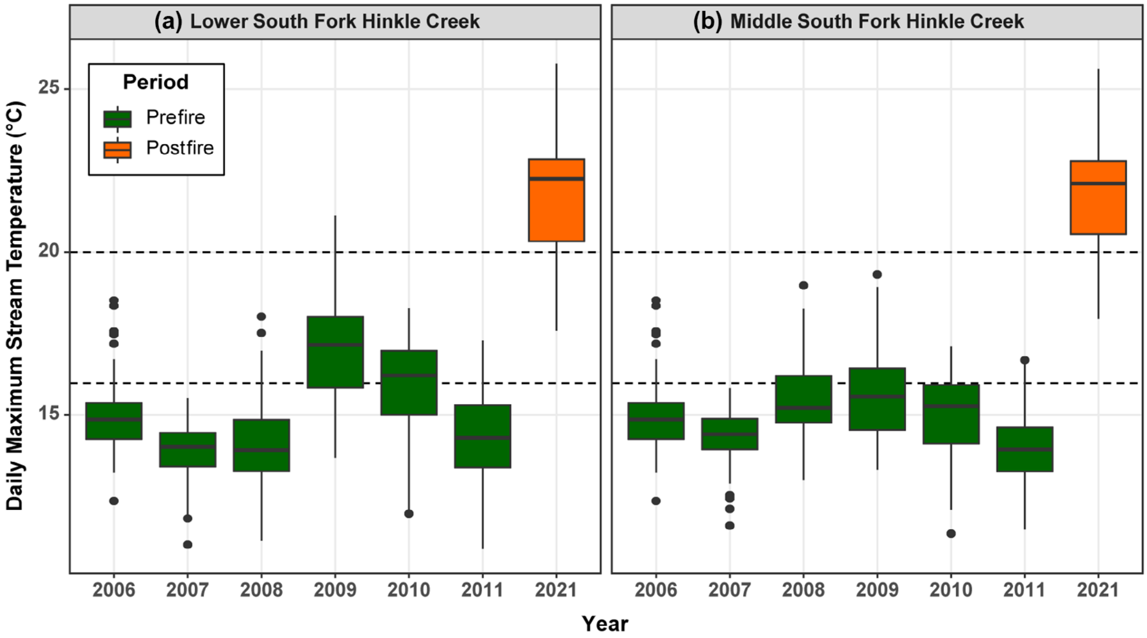

FIGURE 2 Box plot distributions of maximum daily stream temperatures (in degrees Celsius) each day in summer (25 June–25 August) for the years 2006–2011 (green) and 2021 (orange) at stream temperature recording stations in (a) Lower South Fork Hinkle Creek and (b) Middle South Fork Hinkle Creek, in the central Cascade Mountains of western Oregon.

abrupt increases in stream temperatures from 0.8°C to nearly 15°C (Gomez Isaza et al., 2022; Wagner et al., 2014). For example, Dunham et al. (2007) documented increases in maximum stream temperatures by 3–11°C in Idaho streams. However, the effects of wildfire-associated alterations to stream thermal regimes on salmonid fishes can be complicated and do not always confer negative impacts on cold-water fish (Gomez Isaza et al., 2022). As such, it is critical to improve our understanding of the factors driving the direction and magnitude of fish responses to postfire changes in stream temperature. Thus, descriptions of observations, and the context dependency of those observations, can help inform our understanding of the likely responses to wildfires and other disturbances, such as climate change.

Although salmonid fish are assumed to be highly sensitive to warm stream temperatures (McCullough et al., 2009), in many laboratory studies, cutthroat trout and *O. mykiss* can routinely survive maximum temperatures up to 25°C or more (Johnstone & Rahel, 2003; Macnaughton et al., 2021; Underwood et al., 2012). However, fish survival depends not just upon single temperature thresholds, but also relies on other dimensions of the entire stream thermal regime (Steel et al., 2017). In addition to maximum and mean temperatures, daily temperature fluctuations are also important (Steel et al., 2012, 2017). For example, fish responses to elevated temperatures during the day can be mitigated if temperatures are cooler at night (Caissie, 2006; Ryan et al., 2013; Steel et al., 2017). Zeigler et al. (2013) found that trout had lower survival rates in tanks remaining at a constant temperature of 20°C relative to trout held in tanks with the same mean daily temperature but with fluctuations of 2–5°C. Moreover, the duration of elevated temperatures is also important as it governs the exposure of fish to unsuitable thermal conditions. Acclimation temperatures also matter. For example, Underwood et al. (2012) found that cutthroat trout acclimated to 10°C had lower thermal maxima than fish acclimated to 20°C. Collectively, evidence from laboratory experiments can reveal valuable insights for wild populations in natural systems regarding how salmonid fishes deal with different components of stream thermal regimes, but empirical data from natural systems are critical for understanding the degree to which these laboratory studies translate to the field.

The effects of elevated stream temperature on salmonid fishes can also be mediated by the availability and consumption of prey resources (Railsback, 2022). In colder waters, fish metabolic rates are lower and, therefore, they need less food to maintain and grow (Hughes & Grand, 2000). As temperatures warm, metabolic rates increase, and growth rates can also increase but only if there is adequate food. Beyond a given temperature, the metabolic costs exceed what the fish can take in and growth rates decline. If there is inadequate food availability, fish reach this tipping point sooner and, therefore, optimal growth (and therefore also the point at which growth declines) occurs at a lower temperature. But with high food availability, the upper thermal optima and upper thermal limits of trout can increase (Hughes & Grand, 2000; Johnstone & Rahel, 2003; McCullough et al., 2009). This is a key additional contextual point when considering the impacts of wildfire on fish because the loss of riparian vegetation in forested systems often results in increased stream temperatures and also releases benthic autotrophs from light limitation, increasing aquatic productivity (Bixby et al., 2015; Gresswell, 1999; Jager et al., 2021). This simultaneous increase in productivity could impart greater thermal tolerance to fish in the stream than would be present in the same system under lower food availability (Railsback, 2022). Indeed, in systems where temperatures stay below stressful levels after a fire, due to elevated groundwater discharge or advective transport of cooler water from shaded upstream areas due to riparian fire refuge or topographic features, growth rates of trout have increased following fire (Dunham et al., 2007; Rosenberger et al., 2015). As a result, the effects of fire on fish may depend on the interactions between thermal and trophic conditions and available resources (Armstrong et al., 2021; Railsback, 2022; Rosenberger et al., 2015).

When considering impacts of elevated temperature on cold-water fish, acute mortality is important but is it not the only impact. There may be sublethal effects that impact fish responses such as growth, reproduction, and long-term survival (Dunham et al., 2007; Gomez Isaza et al., 2022; Spanjer et al., 2022). For example, Beakes et al. (2014) suggested in a bioenergetics analysis that increases in stream temperature of as little as 0.6°C following a fire could increase metabolic demands on fish and ultimately impact growth and survival. Li et al. (1994) invoked additional physiological stress in stream reaches with elevated temperatures in eastern Oregon streams as the likely driver of reduced fish densities in those reaches. Given the potential for delayed or sublethal effects of elevated temperatures on stream fish, we felt it was important to evaluate whether fish found in a system with elevated temperatures early in the summer would still be present after 2 months or more of exposure to these elevated and potentially stressful temperatures. To address this, we conducted fish surveys in our study stream both early in the summer (after fish had been exposed to elevated temperatures for a few weeks) and late in the summer (after fish had been exposed to elevated temperatures for two additional months).

As climate change leads to potential changes in stream temperature, studies have speculated about how potential increases in stream temperatures above 16, 18, and 20°C through the summer may affect native salmonids in the wild (Arismendi et al., 2012; Isaak et al., 2012, 2018; Spanjer et al., 2022; Wenger et al., 2011). Whereas the magnitude of stream thermal responses to the slow but steady increase in regional temperatures remains uncertain and hard to predict (Arismendi et al., 2012), wildfire is a clear and rapidly accelerating effect of climate change (coupled with legacies of historic land management) in the western United States that has potential to substantially increase stream temperatures (Ball et al., 2021; Koontz et al., 2018). When wildfires burn riparian forests and remove shade from headwater ecosystems, stream temperature can increase substantially (Dunham et al., 2007). As a result, fires are acute natural events that allow us to better understand how fish in natural systems respond to increases in stream temperature across the western United States (Isaak et al., 2012; Jager et al., 2021; Wenger et al., 2011).

In the current study, we assessed a burned over watershed in the first summer after a severe wildfire impacted the system. We deployed water temperature loggers throughout streams in the South Fork Hinkle Creek (SFHC) network (watershed area of 1083 ha) beginning in late June 2021. In mid-July 2021 (15 July–16 July), we conducted quantitative multiple-pass depletion surveys of fish in two ~50 m reaches of the SFHC mainstem (bankfull widths: ~4.9 and 4.0 m for lower and middle Southfork Hinkle Creek, respectively). Reaches were about 700 m apart. We returned in September 2021 (16 September–17 September) and conducted a second survey using identical field methods. Data loggers were deployed within 20 m of the fish survey reaches in late June 2021 (one logger per reach). Loggers recorded the temperature every 15 min in summer 2021 (from 25 June to 25 August). Through this period, the mean daily water temperatures were 18.4 and 18.3°C at lower and middle reaches of SFHC, respectively. Maximum water temperatures in both stream reaches exceeded 16°C every day in this period, and maximum temperatures exceeded 20°C on 53 of the 61 days (Figure 3). Further, during the summer, there were two extended periods, from 27 July to 5 August (10 days) and from 11 August to 16 August (6 days), where stream temperatures never dropped below 16°C. Analysis of the full dataset (15-min measurements) over this period indicated that stream temperatures exceeded 16°C for ~80% of the time and 20°C for ~30% of the time in both reaches (Figure 3).

Given concerns about the impacts of mean temperature increases as low as 0.6°C on stream salmonid populations (Beakes et al., 2014), and given that stream temperatures consistently exceeded what are commonly considered thermally stressful and suboptimal levels throughout the summer in our study sites (Huff et al., 2005; Isaak et al., 2018), we expected a decline in fish abundance and condition from July to September. However, contrary to

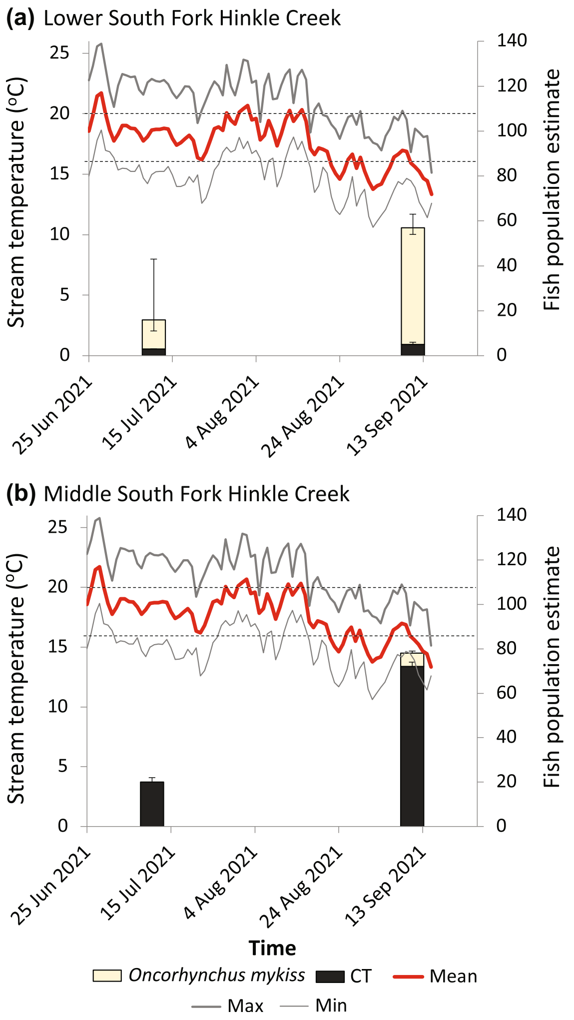

FIGURE 3 Stream temperature (in degrees Celsius; continuous lines) and *O. mykiss* and cutthroat trout (CT) abundance estimates (with 95% CIs; bar plots) during summer 2021 in (a) Lower Southfork Hinkle Creek and (b) Middle Southfork Hinkle Creek. For stream temperature, the central red line is the daily mean, the upper gray line is the daily maximum, and the lower gray line is the daily minimum. Horizontal dotted lines indicate stream temperatures of 16 and 20°C.

our expectations, through the summer of 2021 when stream temperatures regularly exceeded 20°C, fish abundances did not decline. In fact, fish abundances persisted and even increased by more than threefold in both of the study reaches. The density of age 1 and older salmonids (cutthroat trout and *O. mykiss* together) in our study reaches in July 2021 were 0.14 fish m^{-2} in Middle South Fork Hinkle Creek (MSFHC) and 0.11 fish m^{-2} in Lower South Fork Hinkle Creek (LSFHC). This was largely consistent with an earlier study from this area in which salmonid densities in the SFHC mainstem in late summer averaged 0.18 fish m^{-2} over a 5-year period (Bateman et al., 2016). Although our July 2021 abundance estimates were slightly below those reported by Bateman et al. (2016), this earlier study sampled only from pools, and we sampled from all habitats in our survey reaches. Pools have higher densities of salmonid fish than riffles or runs in these systems, and therefore we would expect a whole reach survey to yield slightly lower density estimates. We therefore concluded that the density of salmonids had not declined substantially relative to historic levels at the start of our study. By the end of summer, salmonid densities in our study reaches increased to 0.56 fish m^{-2} in MSFHC and 0.41 fish m^{-2} in LSFHC, and this increase in density was due primarily to an increase in fish abundance, not a reduction in stream wetted widths (Figure 3). Mean condition factor based on total length (in centimeters) and weight (in grams) of each fish declined slightly for cutthroat trout, dropping from 0.92 to 0.85 in MSFHC and 0.88 to 0.86 in LSFHC. Condition factor for *O. mykiss* declined from 1.00 to 0.90 in LSFCH. These declines are likely attributable to a combination of increased metabolic demand associated with warmer temperatures (Beakes et al., 2014; Railsback, 2022) and a density-dependent response to the more than tripling of fish abundances in each of the two reaches through the summer. Although condition factors were lower than previously documented in study watersheds (Bateman et al., 2016; Berger & Gresswell, 2009), condition remained within the ranges seen for salmonids in the western Cascades (Kaylor et al., 2019).

The persistence of trout in a stream system that had elevated temperatures after a fire is not unprecedented. Indeed, a number of studies have found that cutthroat and *O. mykiss* survived or even thrived in the summers after wildfire removed most of the riparian canopy or after other factors increased stream temperatures (Dunham et al., 2007; Hillyard & Keeley, 2012; LeMoine et al., 2020; Rosenberger et al., 2015). However, most of these studies are from regions that are generally warmer in summer and have greater fire frequency than the cool, shaded headwaters of the western Cascade Mountains where historic fire return intervals are 300 years or more (Reilly et al., 2017). For example, Huff et al. (2005) surveyed streams across Oregon and from that survey determined that the upper limits of the realized thermal niche for cutthroat trout and *O. mykiss* in the western cascades were 15.2 and 16.2°C, respectively (Figure 3). Realized niches are a product of the interaction between abiotic physiological constraints and biotic interactions (Colwell & Rangel, 2009). Although temperatures increased beyond the typical realized niche of these salmonids for the Cascade Mountains of Oregon, they did so in a portion of the stream network where classically "warm water" species are absent. Therefore, in this case, competition with warm water species was not a factor—thus, salmonid persistence fell more in line with the fundamental niche of the species, which laboratory studies for various cutthroat trout and *O. mykiss* sub-species suggest can exceed mean water temperatures of 18.4°C and maximum water temperature of 24°C in a fluctuating daily temperature regime (e.g., Johnstone & Rahel, 2003; Zeigler et al., 2013).

In addition to a thermal tolerance that substantially exceeds the previous realized niche of cutthroat trout and *O. mykiss* in this system, a combination of other factors could also have contributed to the persistence of salmonids in Hinkle Creek through summer 2021, including a high abundance of cooler microhabitats created by groundwater discharge, physiological recovery at night when temperatures cooled, and an increase in food availability due to increases in autotrophs at the base of stream food webs, which allowed consumption to increase with metabolic demands as temperatures rose (Railsback, 2022). Although we did not tag fish, since our study encompassed only about 2 months, there was not a long enough time period to recruit younger fish into adult populations within the reaches, and we conclude that the increases in fish abundance observed in our study were driven by the movement of individuals into the reaches. The influx of individuals into the study sections may reflect the movement of fish from lower in the mainstem where temperature may indeed have reached near-lethal levels. Overall, our results do not suggest a strong negative response over the duration of the summer, but these reflect only responses in the first year after the fire. Given the short-term nature of these observations, more research is needed to elucidate driving mechanisms and to monitor how initial patterns of persistence continue through time.

We stress that our observations do not indicate wildfires pose no substantial threats to trout populations. We did not assess long-term or sublethal implications of observed temperature increases that would extend beyond 2 months, such as maturity and spawning phenology (Rosenberger et al., 2015; Warren et al., 2012). Further, greater temperatures are only one of multiple secondary impacts that a fire can have on aquatic ecosystems. Elevated sediment influxes following wildfires can lead to substantial declines in dissolved oxygen (Bladon et al., 2014; Gomez Isaza et al., 2022), reduced habitat complexity, and loss of spawning beds due to sediment deposition (Bixby et al., 2015; Gresswell, 1999). While some sediment and ash inevitably entered our study streams in winter 2020 and 2021, there were no major mass wasting or sediment debris flow events in this system, predominantly due to an abnormally dry initial postfire winter. This allowed us to evaluate fish in summer 2021 with a focus principally on stream temperature effects that were largely independent from the impacts of sediment and ash.

Under current climate change trajectories, wildfire frequency, extent, and severity are all projected to increase throughout western North America (Ball et al., 2021). Therefore, it is increasingly certain that more trout will experience disturbances like the 2020 Labor Day fires in Oregon (Bixby et al., 2015; Koontz et al., 2018). Salmonid fish in Hinkle Creek persisted in water temperatures that substantially exceeded the conditions they are normally found in for this region, but were within their thermal tolerance range from laboratory studies. Our results highlight the transferability of these controlled laboratory studies to field conditions, and we conclude that cutthroat trout and *O. mykiss* within Hinkle Creek appeared resilient to temperature increases that frequently occur in headwater streams during the summer after a severe wildfire (Isaak et al., 2018; Lewis et al., 2014). This result has clear implications beyond Hinkle Creek; however, the many complex interactions between characteristics of a given fire (e.g., burn severity, proportion of watershed burned), catchment physiology (e.g., slope, aspect), dominant runoff mechanisms driving streamflow (e.g., ground water sources, shallow sub-surface runoff), and local biota could create unique habitat responses and confer differential impacts on fish populations and fish community resilience to fire. Long-term conservation of stream ecosystems and stream fish populations under increasing occurrence of large, high severity wildfires will require untangling the complexity of these interacting factors.

AUTHOR CONTRIBUTIONS

Dana R. Warren wrote the first draft, edited the manuscript, and was involved in fieldwork. David A. Roon and Allison G. Swartz edited the manuscript and were involved in fieldwork and data analysis. Kevin D. Bladon edited the manuscript and was involved in fieldwork, and was the lead principal investigator of funding awards.

ACKNOWLEDGMENTS

The authors thank Kate McCredie, Maddie Maffia, Ellen Luedloff, and Melissa Mauk for their help in the field. Matt Kaylor, Jason Dunham, J. Pastor, and two anonymous reviewers provided valuable feedback on earlier drafts of this note. The authors also thank the National Council for Air and Stream Improvement, Oregon Forest Industries Council, Roseburg Forest Products, and the Oregon State University Fish and Wildlife Habitat in Managed Forests program for facilitating this research. All fish were collected under OSU IACUC-2021-0182.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Warren et al., 2022) are available from the Oregon State University library: https://ir.library.oregonstate.edu/concern/datasets/bk128k15d.

ORCID

Dana R. Warren https://orcid.org/0000-0001-5282-7972
David A. Roon https://orcid.org/0000-0002-3284-5791
Allison G. Swartz https://orcid.org/0000-0002-2006-1455
Kevin D. Bladon https://orcid.org/0000-0002-4182-6883

REFERENCES

Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggety, and D. Hockman-Wert. 2012. "The Paradox of Cooling Streams in a Warming World: Regional Climate Trends Do Not Parallel Variable Local Trends in Stream Temperature in the Pacific Northwest." *Geophysical Research Letter* 39: L10401.

Armstrong, J. B., A. H. Fullerton, C. E. Jordan, J. L. Ebersole, J. R. Bellmore, I. Arismendi, B. E. Penaluna, and G. H. Reeves. 2021. "The Importance of Warm Habitat to the Growth Regime of Cold-Water Fishes." *Nature Climate Change* 11: 354–61.

Ball, G., P. Regier, R. Gonzalez-Pinzon, J. Reale, and D. Van Horn. 2021. "Wildfires Increasingly Impact Western US Fluvial Networks." *Nature Communications* 12: 2484.

Bateman, D. S., M. R. Sloat, R. E. Gresswell, A. M. Berger, D. P. Hockman-Wert, D. W. Leer, and A. E. Skaugset. 2016. "Effects of Stream-Adjacent Logging in Fishless Headwaters on Downstream Coastal Cutthroat Trout." *Canadian Journal of Fisheries and Aquatic Sciences* 73: 1898–913.

Beakes, M. P., J. W. Moore, S. A. Hayes, and S. M. Sogard. 2014. "Wildfire and the Effects of Shifting Stream Temperature on Salmonids." *Ecosphere* 5: 1–14.

Berger, A. M., and R. E. Gresswell. 2009. "Factors Influencing Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) Seasonal Survival Rates: A Spatially Continuous Approach within Stream Networks." *Canadian Journal of Fisheries and Aquatic Sciences* 66: 613–22.

Bixby, R. J., S. D. Cooper, R. E. Gresswell, L. E. Brown, C. N. Dahm, and K. A. Dwire. 2015. "Fire Effects on Aquatic Ecosystems: An Assessment of the Current State of the Science." *Freshwater Science* 34: 1340–50.

Bladon, K. D., M. B. Emelko, U. Silins, and M. Stone. 2014. "Wildfire and the Future of Water Supply." *Environmental Science & Technology* 48: 8936–43.

Caissie, D. 2006. "The Thermal Regime of Rivers: A Review." *Freshwater Biology* 51: 1389–406.

Colwell, R. K., and T. F. Rangel. 2009. "Hutchinson's Duality: The Once and Future Niche." *Proceedings of the National Academy of Sciences of the United States of America* 106: 19651–8.

Dunham, J. B., A. E. Rosenberger, C. H. Luce, and B. E. Rieman. 2007. "Influences of Wildfire and Channel Reorganization on Spatial and Temporal Variation in Stream Temperature and the Distribution of Fish and Amphibians." *Ecosystems* 10: 335–46.

Gomez Isaza, D. F., R. L. Cramp, and C. E. Franklin. 2022. "Fire and Rain: A Systematic Reivew of the Impacts of Iwldfire and Associated Runoff on Aquatic Fauna." *Global Change Biology* 28: 2578–95.

Gresswell, R. E. 1999. "Fire and Aquatic Ecosystems in Forested Biomes of North America." *Transactions of the American Fisheries Society* 128: 193–221.

Hillyard, R. W., and E. R. Keeley. 2012. "Temperature-Related Changes in Habitat Quality and Use by Bonneville Cutthroat Trout in Regulated and Unregulated River Segments." *Transactions of the American Fisheries Society* 141: 1649–63.

Huff, D. D., S. L. Hubler, and A. N. Borisenko. 2005. "Using Field Data to Estimate the Realized Thermal Niche of Aquatic Vertebrates." *North American Journal of Fisheries Management* 25: 346–60.

Hughes, N. F., and T. C. Grand. 2000. "Physiological Ecology Meets the Ideal-Free Distribution: Predicting the Distribution of Size-Structured Fish Populations across Temperature Gradients." *Environmental Biology of Fishes* 59: 285–98.

Isaak, D. J., C. H. Luce, D. L. Horan, G. L. Chandler, S. P. Wollrab, and D. E. Nagel. 2018. "Global Warming of Salmon and Trout Rivers in the Northwestern U.S.: Road to Ruin or Path through Purgatory?" *Transactions of the American Fisheries Society* 147: 566–87.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. "Climate Change Effects on Stream and River Temperatures across the Northwest US from 1980-2009 and Implications for Salmonid Fishes." *Climatic Change* 113: 499–524.

Jager, H. I., J. W. Long, R. L. Malison, B. P. Murphy, A. Rust, L. G. M. Silva, R. Sollmann, et al. 2021. "Resilience of Terrestrial and Aquatic Fauna to Historical and Future Wildfire Regimes in Western North America." *Ecology and Evolution* 11: 12259–84.

Johnstone, H. C., and F. J. Rahel. 2003. "Assessing Temperature Tolerance of Bonneville Cutthroat Trout Based on Constant and Cycling Thermal Regimes." *Transactions of the American Fisheries Society* 132: 92–9.

Kaylor, M. J., B. J. VerWey, A. Cortes, and D. R. Warren. 2019. "Drought Impacts to Trout and Salamanders in Cool, Forested Headwater Ecosystems in the Western Cascade Mountains, OR." *Hydrobiologia* 833: 65–80.

Koontz, E. D., E. A. Steel, and J. D. Olden. 2018. "Stream Thermal Responses to Wildfire in the Pacific Northwest." *Freshwater Science* 37: 731–46.

LeMoine, M. T., L. A. Eby, C. G. Clancy, L. G. Nyce, M. J. Jakober, and D. J. Isaak. 2020. "Landscape Resistance Mediates Native Fish Species Distribution Shifts and Vulnerabiilty to Climate Change in Riverscapes." *Global Change Biology* 26: 5492–508.

Lewis, T. L., M. S. Lindberg, J. A. Schmutz, and M. R. Bertram. 2014. "Multi-Trophic Resilience of Boreal Lake Ecosystems to Forest Fires." *Ecology* 95: 1253–63.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. "Cumulative Effects of Riparian Disturbances along High Desert Trout Streams of the John Day Basin, Oregon." *Transactions of the American Fisheries Society* 123: 627–40.

Macnaughton, C. J., T. C. Durhack, N. J. Mochnacz, and E. C. Enders. 2021. "Metabolic Performance and Thermal Preference of Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and Non-native Trout across an Ecologically Relevant

Range of Temperatures." *Canadian Journal of Fisheries and Aquatic Sciences* 78: 1247–56.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. "Temperature as an Ecological Resource." *American Zoologist* 19: 331–43.

McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, et al. 2009. "Research in Thermal Biology: Burning Questions for Coldwater Stream Fishes." *Reviews in Fisheries Science* 17: 90–115.

Railsback, S. F. 2022. "What we don't Know about the Effects of Temperature on Salmonid Growth." *Transactions of the American Fisheries Society* 151: 3–12.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. "Contemporary Patterns of Fire Extent and Severity in Forests of the Pacific Northwest, USA (1985-2010)." *Ecosphere* 8: e01695.

Robinne, F.-N., D. W. Hallema, K. D. Bladon, and J. M. Buttle. 2020. "Wildfire Impacts on Hydrologic Ecosystem Services in North American High-Latitude Forests: A Scoping Review." *Journal of Hydrology* 581: 124360.

Rosenberger, A. E., J. B. Dunham, J. R. Neuswanger, and S. F. Railsback. 2015. "Legacy Effects of Wildfire on Stream Thermal Regimes and Rainbow Trout Ecology: An Integrated Analysis of Observation and Individual-Based Models." *Freshwater Science* 34: 1571–84.

Ryan, D. K., J. M. Yearsley, and M. Kelly-Quinn. 2013. "Quanitfying the Effect of Semi-Natural Riparian Cover on Stream Temperatures: Implications for Salmonid Habitat Management." *Fisheries Management and Ecology* 20: 494–507.

Sauter, S. T., J. McMillan, and J.B. Dunham. 2001. "Salmonid Behavior and Water Temperature." EPA The Region 10 Report.

Silins, U., K. D. Bladon, E. N. Kelly, E. Esch, J. R. Spence, M. Stone, M. B. Emelko, et al. 2014. "Five-Year Legacy of Wildfire and Salvage Logging Impacts on Nutrient Runoff and Aquatic Plant, Invertebrate, and Fish Productivity." *Ecohydrology* 7: 1508–23.

Spanjer, A. R., A. S. Gendaszek, E. J. Wulfkuhle, R. W. Black, and K. L. Jaeger. 2022. "Assessing Climate Change Impacts on Pacific Salmon and Trout Using Bioenergetics and Spatiotemporal Explicit River Temperature Predictions under Varying Riparian Conditions." *PLoS One* 17: e0266871.

Steel, E. A., T. J. Beechie, C. E. Torgersen, and A. H. Fullerton. 2017. "Envisioning, Quanitfying, and Managing Thermal Regimes on River Networks." *Bioscience* 67: 506–22.

Steel, E. A., A. Tillotson, D. A. Larsen, A. H. Fullerton, K. P. Denton, and B. R. Beckman. 2012. "Beyond the Mean: The Role of Variability in Predicting Ecological Effects of Stream Temperature on Salmon." *Ecosphere* 3: 1–11.

Underwood, Z. E., C. A. Myrick, and K. B. Rogers. 2012. "Effect of Acclimation Temperature on the Upper Thermal Tolerance of Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus*: Thermal Limits of a North American Salmonid." *Journal of Fish Biology* 80: 2420–33.

Wagner, M. J., K. D. Bladon, U. Silins, C. H. S. Williams, A. M. Martens, S. Boon, R. J. MacDonald, M. Stone, M. B. Emelko, and A. Anderson. 2014. "Catchment-Scale Stream Temperature Response to Land Disturbance by Wildfire Governed by Surface-Subsurface Energy Exchange and Atmospheric Controls." *Journal of Hydrology* 517: 328–38.

Warren, D. R., K. D. Bladon, D. A. Roon, and A. G. Swartz. 2022. "Fish and Temperature Data from Hinkle Creek Summer 2021 (v. 1) [Data set]." Oregon State University. https://doi.org/10.7267/BK128K15D.

Warren, D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon, and C. E. Kraft. 2012. "Elevated Summer Temperatures Delay Spawning and Reduce Redd Construction for Resident Brook Trout (*Salvelinus fontinalis*)." *Global Change Biology* 18: 1804–11.

Wenger, S. J., D. J. Isaak, J. B. Dunham, K. D. Fausch, C. H. Luce, H. M. Neville, B. E. Rieman, et al. 2011. "Role of Climate and Invasive Species in Structuring Trout Distributions in the Interior Columbia River Basin, USA." *Canadian Journal of Fisheries and Aquatic Sciences* 68: 988–1008.

Zeigler, M. P., S. F. Brinkman, C. A. Caldwell, A. S. Todd, M. S. Recsetar, and S. A. Bonar. 2013. "Upper Thermal Tolerances of Rio Grande Cutthroat Trout under Constant and Fluctuating Temperatures." *Transactions of the American Fisheries Society* 142: 1395–405.

How to cite this article: Warren, Dana R., David A. Roon, Allison G. Swartz, and Kevin D. Bladon. 2022. "Loss of Riparian Forests from Wildfire Led to Increased Stream Temperatures in Summer, yet Salmonid Fish Persisted." *Ecosphere* 13(9): e4233. https://doi.org/10.1002/ecs2.4233