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Tributary confluences are dynamic thermal refuges for a juvenile salmonid in a warming river network

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Abstract

As rivers warm, cold-water fish species may alleviate thermal stress by moving into localized thermal refuges such as cold-water plumes created by cool tributary inflows. We quantified use of two tributary confluence plumes by juvenile steelhead, *Oncorhynchus mykiss*, throughout the summer, including how trout positioned themselves in relation to temperature within confluence plumes. At two confluences, Cedar and Elder creeks, along the South Fork Eel River, California, USA, we monitored temperatures using in situ logger grids throughout summer 2016. Fish were counted within confluences via snorkel surveys five times a day on 5 days at each site. We found diel and seasonal dependence on confluence use by steelhead, especially at the Cedar Creek confluence, where mainstem temperatures exceeded 28°C. At this site, fish moved into the confluence on the warmest days and warmest times of the day. Fish observed within the Cedar Creek confluence plume were most common in locations between 20–22°C, rather than the coldest locations (14.5°C). At Elder Creek, where mainstem temperatures remained below 24°C, there was little relationship between mainstem temperature and steelhead presence in the confluence plume. At both sites, steelhead distribution within plumes was influenced by spatial variation of temperature and mean temperature in surveyed grid cells. Our results show that cool tributaries flowing into warmer mainstem reaches (over 24°C) likely create important thermal refuges for juvenile steelhead. As mainstem rivers warm with climate change, cool-water tributary inputs may become more important for sustaining cold-water salmonids near the southern end of their range.

KEYWORDS

climate change, Eel River, microhabitat, *Oncorhynchus mykiss*, stream temperatures, thermal refuges, thermal tolerance

1 | INTRODUCTION

The spatial distribution of species is often determined by environmental conditions and physiological limits (Kearney & Porter, 2009).

As global temperatures rise, temperatures may surpass physiological tolerances of species, potentially causing species ranges to constrict at thermal margins (Root et al., 2003). However, large-scale, coarse range shifts can be spatially complex when ecological refuges exist

FIGURE 1 (a) Locations of Elder and Cedar Creek confluences with the South Fork Eel River in northern California. (b) Map of the Cedar Creek confluence grid. (c) Map of the Elder Creek confluence grid [Colour figure can be viewed at wileyonlinelibrary.com]

at finer scales (VanDerWal et al., 2013). Ecological refuges are sites that provide protection from adversity (Berryman & Hawkins, 2006). For example, thermal refuges, such as cold-water microhabitats, allow populations to persist despite warming and are often high priorities for conservation (Davis, Pavlova, Thompson, & Sunnucks, 2013).

In river systems, water temperature often dictates species distributions (Caissie, 2006). Many river systems are predicted to warm with climate change, including those of California (Cloern et al., 2011). Stream temperatures will increase directly with rising air temperatures (Isaak, Wollrab, Horan, & Chandler, 2012). Temperatures will also increase as inflows reduce and evaporation rates increase (Null, Viers, & Mount, 2010), and as flow regime shifts from snow-melt to rain-fall dominated (Barnett, Adam, & Lettenmaier, 2005). As stream temperatures rise, cold-water species may rely on thermal refuges to persist during warm periods.

Cold-water-dependent salmonid fishes may be especially reliant on thermal refuges to minimize physiological stress from increasing river temperatures (Torgersen, Price, Li, & McIntosh, 1999; Ebersole, Wigington, Leibowitz, & Comeleo, 2015). In coastal California, tributary confluences may provide thermal refuges because lower order tributaries are often groundwater-fed and well-shaded, and tend to be cooler than mainstem rivers (Dralle et al., 2018). The inflow from tributaries into mainstem rivers can create cold-water plumes at their confluence (Greer, Carlson, & Thompson, 2019). Tributary confluences have been previously highlighted as refuges for salmonids during periods of high temperatures (Brewitt & Danner, 2014; Sutton, Deas, Tanaka, Soto, & Corum, 2007). The extent that a confluence is a thermal refuge may depend on spatial variation in temperature, such as the temperature difference between tributary and mainstem, as well as temporal variation, such as seasonal fluctuations in temperatures (Dugdale, Bergerson, & St-Hilaire, 2013). Previous studies have found salmonids moving into tributary confluences when mainstem temperatures increase above 22°C (Sutton et al., 2007; Sutton & Soto, 2012). However, less is known about which tributary confluences are important refuges and how fish position themselves within confluence plumes.

Here, we investigated the use of tributary confluences as thermal refuges by a juvenile salmonid fish, steelhead trout (*Oncorhynchus mykiss*), in the South Fork Eel River in northern California. First, we characterized water temperature patterns at two confluence sites. Second, we evaluated the seasonal and daily patterns of steelhead occupancy of each site. We predicted that more steelhead would occupy confluence plumes as mainstem temperatures warmed, given that mainstem temperature was a strong predictor of steelhead use of confluence plumes in similar studies (Brewitt & Danner, 2014; Sutton et al., 2007). Third, we tested if trout were non-randomly distributed in the confluence plume, indicating microhabitat selection. We predicted that steelhead would exhibit thermal regulation and track water temperatures in the range of 11–19°C, in alignment with other studies of steelhead performance at different temperatures (Myrick & Cech, 2001). Finally, we predicted that increases in mainstem temperature would be associated with a stronger preference for cold-water habitat within confluence plumes.

2 | METHODS

2.1 | Study system

We studied two confluences within the South Fork Eel River watershed: the confluences of Cedar Creek (drainage area: 39.5 km²) and Elder Creek (drainage area: 16.9 km²) with the mainstem South Fork Eel River (Figure 1). Cedar Creek enters the South Fork Eel River at 527.3 km² drainage area at an open, shallow riffle (39 cm average depth, June 2016) with little riparian shading. Dispersed boulders and cobbles create a complex flow environment. The Elder Creek confluence is 26 km upstream of the Cedar site, in the headwaters of the South Fork Eel River on the University of California Angelo Coast Range Reserve, drainage area of 145.9 km². Elder Creek flows into a well-shaded, slow-moving pool (81 cm average depth, June 2016). With the exception of the inflow from Elder Creek, flow was parallel to the channel. The confluence pool was comprised of small cobbles and sand with a few large boulders. Compared to the Elder Creek confluence, the Cedar Creek confluence tends to be warmer because of its larger area, reduced riparian shading and exposure to radiative warming.

2.2 | Temperature monitoring at confluences using in-stream grids

We established grids in the mainstem channels at both confluence sites to organize collection of temperature data and fish counts in 2016. We created grids by anchoring rebar into the streambed to form cross-stream rows and along-stream columns. Grids were situated to capture the cold-water plumes of the incoming tributaries (which we first observed using visual tracers) in early June. The Elder confluence grid included 6 rows and 4 columns, totalling 24 cells that spanned 11.6 m along and 7.5 m across the channel (grid extended two-thirds across the channel, where the cold-water plume was no longer detected). The Cedar Creek confluence grid included 8 rows and 6 columns, totalling 48 observation cells that spanned 20.4 m along and 11.0 m across the channel. Grid cells ranged from 3.8–18.0 m^2 at Elder Creek and 3.0–14.9 m^2 at Cedar Creek. We calculated the volume of each cell by averaging ten random depths measured at installation.

We installed three Onset® HOBO Data Loggers at each rebar stake, one just below surface water level, one at mid-depth and one 2 cm above the bed. Where water depth was <0.5 m (n = 6 at Cedar), we installed two loggers. Where water depth was >1 m deep (n = 10 at Elder), we installed four loggers. We deployed 97 loggers at Elder Creek confluence and 118 loggers at Cedar Creek confluence. Temperature was also logged upstream of each confluence and in each tributary. All loggers recorded temperature hourly. Temperature data are reported from June 19 to August 31, 2016 (74 days).

2.3 | Fish snorkeling surveys at confluences using in-stream grids

We performed snorkel surveys to count fish and record their positions in the confluence plumes. We surveyed on 5 days throughout the summer and selected for a range of cooler to warmer days. Elder Creek confluence was surveyed on June 20, July 5, July 18, July 21 and August 4, and Cedar Creek confluence was surveyed on June 20, July 4, July 18, July 24 and July 30. Each day, pairs of snorkelers performed 5 surveys, once at 9:00, 11:30, 14:00, 16:30 and 19:00. In total, we conducted 50 snorkel surveys.

The grid cells delineated by the rebar stakes guided snorkelers for surveys. On each survey, two snorkelers split the confluence grid in half length-wise (parallel to river flow). Snorkelers entered the mainstem downstream of the grid, and swam upstream through the columns, recording fish counts for each cell. Since fish upstream of snorkelers remained largely undisturbed, snorkelers counted the number of each fish species in each cell before entering from downstream. Snorkelers moved slowly in tandem and counted from a distance to avoid disturbing fish. The same pair of snorkelers conducted all snorkel surveys at a given site. Snorkelers minimized double counting by moving cautiously and communicating frequently. Surveys ranged from 10 to 40 min.

Steelhead trout, coho salmon (*O. kisutch)* and Chinook salmon (*O. tshawytscha)* occur in the South Fork, but we primarily observed juvenile steelhead trout at our study sties. Observed steelhead were presumed to be either produced from the corresponding tributary or upstream of the mainstem. The largest *O. mykiss* were assumed to be resident trout, but the majority of recorded steelhead were rearing juveniles. Other fish species were counted but excluded from analysis.

2.3.1 | Objective 1: Characterize temperature patterns at confluence sites

To evaluate differences in thermal regimes between Elder and Cedar confluence sites, we first compared temperatures in the mainstem upstream of each confluence. We calculated the number of days in which any hourly mainstem temperature was above a 21°C threshold, as a metric for how often there was potential thermal stress on juvenile steelhead and when fish may seek thermal refuge. We chose 21°C because it is above steelhead preferred temperatures of 11–19°C (Myrick & Cech, 2001), and is a threshold at which they experience lower growth rates, reduced feeding and increased aggression (Carter, 2005; Nielsen, Lisle, & Ozaki, 1994; Sullivan, Martin, Cardwell, Toll, & Duke, 2000). Additionally, this value is close to 22°C, above which juvenile steelhead have been observed to move into cold-water refuge in the nearby Klamath River (Sutton et al., 2007; Brewitt & Danner, 2014), suggesting a physiological threshold near this point.

To analyse temperature variation within each plume, we interpolated temperatures spatially based on the sensors installed on the rebar stakes. All calculations were performed using the software MATLAB (The Mathworks, 2017). The physical grid system of the snorkel survey was mapped to a logical grid using bilinear interpolation, allowing for the oddly-shaped grid cell polyhedrons to transform into simple cubes. We used Chebyshev nodes to densely populate the edges of the grid cells to reduce edge effect error (Fink & Mathews, 1999). We then used MATLAB's function "scatteredInterpolant" to create an interpolated temperature field for each snorkel survey. We used the interpolated temperature field to compute spatial statistics for each grid cell for each survey. The statistics we computed for each grid cell are: mean temperature, variance of temperature, range of temperature and maximum temperature spatial gradient—which may be important if juvenile steelhead prefer locations where they can quickly move between temperatures. The maximum spatial gradient metric describes the greatest difference in temperature over any Cartesian distance in the three-dimensional cube. In other words, if temperature is a function of space $T(x, y, z)$, then maximum gradient is the maximum magnitude of dT/dx, dT/dy and dT/dz.

2.3.2 | Objective 2: Evaluate if and when confluence sites are used by juvenile steelhead

We compared the number of juvenile steelhead that used each confluence site across the summer and within each survey day. We summed the number of steelhead trout in each confluence site for

each survey and standardized counts by the volume of each confluence plume (surface area × average depth).

2.3.3 | Objective 3: Evaluate whether juvenile steelhead are distributed randomly within confluence plumes

To characterize the pattern of steelhead distribution within each confluence plume, we calculated Global Moran's I values for each survey in ArcGIS v10.3.1. The Global Moran's I is a metric used to test the null hypothesis that points are distributed randomly in space. A Moran's I value close to −1 implies that steelhead are uniformly spread across the confluence site, a value close to 1 implies steelhead are clumped at high-density pockets, and a value close to 0 suggests spatial randomness.

2.3.4 | Objective 4: Explore the role of temperature in determining juvenile steelhead positioning within confluence plumes

Model selection to assess which temperature variables best predict steelhead positioning

We used linear mixed effects modelling to relate temperature variations within the plume to (log-transformed) density of juvenile steelhead in each grid cell. All models used the grid cell-level temperature statistics for each survey (mean temperature, its square, temperature variance, temperature range and the maximum temperature gradient) as fixed effects. We included the quadratic term (square of mean temperature) because aspects of salmonid physiology often have a quadratic relationship with temperature (e.g., Railsback & Rose, 2017) and because preliminary exploration indicated a non-linear relationship between temperature and steelhead density. Date and time were included as random effects to account for non-independence of these sampling events. Specifications for all models we explored are in Table 1. We excluded maximum temperature from models because it was highly correlated to mean temperature ($r^2 > 0.9$, Table S1). We used Akaike's Information Criteria (AIC), implemented in MuMln package (Barton, 2019) in R, to identify the best supported model at each site. We conducted the model selection process twice, the first time including all data points and the second time removing grid cells with

zero steelhead to explore the influence of zero-inflation. We took this extra step because many grid cells had no steelhead, and the inclusion of zero counts from these cells had potential to strengthen the statistical relationships between temperature and fish density.

Analyses of temporal differences in steelhead positioning within the confluence

Since mean cell temperature emerged as an important predictor (see Results), we tested if the relationship between mean temperature and steelhead density differed within and among days. We regressed steelhead density against grid cell mean temperature for each survey using the best supported relationship between mean temperature and density (see Results), totalling 25 regressions per site.

At the Cedar confluence, the strength of the relationship between steelhead density and mean temperature differed across season and time of day (see Results), so we conducted an additional analysis to assess if this pattern was driven by the temperature difference between mainstem and tributary. We explored how r^2 values for the regressions between steelhead density and grid cell mean temperature varied with the temperature difference between tributary and mainstem at the time of the survey. A positive relationship indicates that mean temperature better predicts fish positioning within the confluence as the mainstem becomes increasingly warmer than the tributary.

3 | RESULTS

3.1 | Objective 1: Characterize temperature patterns at confluence sites

Stream temperatures at both sites peaked in late July and early August (Figure 2). Cedar and Elder creek temperatures were similar, ranging from 11.8 to 19.9°C over the course of the summer, with Cedar Creek being 0.8°C warmer on average than Elder Creek (Figure 2). Temperatures of the South Fork Eel River upstream of each confluence differed between sites. From June 20 to August 4, the average mainstem temperature upstream of Cedar Creek was 4.2°C warmer than upstream of Elder Creek. Mainstem temperature upstream of Cedar Creek ranged from 15.1 to 26.1°C (mean daily minimum to mean daily maximum), whereas mainstem upstream of Elder Creek ranged from 14.2 to 21.6°C. The mean temperature difference

TABLE 1 Comparison between models that predict steelhead density as a function of temperature variation, presented separately for Cedar Creek and Elder Creek

Cedar confluence models			Elder confluence models		
Variables	AIC	ΔAIC	Variables	AIC	ΔAIC
Mean + mean^2 + variance	1,287.4	0.0	Mean + variance	−64.1	0.0
Mean + mean^2	1,329.0	41.6	Mean + range	−8.1	56.0
Mean + mean^2 + gradient	1,332.6	45.2	Mean	0.1	64.2
Mean + mean^2 + range	1,333.5	46.1	Mean + mean^2	4.2	68.3
Mean	1,442.1	154.7	Mean + gradient	6.2	70.3

Note: All models included day and time as random effects to account for non-independence of grid-cell level observations within each survey.
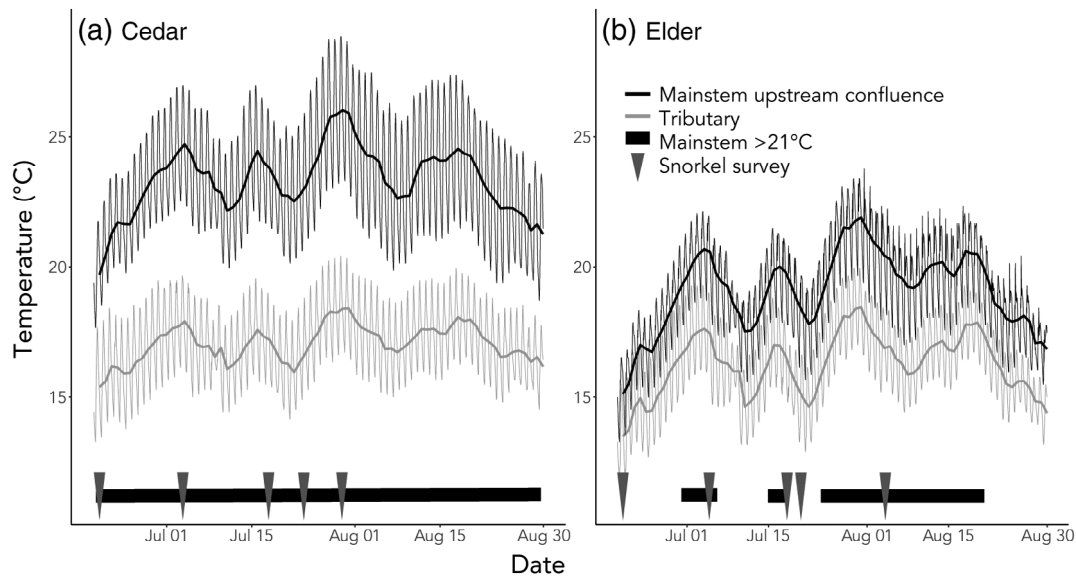
FIGURE 2 Water temperature recorded at Cedar Creek (a) and Elder Creek (b) from June 19–August 30, 2016. Two hourly time series are displayed for each site: temperature of the South Fork Eel River upstream of the confluence (black), and temperature of the tributary (grey). The bold lines represent the daily mean temperature. The horizontal black line at the bottom of the plot highlights periods in which steelhead may experience thermal stress (when mainstem temperature >21°C, see Methods). Grey arrows represent snorkel survey dates

(mean difference in daily means) between the mainstem and tributary was 6.3°C at Cedar and 2.8°C at Elder. Mainstem temperatures were above the threshold temperature of 21°C, when thermal stress may occur for steelhead (see Methods), for 71 days at the Cedar site and 37 days at the Elder site (Figure 2).

The two tributaries created cold-water plumes that diffused into warmer mainstem temperatures across the river channel. This pattern was especially prominent at Cedar Creek where the water temperature difference between mainstem and tributary was greater overall (Figure 4, see Figure S1 for all 25 snorkels). In comparison, Elder Creek was only slightly cooler than ambient mainstem temperatures.

3.2 | Objective 2: Evaluate if and when confluence sites are used by juvenile steelhead

We observed an average of 148.2 steelhead (1.56 steelhead/m^3) per survey at the Cedar Creek confluence (0.84–2.22 steelhead/m^3) compared to 7.3 steelhead (0.05 steelhead/m^3) per survey at the Elder Creek confluence (0–0.23 steelhead/m^3). During the day, steelhead density reached its maximum during the 16:30 survey and declined at the 19:00 survey (Figure 3). As mainstem temperatures warmed through the summer (Figure 2), we observed more fish in both confluence sites. At Elder Creek, we counted 11 fish on the first day (June 20) and 116 fish on the last day (August 4, Figure 3). At Cedar Creek, we counted 546 fish on the first day (June 20) and 821 fish on the last day (July 30, Figure 3).

During our surveys at Cedar Creek, most juvenile steelhead were observed to be holding in fast waters or in pockets behind

boulders, and actively foraging with infrequent aggressive behaviours. At Elder Creek, juvenile steelhead were mostly observed to be foraging along substrate or swimming through the water column (not holding a foraging position). Little interaction among steelhead was observed. At the Cedar site, we seldom observed northern pikeminnow (*Ptychocheilus oregonensis*), a known invasive predator of steelhead (<2% of total fish counts). Since most pikeminnow were <5 cm and not big enough to prey on most juvenile steelhead observed, we assumed steelhead distribution was not significantly influenced by pikeminnow presence.

3.3 | Objective 3: Evaluate whether juvenile steelhead are distributed randomly within confluence plumes

At the Cedar confluence, steelhead were distributed randomly throughout the survey grid when mainstem temperatures were cool. Moran's I was close to 0 (Table S2) for all five snorkel surveys on June 20, with the exception of 11:30, and during the 9:00 snorkel surveys on all subsequent surveys. By 11:30, steelhead were clustered in the cold-water zone within the plume (positive and significant Moran's I, Table S2). Steelhead were increasingly clustered as the summer progressed (Table S2). Grid cells with the highest density of steelhead tended to be located at the edge of the cold-water plume, where mainstem and tributary waters mixed (Figure 4). In contrast, steelhead within Elder Creek confluence tended to be randomly distributed throughout the day and the summer (non-significant Moran's I values, Table S2, Figure S2).
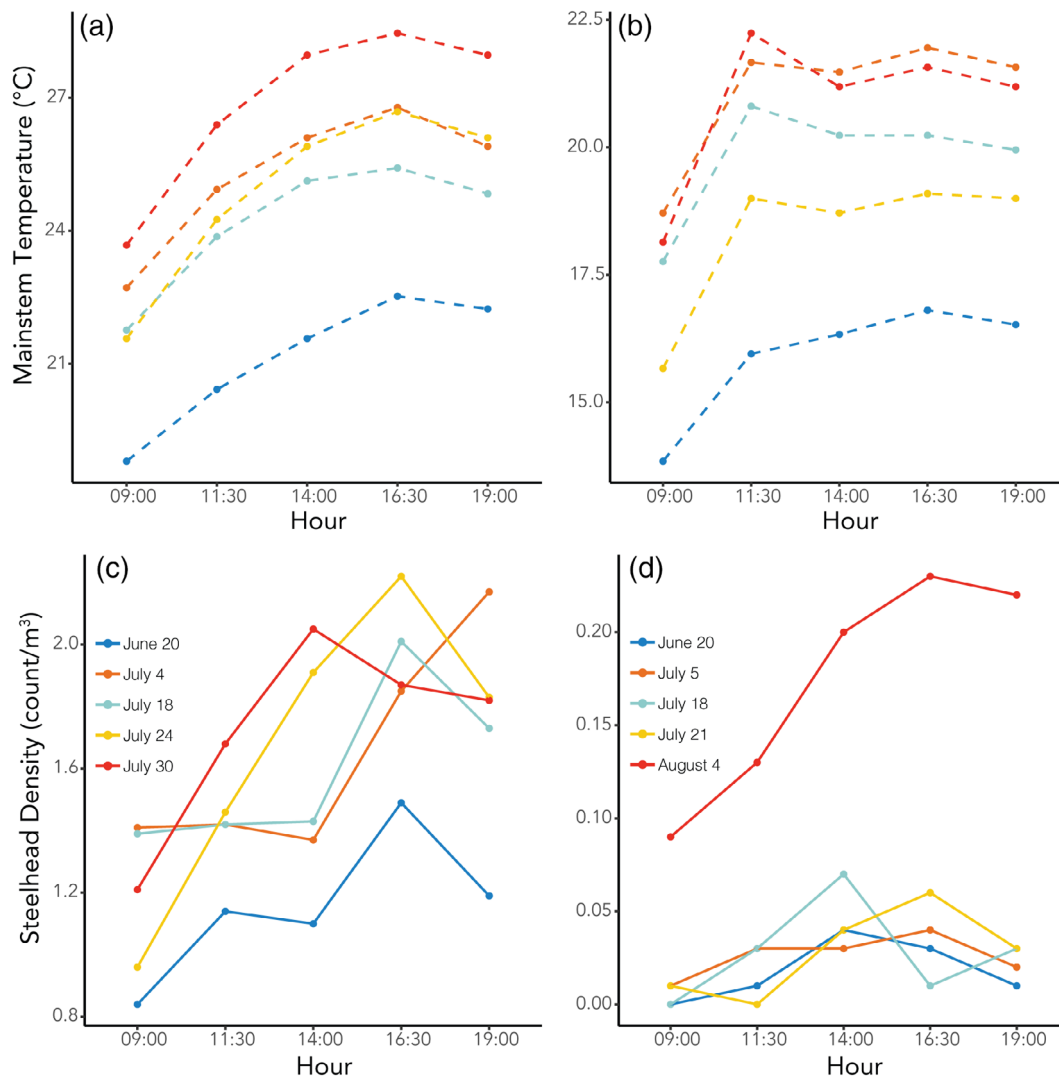
FIGURE 3 Recorded temperature of the South Fork Eel River at the start of each survey upstream of (a) Cedar Creek and (b) Elder Creek. Fish density in the confluence during each survey at (c) Cedar and (d) Elder. Days are coloured by rank in overall temperature from coolest to warmest (blue to red) [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Objective 4: Explore the role of temperature in determining juvenile steelhead positioning within confluence plumes

At both sites, steelhead density within the confluence plume was best predicted by a model that included the spatial mean and variance in temperature (Table 1). The results did not change if we excluded cells with zero steelhead observed (Figure S3), so following analyses include the entire dataset (Wang, Kelson, Greer, Thompson, & Carlson, 2020). At Cedar Creek confluence, the best supported model included mean temperature, variance in temperature and mean temperature squared (Table 1). This model revealed that juvenile steelhead density was strongly related to mean temperature (parameter coefficient estimate (est. ± standard error [SE] = 0.77 ± 0.10, t_{791} = 7.4, p < 0.001), mean temperature squared

(est. ± SE = −0.02 ± 0.002, t_{791} = −8.9, p < 0.001), and the variance in temperature (est. ± SE = 0.14 ± 0.02, t_{778} = 0.15, p < 0.001). Fish counts were mapped over the interpolated mean temperature surfaces (Figures 4 and S1) and temperature variance (Figure S4). During morning hours and early summer days, steelhead showed no strong pattern with mean temperature and temperature variance (i.e., June 20 9:00 and July 24 9:00, Figures S1 and S4). As the day and summer progressed, steelhead concentrated in grid cells of high temperature variance and around 21°C (see distributions on July 24 19:00 and July 4 19:00, Figures S1 and S4), even though cooler temperatures existed within the plume.

At Elder Creek confluence, the best supported model included mean temperature and variance in temperature (Table 1). Steelhead density increased with variance in temperature (est. ± SE = 0.22 ± 0.02, t_{182} = 9.6, p < 0.001) and, to a lesser degree, mean
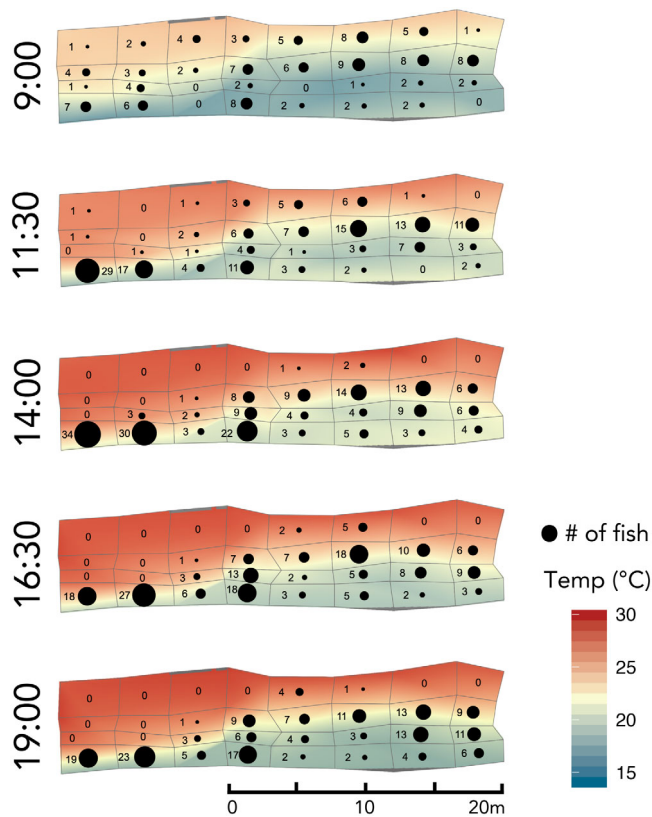
FIGURE 4 Fish counts from the Cedar Creek confluence plume overlaid on interpolated mean temperature for the July 30, 2016 surveys (plots for all dates and confluence sites included in the supporting figures) [Colour figure can be viewed at wileyonlinelibrary.com]

temperature (est. ± *SE* = 0.002 ± 0.008, t_{28} = 0.2, *p* = 0.82). Throughout the day and summer, steelhead within the Elder confluence plume showed no pattern with temperature and temperature variance (e.g. July 18 11:30, Figures S2 and S5). One exception occurred on August 4, when steelhead concentrated along the cold-water zone perimeter (Figures S2 and S5).

3.4.1 | Seasonal and daily variation in relationship between temperature and steelhead positioning within the confluence

We further explored the relationship between mean grid cell temperature and steelhead density to test for behavioural thermoregulation. We found no relationship between steelhead density and temperature at Elder (Figure S6). At Cedar, the strength of the quadratic relationship between steelhead density and temperature within the confluence plume varied daily and through the summer. We found that significant relationships between temperature and fish density emerged on the warmest days and the warmest times of day (Figure 5). On three warm days (July 4, 24, 30), there were significant quadratic relationships at 11:30, 14:00, 16:30 and

19:00. For the subset of statistically significant quadratic relationships, steelhead densities were highest for grid cells that had a mean temperature of 20.8°C, with an interquartile range of 19.7–21.6°C.

We found that the temperature difference between Cedar Creek and the mainstem explained considerable variation in the relationship between steelhead density and mean temperature of grid cell. R^2 values were positively related to the mainstem-confluence temperature difference ($F_{1, 23}$ = 10.06, *p* < .05, r^2 = .27) (Figure 6).

4 | DISCUSSION

The two tributary confluences in this study differed in their importance as thermal refuges for juvenile steelhead. While Cedar Creek and Elder Creek were relatively similar in temperature (11.8–19.9°C), the South Fork Eel River mainstem temperatures at Cedar Creek were much warmer (mean daily min-max of the South Fork Eel River at, Cedar Creek: 15.1–26.1°C, and at Elder Creek: 14.2–21.6°C). Consequently, the number of days in which steelhead experienced potential thermal stress (mainstem temperature > 21°C) was greater at Cedar Creek confluence compared to Elder Creek confluence (71 vs. 32 days). Likewise, there was a higher abundance and density of juvenile steelhead at Cedar Confluence, and in this confluence, fish density increased especially during warm days and warm times of the day (density: 0.84–2.22 steelhead/m³ at Cedar vs. 0–0.23 steelhead/m³ at Elder). Within the Cedar confluence, juvenile steelhead favoured microhabitats associated with lower mean temperatures and higher variance in temperature, which were located along the mixing zone of tributary and mainstem waters. Juvenile steelhead exhibited evidence of behavioural thermoregulation by selecting microhabitats associated with temperatures between 20–22°C despite the availability of cooler microhabitats closer to the tributary. Together, these results highlight that juvenile steelhead use cold-water confluences when and where mainstem temperatures are warm, and that juvenile steelhead within confluences display microhabitat selection.

4.1 | Spatial and temporal differences in the importance of confluences as thermal refuges

We found spatial variation in the importance of tributary confluences as thermal refuges. More steelhead used the Cedar Creek plume than the Elder Creek plume, which is consistent with temperature differences between these sites. The mean daily maximum temperature of the South Fork Eel River upstream of Elder Creek was 21.6°C. On the other hand, the mean daily maximum temperature upstream of Cedar Creek was much warmer (26.1°C) and reached an instantaneous high of 28.8°C. This temperature is close to 29.6°C, the critical thermal maximum temperature for juvenile steelhead (Myrick & Cech, 2005), and is well above 25°C, the temperature at which steelhead have nearly zero growth (Myrick & Cech, 2005), elevated homeostatic
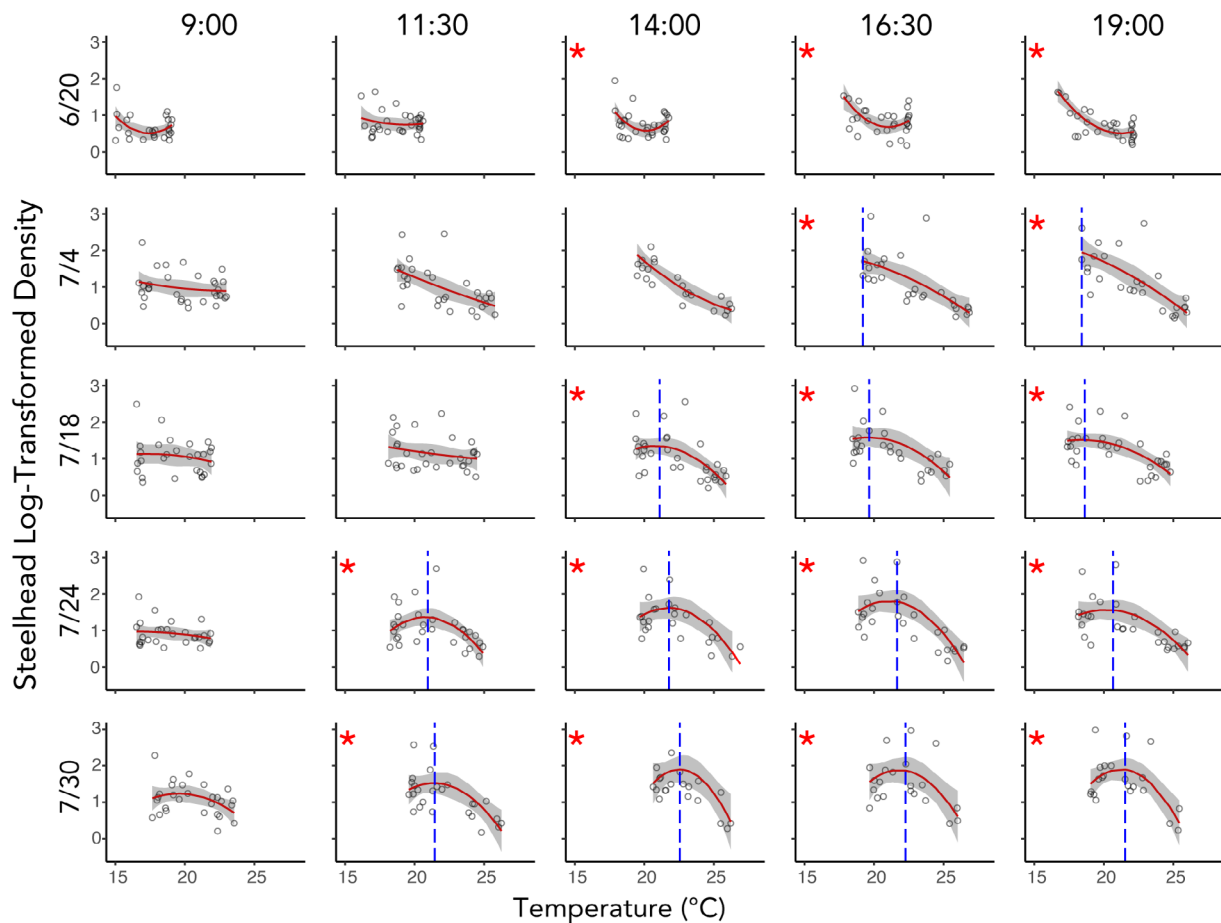
FIGURE 5 Quadratic regression models of log steelhead density versus mean temperature (red line) based on data collected at the grid cell level displayed for each survey date and time, with the 95% confidence interval in grey. Statistically significant ($p < .05$) models are marked with an asterisk. The temperature associated with the maximum estimated log steelhead density (the optimum temperature) is denoted with a dashed blue line [Colour figure can be viewed at wileyonlinelibrary.com]
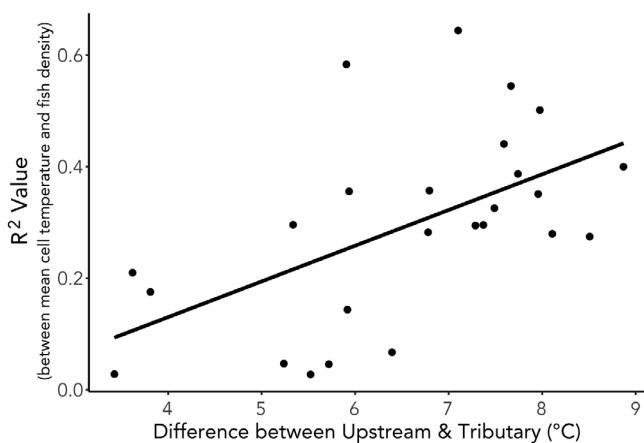

FIGURE 6 The R^2 value for each quadratic model of log steelhead density versus grid cell level mean water temperature (models in Figure 5) was positively correlated with the temperature difference between the South Fork Eel River (measured upstream of the confluence) and the Cedar Creek tributary inflow

stress levels (Campbell, Emlen, & Hershberger, 1998), and experience impaired smoltification (Marine & Cech, 2004). Additionally, our findings that juvenile steelhead increased their use of thermal refuges when mainstem temperatures increased above 21°C is consistent with research in nearby river systems (Nielsen et al., 1994; Brewitt & Danner, 2014; Sutton et al., 2007). Below this threshold, juvenile steelhead may avoid overcrowding by using the full extent of the river habitat, which tends to be more productive than confluence plume habitats (Kiffney, Greene, Hall, & Davies, 2006).

Additionally, we observed that more steelhead moved into confluences *when* mainstem temperatures were warmer. We observed more fish in the confluence plumes during the hottest time of the day (during our 16:30 survey) and in the late summer. This result mirrors previous observations of increased salmon in thermal refuges during the late afternoon (Sutton et al., 2007) and on days with larger diel swings in mainstem temperature (Brewitt & Danner, 2014). Our study confirms that tributary confluences are most important to salmonids when temperatures are warmest late in the day and late in the summer.

Although thermal differences between these two sites seem to be important drivers of steelhead distribution, other factors may partially explain why more steelhead were observed at Cedar confluence. Cedar Creek is further downstream, and drains a larger area than Elder Creek, so more juvenile steelhead have access to the Cedar site. Additionally, the mainstem surrounding Cedar Creek has more suitable physical microhabitats, such as large boulders for cover or food availability than Elder confluence, which could attract higher numbers of juvenile steelhead early in the summer. Future studies could incorporate more tributary confluences and examine variables such as food, habitat suitability, and fish mobility to evaluate differences in steelhead use among confluences.

4.1.1 | Behavioural regulation by juvenile steelhead

Our findings show that micro-spatial thermal variation within confluence plumes influences steelhead positioning. Surprisingly, juvenile steelhead trout were not found in the coldest water available within confluence plumes, and instead occupied micro-habitats with mean temperatures from 20 to 22°C (Figure 5). This temperature range can provide opportunity for fast growth for steelhead given sufficient food resources (Myrick & Cech, 2001).

Another intriguing result is that juvenile steelhead tended to cluster in areas with high temperature variance, particularly along the mixing zone of tributary and mainstem waters (Figure S4). These thermally variable locations may allow steelhead to thermoregulate at very fine scales, that is, within grid cells. Food availability and flow velocity might also vary along these boundaries and influence steelhead positioning. For example, Brewitt, Danner, and Moore (2017) found that steelhead in the Klamath River behaviourally thermoregulated by holding in thermal refuges, but moved in and out to feed on mainstem invertebrates. The role of food availability should be further explored to better understand fish micro-habitat selection in thermal refuges.

4.1.2 | Identifying important tributary confluences and thermal refuges

Identifying factors that influence the potential importance of a given confluence as a thermal refuge for cold-water fish is a high priority conservation target (Isaak et al., 2012; Kurylyk, Macquarrie, Linnansaari, Cunjak, & Curry, 2015), and we highlight a few general observations from our study. First, tributaries that supply a steady volume of cold water, or subsurface flow, into the mainstem throughout the hot summer are likely to create cold-water plumes and provide thermal heterogeneity in the mainstem rivers (Dugdale et al., 2013).

Second, confluences where nearby mainstem temperatures frequently exceed lethal temperatures are especially important as refuges. Since coarse climate models predict declines in the number of available thermal refuges for salmonids (Daigle, Jeong, & Lapointe, 2015), sites that are not currently used as thermal refuges but provide cold water outflow

all summer (e.g., Elder Creek) may become more important as mainstem temperatures warm with climate change.

We recommend avoiding definitions of thermal refuges that strictly use temperature thresholds. Thermal refuges for salmonid fishes have been defined using many approaches including areas with temperatures <23°C (Sutton et al., 2007), temperatures lower than the mean mainstem temperature (Baird & Krueger, 2003), and temperatures >3°C cooler than surrounding areas (Brewitt & Danner, 2014; Ebersole et al., 2015). However, Greer et al. (2019) demonstrated that different threshold-based definitions can lead to different conclusions about thermal refuge status and can over-simplify the nuances of a refuge. Thermal refuge evaluation should recognize the complex spatial and temporal patterns that characterize habitats and holistically incorporate other parameters, such as food availability (Brewitt et al., 2017).

Once identified as potential thermal refuges, tributary confluences could be managed to augment use of these thermal refuges by target species. For example, Biron and Lapointe (2004) placed channel deflectors in the mainstem just upstream of tributary confluence to allow for a further extension of cold-water plume into the river channel. However, this strategy would inhibit mixing of tributary and mainstem waters, and we found juvenile steelhead preferred these thermally mixed regions, which allow them to thermoregulate while feeding (Brewitt et al., 2017). On the other hand, management strategies such as riparian shading can reduce water temperature by up to 4°C (Ebersole et al., 2015) and provide cover from avian predators (Kurylyk et al., 2015), all while maintaining relatively undisturbed flows.

5 | CONCLUSIONS

Thermal refuges may be critical for the survival of salmonids during summer heat events (Torgersen et al., 1999; Mohseni, Stefan, & Eaton, 2003; Caissie, 2006). As rivers warm and the need for thermal refuges increases, so does the need to predict where critical thermal refuges are likely to exist and how they may be used by threatened species. We suggest that the tributary confluences are especially important where a high-volume cold-water tributary or subsurface seep flows into a relatively warm mainstem river. These cold-water zones may allow for the persistence of cold-water fishes in river reaches that are otherwise thermally unsuitable.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data avaailability statement: The data that support the findings of this study are openly available in [Dryad] at [https://doi.org/10.6078/D1J69Q].

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