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RESEARCH ARTICLE

Restored off-channel pond habitats create thermal regime diversity and refuges within a Mediterranean-climate watershed

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Cool-water habitats provide increasingly vital refuges for cold-water fish living on the margins of their historical ranges; consequently, efforts to enhance or create cool-water habitat are becoming a major focus of river restoration practices. However, the effectiveness of restoration projects for providing thermal refuge and creating diverse temperature regimes at the watershed scale remains unclear. In the Klamath River in northern California, the Karuk Tribe Fisheries Program, the Mid-Klamath Watershed Council, and the U.S. Forest Service constructed a series of off-channel ponds that recreate floodplain habitat and support juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) along the Klamath River and its tributaries. We instrumented these ponds and applied multivariate autoregressive time series models of fine-scale temperature data from ponds, tributaries, and the mainstem Klamath River to assess how off-channel ponds contributed to thermal regime diversity and thermal refuge habitat in the Klamath riverscape. Our analysis demonstrated that ponds provide diverse thermal habitats that are significantly cooler than creek or mainstem river habitats, even during severe drought. Wavelet analysis of long-term (10 years) temperature data indicated that thermal buffering (i.e. dampening of diel variation) increased over time but was disrupted by drought conditions in 2021. Our analysis demonstrates that in certain situations, human-made off-channel ponds can increase thermal diversity in modified riverscapes even during drought conditions, potentially benefiting floodplain-dependent cold-water species. Restoration actions that create and maintain thermal regime diversity and thermal refuges will become an essential tool to conserve biodiversity in climate-sensitive watersheds.

Key words: drought, habitat diversity, river restoration, salmonids, thermal refuge, thermal regimes, time series modeling

Implications for Practice

- River floodplain restoration projects that create thermal refuge can help maintain suitably cool habitat in the face of climate extremes like drought and heat waves.
- Even during a severe drought, restored off-channel ponds in the Klamath River maintained diverse thermal regimes and created thermal refuge habitats that likely benefited cold-water fishes.
- Building off-channel ponds connected to river mainstems is a relatively quick way of creating thermal habitat diversity in a watershed.
- As climate change and drought increase the importance of thermal refuge habitats in riverscapes around the world, managing thermal regimes will be increasingly critical to the integrity of river ecosystems and to river restoration efforts.

Introduction

Restoring river habitat to support healthy fisheries, ecosystems, and human communities is a global conservation priority, especially as regional climates change (Palmer et al. 2008). River ecosystems are particularly sensitive to climate change, and studies have identified significant climate-related increases in water temperature and thermal heterogeneity across riverscapes (e.g. Isaak et al. 2012). Changing thermal regimes can have major impacts on aquatic species, which are highly sensitive to large changes in water temperature due to climate or other factors (e.g. Woodward et al. 2010; Sullivan et al. 2021). As irregular climate patterns such as extreme drought and variable temperatures become more common (Swain et al. 2018), understanding how watershed thermal regimes are poised to change is an increasingly important aspect of planning river conservation and restoration actions (Olden & Naiman 2010; Arismendi et al. 2013; Steel et al. 2017).

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To address the thermal requirements of aquatic species in a changing climate, thermal refuges are an increasingly important riverscape feature. A freshwater thermal refuge is a spatiotemporally distinct habitat patch that organisms use to avoid stressful temperatures elsewhere in the river (Sullivan et al. 2021). In particular, cool-water refuges are critical for populations of aquatic species that exist in marginal habitats and frequently experience heat stress (Ebersole et al. 2020; Armstrong et al. 2021). Cool-water thermal refuges can form in many ways within a river system: tributary confluences (e.g. Brewitt et al. 2017), groundwater upwellings (e.g. Bilby 1984; Dugdale et al. 2015), deep pools (e.g. Tate et al. 2007), and off-channel floodplain areas (e.g. Dugdale et al. 2013) can all provide cooler habitats compared to the predominant temperature in the mainstem river (Sullivan et al. 2021). Cold-water fish such as salmonids especially benefit from cool-water refuges. Studies on both Pacific salmonids (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) have shown that access to cool-water refuges allows salmonids to avoid stressful or lethal water temperatures during summer heat waves (Dugdale et al. 2015; Hess et al. 2016). Coho salmon and steelhead with access to cool-water refuges have been shown to forage more efficiently by reducing heat stress in cooler areas and foraging in warmer, more prey-dense parts of the watershed (Brewitt et al. 2017). In northern California, thermal refuges have been shown to reduce exposure of juvenile coho salmon to the myxozoan parasite, *Ceratonova shasta*, because cooler areas have fewer parasitic spores and alleviate disease effects (Chiaramonte et al. 2016). Cool-water refuges in the Klamath watershed have also been shown to reduce lamprey wounds on redband trout (Ortega et al. 2023). Understanding thermal refuge dynamics in rivers that support coldwater fish is critical for conserving, restoring, and managing these ecosystems.

A key challenge to managing thermal refuges is understanding the timing and spatial distribution of thermal regimes throughout a riverscape. Coldwater fishes, for example can thrive in riverscapes with diverse thermal regimes that create areas with warmer water and more food availability, and areas with cooler water and less food but that act as refuges from high temperatures, floods, droughts, disease, and invasive species (e.g. Brewitt et al. 2017; Ebersole et al. 2020). Historically, thermal refuge habitats in stream systems were created by complex floodplain features such as oxbow lakes, springs, seeps, and seasonal flooding (Sullivan et al. 2021). Thermal regimes in such floodplain habitats are often dictated by geomorphic and hydrologic context, and temperatures in floodplain waters can vary greatly depending on elevation, climate, groundwater influence, water level, and connectivity to other waterbodies (Arscott et al. 2001). In particular, connections between groundwater and floodplain habitats are complex, and variability in the temperature and flow of groundwater can create thermal mosaics across habitats (Arrigoni et al. 2008). Connections to groundwater can also influence the dissolved oxygen (DO) concentration in water: depending on the source, groundwater that creates cooler thermal habitats can have high or low DO concentrations, which influences the quality of floodplain habitat for fish (Larsen & Woelfle-Erskine 2018). In many cases, channelization, river regulation, riverbank development, agriculture, and water diversions have damaged river–floodplain connections, and these habitats are often no longer accessible to fish (Bond et al. 2019).

In certain contexts, restoration efforts that focus on reestablishing connections between rivers and floodplains and reactivating floodplains as thermal refuges can help restore thermal refuge options in degraded watersheds (Steel et al. 2017). This approach is exemplified in the Klamath River watershed in northern California. To create refuge habitat for juvenile coho (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*), the Karuk Tribe Fisheries Program (KFP), in collaboration with the U.S. Forest Service and the Mid-Klamath Watershed Council (MKWC), collaborated to construct a series of human-made off-channel ponds throughout the mid-Klamath (MKWC 2014, 2020, 2022; Wickman et al. 2020). These off-channel ponds connect to shallow groundwater within the floodplain (MKWC 2014, 2020, 2022; Wickman et al. 2020). Groundwater upwelling into the ponds is thought to sustain these ponds as cool-water refuges during hotter periods of the summer. These ponds are especially important cool-water habitat during extreme drought, when fish need refuge from high water temperatures caused by low flow and extreme air temperatures (Maher et al. 2019). Juvenile coho salmon in the Klamath River begin to seek cooler waters at around 19°C, which occurs with increasing frequency in the Klamath River during summer, making the ponds a potentially critical refuge habitat (Sutton & Soto 2012; Asarian et al. 2020). Efforts to restore, create, or maintain cool-water refuge habitat are crucial restoration actions in systems like the Klamath River that support cold-water fishes. However, it is unclear whether localized restoration projects like off-channel ponds create a diverse selection of thermal refuges at a riverscape scale, particularly during stressful periods such as droughts. Additionally, few studies examine the long-term outcomes of thermal habitat restoration in a riverscape throughout recurring periods of drought. In this study, we analyze a decade of temperature data to explore thermal refuges and thermal regime diversity created by off-channel ponds in the mid-Klamath riverscape. We also measured DO in the off-channel ponds as a possible source of stress limiting refuge potential. We hypothesized that off-channel ponds would create cool thermal refuges because of groundwater connections, and that off-channel ponds would contribute to thermal regime diversity by adding unique regimes to the riverscape. Specifically, we predicted that: (1) off-channel ponds would have significantly different thermal regimes compared to creeks and the mainstem river; (2) off-channel ponds would provide cooler and more thermally stable habitats compared to creek and river habitats on daily and seasonal scales; and (3) thermal regime stability in ponds would increase over time. Testing these predictions may help reveal the potential and limitations of off-channel ponds for creating thermal refuges in degraded watersheds, especially under changing climate conditions.

Methods

Study Site

The Klamath River begins at Klamath Lake in southern Oregon and flows southwest through northern California to the Pacific

Ocean. The watershed is heavily impacted by hydropower dams, agricultural water diversions, megafires, and poor water quality (including high water temperatures) that have devastated populations of native salmonids (Asarian et al. 2020; Sarna-Wojcicki et al. 2019). To create cool-water refuge habitat, the KFP, National Forest Service, and MKWC have constructed a variety of off-channel, groundwater-fed ponds that provide habitat for juvenile coho salmon and steelhead (see summary of previous research and findings on these systems in Table 1). Our study focused on nine human-made ponds constructed between 2010 and 2019 in the mid-Klamath watershed. The ponds are located on Horse Creek and Seiad Creek (Fig. 1), which are both tributaries to the Klamath River. Goodman Pond is adjacent to Middle Creek, a tributary of Horse Creek. Ponds are human-made and are fed mainly by groundwater before flowing into the creek. Ponds range between 0.7 and 1.1 m average water depth during the summer but sustain higher water levels during the wet season (see Table 1).

As newly constructed habitats, these off-channel ponds were excavated with backhoes. They were sparsely vegetated at the start, and had large woody debris purposefully placed to enhance habitat heterogeneity. After construction, banks were stabilized with native grass seeding and weed-free straw, and additional native riparian plants were planted and tended at some ponds (MKWC 2014, 2020, 2022; Wickman et al. 2020). Aquatic vegetation was left to develop as time went on. As a result, ponds initially received full sun exposure, and the development and ongoing restoration plantings of riparian canopy cover and aquatic vegetation could influence thermal stability in these ponds over time.

Data Collection

We examined water temperature and air temperature regimes in the Mid-Klamath riverscape using temperature sensors and data from long-term monitoring programs. These datasets included several habitat types: off-channel ponds, creeks, and the mainstem Klamath River. Importantly, much of our data collection took place during the severe drought of 2020–2021, the second driest year on record in California (California Department of Water Resources 2021).

In July 2020, we deployed 30 temperature sensors (HOBO MX2201, Onset Corporation, Bourne, Massachusetts, U.S.A.) programmed to measure temperature every 15 minutes in ponds

Table 1. Evidence of salmonid use in off-channel ponds. Upper Lawrence and Lower Lawrence Ponds are the only ponds not included here.

Citation	*Findings relevant to this study*	*Ponds/creeks included in this study*
Witmore (2014)	• Evaluated movement patterns of juvenile coho in and out of ponds. • Juvenile coho growth and retention depends on pond-specific characteristics.	Alexander Pond
Krall (2016)	• Assessed accessibility, habitat conditions, food availability, and salmon density in ponds. • Recorded high salmon occupancy in ponds in the summer, but access to ponds was sometimes restricted. • Estimated salmon growth rates in ponds; growth rates mostly depend on fish density.	Alexander Pond, Stender Pond, Lower Seiad Pond, May Pond
Gorman (2016)	• Used Passive Integrated Transponder (PIT) tag data to track salmon rearing in off-channel ponds and non-natal tributaries. • Non-natal rearing in habitats like off-channel ponds can contribute to adult returns.	May Pond, Seiad Creek, Horse Creek
Faukner et al. (2019)	• Described numbers of juvenile coho PIT tagged in pond or creek locations in the mid-Klamath river watershed. • Fish tagged in off-channel ponds have low detection rates.	Horse Creek, Seiad Creek, Alexander Pond, Stender Pond, May Pond, Durazo Pond
Maher et al. (2019)	• Evaluated temperature, DO, and fish presence in Fish Gulch pond and Horse Creek. • Recorded acceptable temperature and DO levels for juvenile coho and steelhead.	Fish Gulch Pond, Horse Creek
MKWC (2014)	• Monitoring report detailing fish counts and temperature dynamics between 2010 and 2014. • Found that the pond buffered water temperatures and supported up to 1500 juvenile coho salmon in winter 2014.	Alexander Pond
Wickman et al. (2020)	• Monitoring report detailing fish counts and temperature dynamics between 2014 and 2019. • Pond supported about 300 juvenile coho salmon in 2019	Durazo Pond
MKWC (2022)	• Monitoring report detailing fish counts and temperature dynamics between 2016 and 2022. • Pond supported about 1300 juvenile coho salmon in January 2022.	Goodman Pond
MKWC (2020)	• Monitoring report detailing fish counts and temperature dynamics between 2014 and 2019. • Pond supported about 200 juvenile coho salmon in 2018.	May Pond

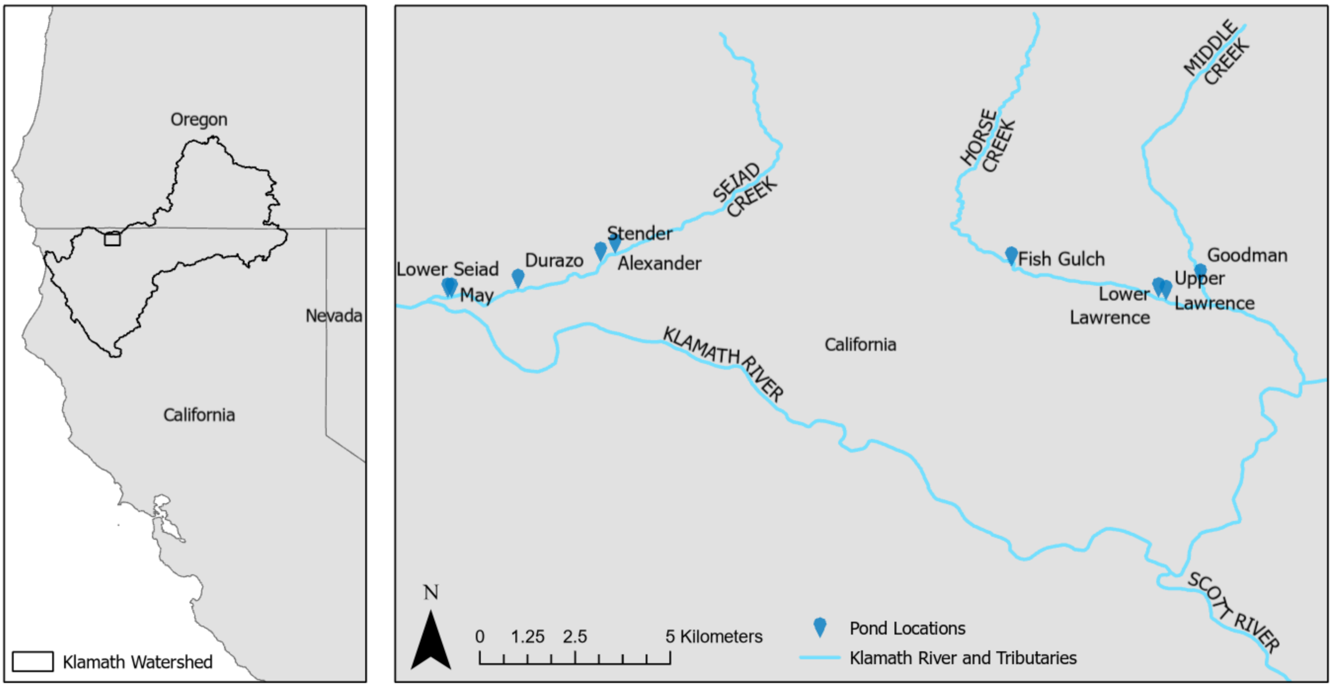

Figure 1. Seiad Creek and Horse Creek are neighboring watersheds feeding the Klamath River in northern California, United States. This study included five ponds on Seiad Creek (Alexander, Stender, Durazo, Lower Seiad, and May) and four ponds on Horse Creek (Fish Gulch, Goodman, Upper Lawrence, and Lower Lawrence). Goodman Pond is on Middle Creek, a tributary of Horse Creek.

and creeks. We placed one to four sensors in each pond to capture local-scale temperature variation. Sensors were installed at approximately one-third the water depth (at time of placement), except for two sensors in Goodman Pond, one in Upper Lawrence Pond, and one in Lower Lawrence Pond, where sensors were placed on the bottom of the pond. Sensors were placed near the outlet, around the sides, and as close to the center of the pond as possible. We chose these locations to capture within-pond variation in thermal habitat, to maximize access and safety, and to facilitate future monitoring. We also placed one sensor in the creek upstream of the outlet of each pond. We placed sensors between 7 and 13 July, 2020 and read them out between 11 and 13 July, 2021. We removed incomplete sensor time series ($n = 6$ pond sensors and $n = 3$ creek sensors) resulting either from sensor malfunction or sensors that were no longer submerged because of drought-related decreases in water level. In ponds and creeks with multiple sensors, we averaged remaining sensor readings to obtain an average time series per site. In the five ponds with only one sensor, we used that sensor's time series. We averaged sensor readings per site because sensors in the same site captured very similar patterns (see Table S1; Fig. S1). We calculated and modeled daily temperature means (instead of using sub-daily data) to avoid having to account for diel periodicity in the multivariate autoregressive model (MAR) models (Hampton et al. 2013; Holmes et al. 2023), which would have made these models unnecessarily complex.

Water levels in the pond fluctuated throughout the year, leading to different depths for the sensors throughout the study period, which could influence temperatures. We removed from analysis sensors that were completely out of the water (thus, recording air temperature rather than water temperature) because of depth fluctuations. To understand how well the remaining sensors represent thermal habitats in the ponds, we took post hoc temperature depth profiles in June 2023 at several locations in each pond (Fig. S2). We found that the location and depth of our long-term temperature sensors placed in 2020 were generally representative of temperatures found in the 2023 depth profiles. To further quantify any error that was introduced by fluctuating water depths throughout the year, we compared sensors at different depths for sites with more than one sensor. We found that sensors at different depths captured very similar patterns (Table S1; Fig. S1), suggesting that even if water depth fluctuated, sensor readings likely stayed relatively consistent.

Klamath River temperature data were collected by the Karuk Tribe and accessed with permission from the Karuk Tribe Water Quality Department (accessed 27 Sep 2022). We used data between May 2020 and February 2021. We used a combination of data readings from the Seiad Valley station as well as interpolated data using a linear regression from the Orleans station when Seiad Valley data was unavailable (5.5% of Seiad Valley data was interpolated). Additionally, we obtained air temperature time series from the National Oceanic and Atmospheric Administration's Climate Data Online database for Siskiyou County, California (NOAA 2020). We used the Slater Butte air sensor, located relatively close (13 km) to our study sites in Seiad Creek. Although these two sites differ in elevation (1423 vs. 430 m), we expected fluctuations in air temperature at these two locations to be correlated, and we note that our models quantify the effects of fluctuations around the mean rather than absolute values of air temperature (see next Section 2.3). Also, we measured DO in a single location in each pond over several days in July 2020 (Fig. S3), and we took post hoc DO and temperature depth profiles in each pond in June 2023 (Fig. S2). Finally, we analyzed historical temperature data from temperature sensors in Alexander and Stender Ponds, provided by MKWC. These are the two oldest ponds in the study and were constructed in 2010, and temperature data were collected hourly in these ponds from 2010 to 2021 via similar sensors to those we deployed (HOBO U22, Onset Corporation, Bourne, Massachusetts, U.S.A.). Each pond had a single HOBO U22 sensor that was placed in an accessible location near large woody debris on the side of the pond and suspended approximately one-third the depth of the pond.

Thermal Diversity

To analyze variation in thermal regimes across the riverscape, we used MAR models. The MAR model is a time series model that takes advantage of temporal correlation in environmental variables to estimate the effects of a particular driver, while also accounting for stochastic process error (Ives et al. 2003; Ruhí et al. 2015). MAR models can also incorporate environmental covariate data, which allows us to quantify the effects of external drivers on the process of interest (in our case, variation in water temperature). A MAR model in the matrix form can be expressed as follows:

$$X_t = BX_{t-1} + Cc_{t-1} + w_t, \text{where } w_t \sim \text{MVN}\,(0, Q) \qquad (1)$$

where temperature at a given day (X_t) is a function of temperature the previous day (X_{t-1}) plus sensitivity to a covariate, here variation in air temperature (Cc_{t-1}); and process error (w_t). As a covariate (c_{t-1}), we used a time series of air temperature with a 1-day time lag, after examining support for other lags (results not shown); and the C matrix captured site-specific sensitivity to air temperature. In turn, process error (w_t) was drawn from a multivariate normal (MVN) distribution, with mean zero and covariance matrix Q. In our case, Q captured stochasticity in water temperature (i.e. temporal variation in water temperature that was unrelated to air temperature). B is an interaction matrix that can model the effect of each state on itself (diagonal parameters) and on each other (off-diagonal parameters). In our case, we set off-diagonal parameters to zero (as we did not expect sites to interact with each other) and estimated the diagonal parameters, often used to capture "density-dependence" in population processes, or pull-back to mean. When analyzing a thermal regime, these B parameters capture how fast temperature goes back to the mean after an anomalously high or low value (in our case, a warmer- or colder-than-average day).

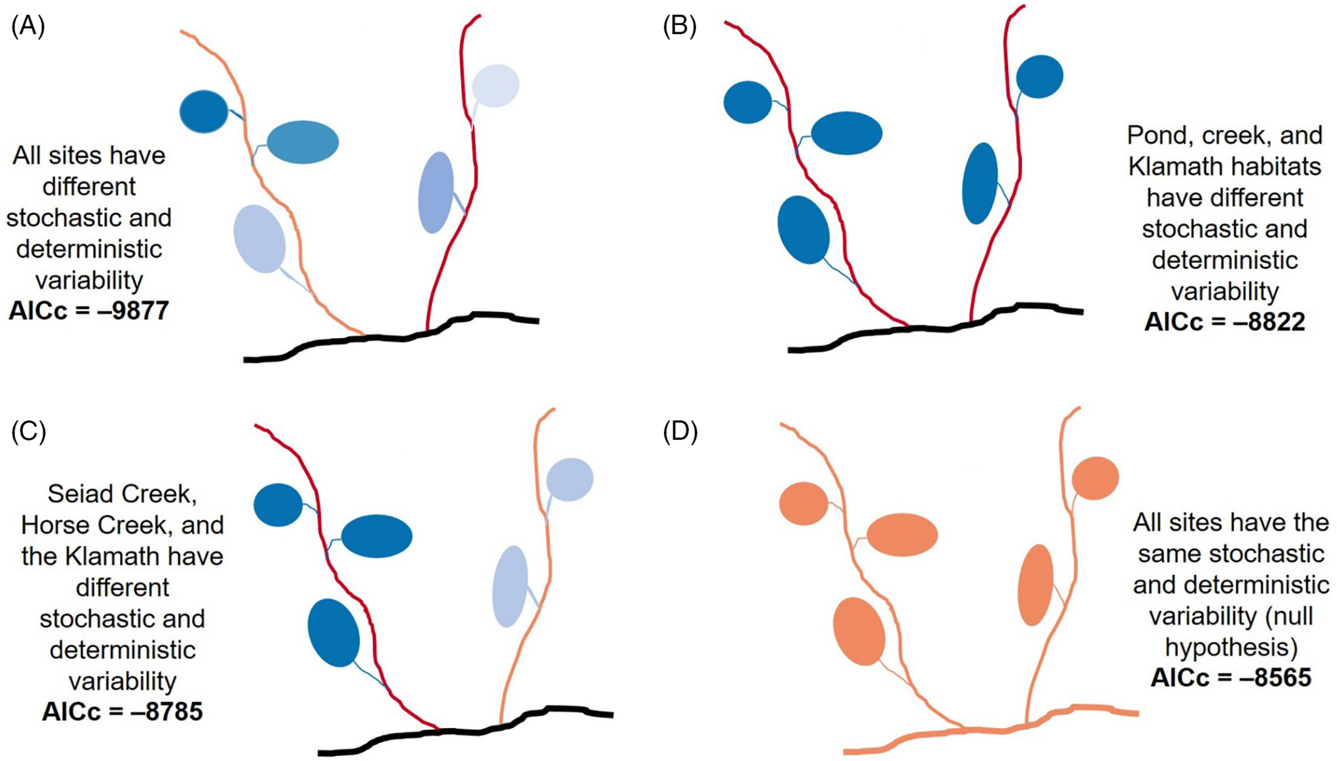

Figure 2. Four hypotheses representing different levels of thermal diversity in the riverscape. In the multivariate autoregressive (MAR) model, we allowed for different levels of complexity in stochastic variability (Q, variation due to random chance) and deterministic variability (C, variation due to changes in air temperature), ranging from a complex array of site-specific regimes (A) to a simple, watershed-wide thermal regime (D). Colors represent different configurations of deterministic and stochastic variability in ponds, creeks, and the mainstem river. We compared the four models using Akaike's information criterion corrected for small sample size (AICc), in which the best supported model has the lowest AICc score.

To test our first prediction that off-channel ponds have significantly different thermal regimes compared to creeks and the mainstem, we developed four MAR model hypotheses that represent different levels of complexity in thermal regimes (as in Leathers et al. 2022). Each hypothesis was tested by manipulating the matrices of the MAR model, capturing stochastic or "unexplained" variation (*Q* matrix), and deterministic or covariate-explained variation (*C* matrix). This strategy allowed modeling mean daily temperatures among pond, creek, and river habitats in different ways (Fig. 2). The first hypothesis was that all sites had different levels of stochastic and deterministic variability (i.e. as many thermal regimes as sites). The second hypothesis was that each habitat type (pond, creek, and river) had some typical level of stochastic and deterministic variability, but sites within the same habitat type did not differ from each other. The third hypothesis predicted that stochastic and deterministic variability depended on the watershed (Horse Creek vs. Seiad Creek vs. Klamath River), but not the specific site or habitat type. The fourth hypothesis predicted that all sites would have the same level of stochastic and deterministic variability (i.e. a single, watershed-level thermal regime). We used Akaike's information criterion corrected for small sample size (AICc) to compare support for the different hypotheses. All data and covariate data was *z*-scored, and model outputs were examined for normality and autocorrelation of residuals via the autocorrelation function. We used the MARSS package version 3.11.3 (Holmes et al. 2023) in R (R Development Core Team 2021).

Thermal Buffering

To quantify thermal buffering of ponds (relative to creeks), we compared daily maximum temperatures (averaged across all sensors in a site, see Table S1; Fig. S1) in each pond and creek during the three hottest months of 2020 (15 July–15 September), and then ran a one-way analysis of variance (ANOVA) of temperature as a function of site. We repeated the same process for the winter, focusing on daily minimum temperatures during the three coldest months (15 December, 2020–15 February, 2021). We assured that model residuals met assumptions of normality and homogeneity of variances.

We also assessed daily thermal buffering capacity of ponds and creeks by calculating the coefficient of variation (CV) for each day, using 15-minute temperature data. We then averaged daily CVs for each site over the yearlong study period. We used mean CV values to calculate the ratio of creek to pond CV for each pond/tributary pairing. If the creek:pond CV ratio was equal to or less than 1, that suggested no significant buffering took place. If the ratio was greater than 1, we considered the pond to "buffer" thermal fluctuations compared to the creek.

Thermal Stabilization Over Time

We used wavelet analysis to examine thermal regimes in the frequency and time domains, and to determine whether some scales of variation strengthened over time. Wavelet analysis is useful because it localizes the contribution of each frequency to a given time series, and is not sensitive to the assumption of stationarity (Torrence & Compo 1998). Although the wavelet method does not require pre-specifying a frequency of interest, here we focused on temperature variation at diel (24 hours) and seasonal scales (12 months), and asked whether diel and seasonal variation changed over the years. We interpolated missing values in the historical temperature datasets for Alexander and Stender Ponds (3.3 and 3.9% of days, respectively) via an autoregressive integrated moving average model (ARIMA) and a Kalman filter. An ARIMA model is generally expressed as ARIMA(p, d, q), where p is the order of the autoregressive model, that is the dependence of the model on prior values; d is the order of non-seasonal differences, that is degree of differencing of raw observations; and q is the order of the moving average, that is

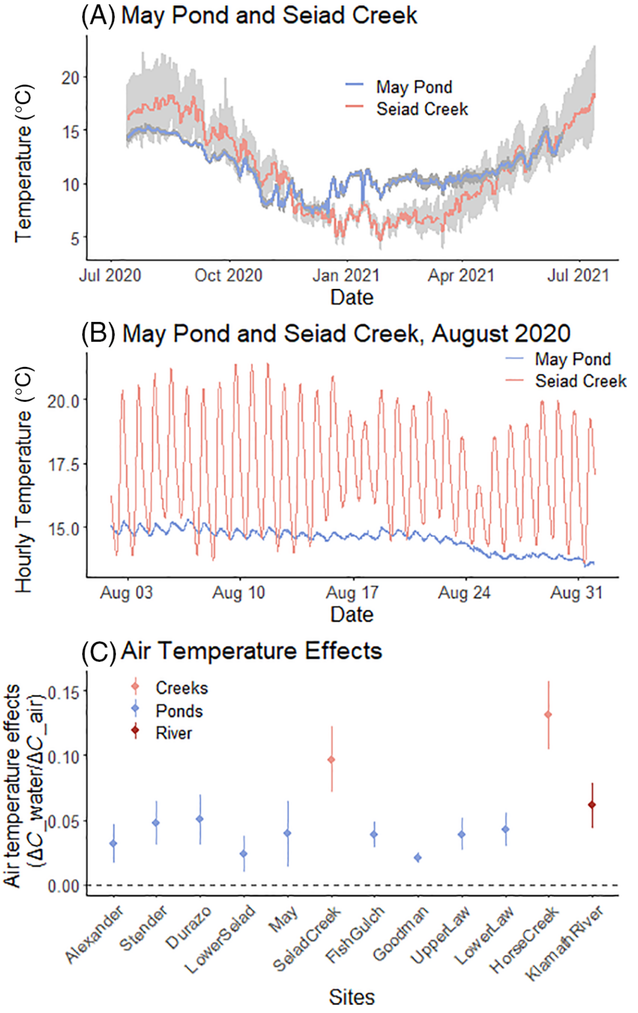

Figure 3. (A) Daily mean temperatures in May Pond (blue) and Seiad Creek (red) throughout the study period. Gray lines display 15-minute temperature readings. (B) Daily temperatures in May Pond (blue) and Seiad Creek (red) in August 2020. May Pond exhibits the strongest thermal buffering. (C) Air temperature (*C*) effects in the best supported multivariate autoregressive model (MAR). Air temperature was a significant covariate for all ponds, and Horse Creek and Seiad Creek had particularly strong air temperature effects compared to ponds. Error bars denote 95% CIs for the air temperature (C) effects.

Table 2. MAR model hypotheses and AICc values. Model 1 was the best supported model with the lowest AICc score.

Hypothesis	*Model number*	*AICc*
All states have *different* levels of stochastic (Q) and deterministic (C) variability	Model 1	−9877
Each *habitat type* (creeks, ponds, Klamath) have different levels of stochastic (Q) and deterministic (C) variability	Model 2	−8822
Each *watershed* (Horse Creek, Seiad Creek, and Mainstem Klamath) have different levels of stochastic (Q) and deterministic (C) variability	Model 3	−8785
All states have *same* levels of stochastic (Q) and deterministic (C) variability	Model 4	−8565

the model's dependence on longer-term values and stochastic "shocks." After identifying the best-fit ARIMA model, we used the Kalman filter to interpolate missing data. We then ran wavelets on the complete time series, using the WaveletComp package in R (Roesch & Schmidbauer 2018). We used the Morlet wavelet function and compared observed power to a null background generated with red noise (i.e. temporally autocorrelated data).

Results

Off-Channel Ponds Increase Thermal Diversity Within the Riverscape

Our analysis of riverscape temperatures showed that thermal regimes varied significantly between linked pond, creek, and river habitats (Fig. 3A). The best supported MAR model (i.e. the model with the lowest AICc score, model 1) allowed all sites (each pond, creek, and river) to have different levels of stochastic (Q) and deterministic (C) variability (Table 2; Fig. 2). As such, we can infer that each pond contributes a distinct thermal regime to the riverscape and increases thermal habitat options. Additionally, previous-day air temperature significantly influenced water temperature at all sites, as evidenced by the air temperature parameter not including zero at any sites. Notably, the creek habitats were more sensitive to air temperature (i.e. higher C parameter values) than pond or river habitats, as indicated by air temperature effects for creeks being higher and not overlapping with pond or with river habitats (Fig. 3C).

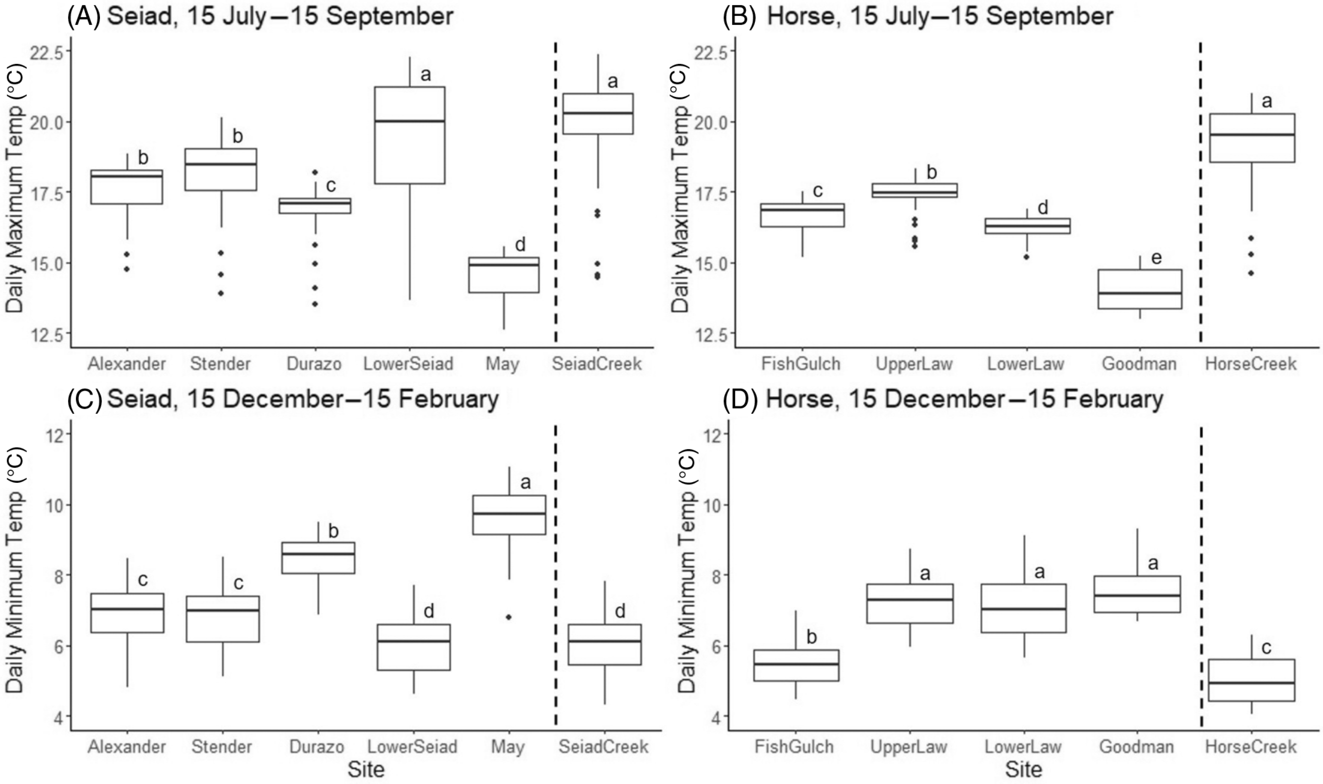

Figure 4. Boxplots showing daily maximum temperatures for the three hottest months in the study period (15 July–15 September, 2020) for (A) Seiad ponds and creek and (B) Horse ponds and creek. All ponds were significantly cooler than creeks except for Lower Seiad Pond. (C) and (D) show boxplots of the daily minimum temperature of the three coldest months in the study period (15 December–15 February, 2020–2021). Ponds were significantly warmer than creeks except for Lower Seiad Pond. Letters represent significant groupings from ANOVA analysis. The vertical dashed line in each graph is a visual aid to separate the pond and creek habitats (ponds are on the left of the line, and creeks are on the right).

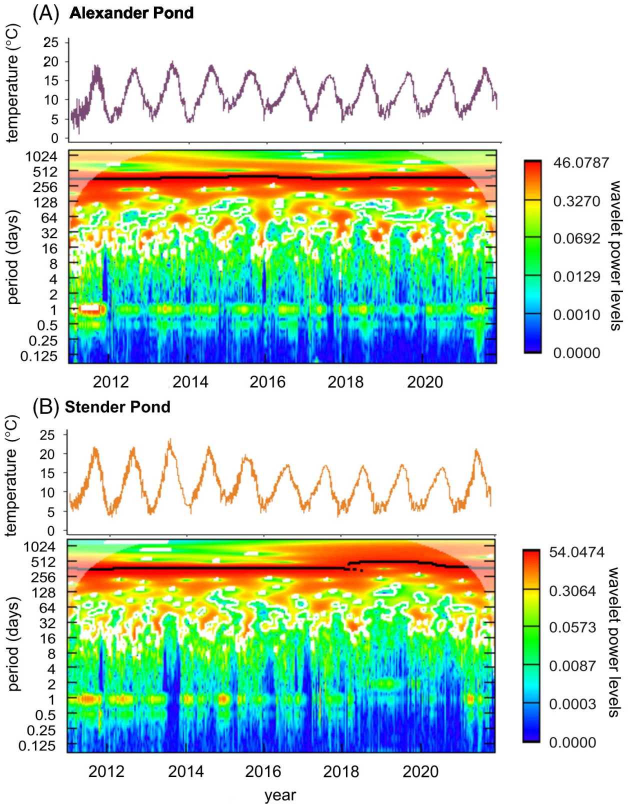

Figure 5. Hourly water temperatures from 2010 to 2020 and wavelet diagrams for Alexander (A) and Stender (B) Ponds. Wavelet diagrams identify the contribution of each frequency to the power, or strength, of a particular thermal regime. More powerful regimes with a stronger frequency are red, and less powerful regimes are blue. Statistically significant frequencies are outlined with a white line. Both ponds exhibit strong seasonal frequencies (period = 365 days) because of strong and regular temperature fluctuations in winter and summer. Both ponds also show strong frequencies at the daily scale (period = 1 day) because the cycle of day and night creates a strong and regular thermal fluctuation. In both ponds, the daily frequency becomes smaller and less red over time, indicating that daily temperature fluctuations decreased over the 11-year timespan. We predict this decrease in the power of daily regimes is due to the development of aquatic and riparian vegetation that provides shading.

Off-Channel Ponds Provide Diel and Seasonal Thermal Buffering

Ponds buffered extreme hot and cold-water temperatures in winter and summer. Daily maximum temperatures for the three hottest months of the year were significantly cooler in most ponds compared to creeks on both Seiad Creek ($F_{[5,360]} = 125.70$, $p < 0.001$) and Horse Creek ($F_{[4,299]} = 300.90$, $p < 0.001$), except for Lower Seiad Pond, which was not significantly cooler than Seiad Creek in the summer ($p = 0.672$; Fig. 4A & 4B). Daily minimum temperatures for the three coldest months were warmer in ponds compared to creeks on both Seiad Creek ($F_{[5,360]} = 168.80$, $p < 0.001$) and Horse Creek ($F_{[4,300]}$- $= 170.00$, $p < 0.001$; Fig. 4C & 4D), again with the exception of Lower Seiad Pond, which was not significantly warmer than Seiad Creek in the winter ($p = 0.999$).

Ponds also buffered daily water temperatures compared to creeks. The ratio of creek CV to pond CV was greater than one for all ponds, indicating that daily pond temperature varies less than creek temperature. However, we observed variation in the magnitude of buffering: the highest buffering was in May Pond (creek:pond CV = 5.3; Fig. 3B) and Goodman Pond (creek:pond CV = 5.06), and other ponds exhibited less than half that value (Table S2).

Off-Channel Ponds Thermally Stabilize Over Time

Wavelet analysis of the long-term series for Alexander and Stender Ponds (2010–2021) indicated fluctuations at the seasonal (1 year) scale and at the 24-hour scale (Fig. 5). The annual signal remained important across the whole decade, indicating predictable, seasonal fluctuations in water temperature (i.e. winter vs. summer). However, the strength of the 24-hour signal declined over time (despite a small spike in 2021), suggesting that diel fluctuations in temperature (i.e. day vs. night) became less pronounced as pond succession advanced.

Discussion

Cool-water thermal refuges are increasingly critical habitat features for cold-water fishes in watersheds experiencing warming conditions (e.g. Steel et al. 2017). Restoration projects that create a diverse suite of cool-water thermal refuges, such as the off-channel ponds in this study, are examples of floodplain restoration practices that create large volumes of cooler water and restore thermal regimes; however, to what extent these habitats may be valuable under warmer, drier futures remains largely unknown. We found that (1) human-made, off-channel ponds had thermal regimes that were significantly different than their adjacent creek and the mainstem Klamath River; (2) ponds provided cooler and more thermally stable habitats compared to creek and river habitats; and (3) thermal regime stability in ponds generally increased over time, with some exceptions in a severe drought year. Overall, our study shows that off-channel ponds in the mid-Klamath watershed create thermal regime diversity and thermal refuges within the riverscape, adding to the growing evidence on the potential benefits of this restoration strategy. We contend that this approach may be particularly beneficial in Mediterranean-climate watersheds with seasonally and interannually variable hydroclimates, provided other critical conditions are met (e.g. access to the pond, sufficient DO). Understanding the spatial and temporal dimensions of restored cool-water thermal refuges is becoming critical, given the ongoing and projected warming trends (e.g. Albert et al. 2021).

Off-Channel Ponds Increase Thermal Diversity Within the Riverscape

Based on the results of our MAR model, each of the nine off-channel ponds had a distinct thermal regime and contributed to overall thermal diversity. This finding supports our hypothesis that as large bodies of water with robust groundwater inputs (MKWC 2014, 2020, 2022; Wickman et al. 2020), off-channel ponds represent significantly different thermal habitats compared to creek or river sites. Diverse thermal regime options such as those created by these off-channel ponds are important features within a riverscape. Such habitat diversity allows mobile animals like fish to balance tradeoffs in food abundance and water temperature (e.g. Brewitt et al. 2017). In a system with stressful thermal conditions for salmonids, such as high summer temperatures in the mainstem Klamath River (Sutton & Soto 2012), the diverse thermal options provided by these ponds can be critical for salmonid survival. Other studies in the Klamath River identified tributary mouths as a source of cool thermal refuges for salmonids moving between the mainstem and tributaries (e.g. Sutton et al. 2007; Sutton & Soto 2012; Brewitt et al. 2017). In this ecosystem, juvenile salmonids in the mainstem Klamath River seek thermal refuge when temperatures reach around 19°C (Sutton & Soto 2012). In the summer during our study, daily maximum water temperatures in Horse Creek averaged 19.14°C and Seiad Creek were 19.9°C, slightly exceeding the threshold for salmonids seeking refuge. Ponds, on the other hand, were several degrees cooler, averaging at daily maximums of between 16.1°C in the Horse Creek watershed and 17.4°C in the Seiad Creek watershed during the summer. Thus, our results suggest that off-channel ponds likely provide salmonids with a diversity of thermal habitats across the watershed—a facet of "biocomplexity" that may contribute to stabilizing population portfolios (Hilborn et al. 2003; Schindler et al. 2010). Thanks to the diversity of life-history, behavioral, and physiological traits in salmonid populations (e.g. Barrett & Armstrong 2022), floodplain ponds conferring thermal diversity likely help salmonid metapopulations cope with high summer temperatures.

Off-Channel Ponds Provide Diel and Seasonal Thermal Buffering

In addition to increasing thermal diversity, off-channel ponds also buffered against changes in air temperature—a critical function in light of increasing frequency of heatwaves (Tassone et al. 2022). Our MAR analysis showed that off-channel ponds exhibited significant sensitivity to air temperature, but pond sensitivity was much lower than creek or mainstem river sensitivity. We suspect that ponds are less sensitive to changes in air temperature because they are deeper, have higher thermal mass and volume-to-surface ratios, and are more connected to groundwater compared to creeks (MKWC 2014, 2020, 2022; Wickman et al. 2020). Other studies measuring thermal sensitivity to air temperature in snowmelt-fed streams in California's Sierra Nevada (Leathers et al. 2022), or in high-latitude streams in Alaska (Lisi et al. 2015), have generally reported higher thermal sensitivities than our study. Our measurements reflect an extreme drought period but still exhibited low thermal sensitivity compared to other published values. This highlights the strong buffering potential of ponds against hot periods, which may insure sensitive fish populations against transient heatwaves (Tassone et al. 2022) as well as long-term, directional warming (Arismendi et al. 2013). This is particularly important in the drought-stricken U.S. West: in the Klamath River, summer water temperatures have warmed over the last 20 years due to climate change, reduced snowpack, and decreased flows (Dettinger et al. 2015; Asarian et al. 2020).

We also found that the ponds created daily and seasonal thermal stability compared to adjacent creeks or the mainstem Klamath River. Daily maximum temperatures in the summer were up to 5°C cooler in ponds compared to adjacent creeks, while daily minimum temperatures in the winter were up to 3°C warmer in ponds compared to creeks. Overall, off-channel ponds buffer water temperatures throughout various seasons, meaning they likely stay closer to the physiological optima of cold-water fish in both summer and winter months. This buffering capacity also occurs within a day. Hourly temperature data showed that pond temperatures fluctuated far less than creek temperatures throughout day–night thermal cycles during summer months. Additionally, all ponds had thermal buffering capacity, as described by a ratio of creek to pond CVs as greater than one. Buffering capacity was highest in May Pond (5.3) and Goodman Pond (5.06), which are large, deep ponds with strong groundwater inputs.

Off-Channel Ponds Thermally Stabilize Over Time

The ponds received some assisted revegetation, and they were subsequently colonized by native and invasive vegetation that created canopy cover, habitat structure, and shading over time (T. Soto, Karuk Tribe Fisheries Program, personal observation July 2021). As canopy cover developed, we predicted that daily temperature fluctuations in the ponds would become more stable with increasing shade. As expected, wavelet analysis of Alexander and Stender Pond indicated that daily thermal stability increased over 10 years. However, the pattern of increasing daily thermal stability broke down in 2021, when daily temperatures fluctuated more widely than prior years in Alexander and especially Stender Pond. The years 2020–2021 were exceptionally dry and hot (California Department of Water Resources 2021), but the mechanism that caused pond thermal stability to break down during this drought is not clear, especially given that we did not observe similar patterns during the 2012–2016 drought (Lund et al. 2018). However, even though the daily thermal stability of Stender and Alexander Ponds declined in 2021 compared to prior years, the ponds retained buffering capacity compared to adjacent creeks and provided cooler, more stable thermal environments. This illustrates the importance of analyzing not only temperature averages and extremes, but also the scale and predictability with which regimes fluctuate (Arismendi et al. 2013). Extreme temperature variation at short timescales may be stressful to aquatic species (e.g. Nelson & Palmer 2007), and understanding this variation is important to classifying the impacts of climate events such as the 2021 drought.

Salmonid Conservation

Sullivan et al. (2021) define a thermal refuge in the context of temperate river basins as "a cold-water patch used by poikilotherm (i.e. fishes) avoiding higher temperatures." We have not presented data on fish use of these ponds in this study; however, other studies have shown that juvenile salmonids used these ponds as refuge habitat throughout the year. Annual fish surveys by MKWC and the KFP indicated that these ponds are used by juvenile coho salmon and steelhead, although fish populations, community composition, and age structure in each pond vary by year throughout the watershed. Growth rates of juvenile salmonids rearing in the ponds depend on a variety of factors, including fish density (Witmore 2014; Krall 2016). Other studies of non-natal rearing in the Klamath watershed suggest that non-natal rearing, including in the ponds, can contribute to adult returns (Gorman 2016). Thus, the studied off-channel ponds likely provide important rearing habitats for juvenile salmonids in this watershed.

Critically, habitat intended as refuge can become an ecological trap (Schlaepfer et al. 2002) if a pond becomes isolated and fish are no longer able to leave when needed, e.g. to access better food sources, migrate to the ocean, or avoid predators. In several of these ponds, outflow channels connecting the pond to the creek can dry out by late summer, trapping salmonids in ponds and preventing other individuals from entering until winter rains rewet the outflow channel. In other cases, winter flows may create sediment plugs that cut off outflows. In this system, sediment plugs form most frequently in ponds with weak groundwater inputs and outflow channels connected at 90° to the creek, compared to oblique angled outlets (e.g. MKWC 2014). MKWC and the KFP have been experimenting with rock structures, beaver dam analogs, and post-assisted log structures that increase water level and connectivity of pond outlets. This work highlights an important point: restored floodplain habitats often require continued human intervention to maintain connectivity with the rest of the watershed, which is key to ensuring that these habitats operate as refuges rather than traps. The specific methods for maintaining lateral (river-to-floodplain) connectivity may vary across watersheds that differ in geomorphic and hydrologic background (e.g. Arrigoni et al. 2008). We do note that periodic connectivity is an inherent property of floodplains, and the risk–reward trade-off of using floodplain habitat has existed during the evolution of salmon using floodplains (e.g. Jeffres et al. 2008). Thus, occasional disconnect from the mainstem does not necessarily mean that these habitats are ecological traps. Further research on how intermittent access to pond habitats may affect salmonid behavior, foraging, and survival would help contextualize their role as thermal refuges (e.g. Krall 2016).

Another important consideration when restoring floodplain habitat for salmonids is DO availability. Inadequate levels of DO can impair activity, growth, and survival for juvenile salmonids (Carter 2005). In experimental settings at 15°C, juvenile coho salmon started to display oxygen growth dependence around DO concentrations of 4 mg/L and displayed zero growth below concentrations of 2.3 mg/L (Brett & Blackburn 1981). However, in northern California, juvenile coho salmon have been shown to survive in habitats with low DO concentrations by inhabiting microsites with higher DO (Woelfle-Erskine et al. 2017). In this study, we measured DO at a single location in each pond over several days in July 2020, and we took post hoc DO and temperature depth profiles in each pond in June 2023. In seven out of nine ponds, DO in at least the first 50 cm of the pond was above the 4 mg/L threshold. Additionally, in several ponds we recorded areas with DO supersaturation, likely due to photosynthesis from algae and macrophytes, indicating some pond microhabitats may provide relief from low-DO areas at least during the day (e.g. Woelfle-Erskine et al. 2017). However, Goodman and Lower Lawrence Ponds exhibited many DO measurements below 3 mg/L. Although fish have been recorded using Goodman Pond (e.g. MKWC 2022), this is cause for concern and DO in Goodman and Lower Lawrence ponds should be more thoroughly monitored.

Apart from floodplain restoration in general, our research calls attention to the importance of incorporating thermal regimes into restoration actions in dam-impacted rivers (Olden & Naiman 2010; Wohl et al. 2015; Palmer & Ruhi 2019). In the Klamath River, four dams in the upper part of the watershed are scheduled for removal in 2023 and 2024 (Klamath River Renewal Corporation 2020; Blumm & Illowsky 2022). The off-channel ponds in this study will be used for relocating fish from the mainstem prior to reservoir draw-down to protect them from fine sediment flushing during dam removal (Klamath River Renewal Corporation 2020; T. Soto, Karuk Tribe Fisheries Program, personal observation July 2021). Additionally, new off-channel ponds will be constructed in dam reservoir footprints post-dam removal. In addition to long-term restoration strategies such as dam removal, off-channel ponds offer quick support to depressed coho populations, providing a relatively fast-acting restoration strategy that creates diverse thermal habitats for salmonids.

Our study has shown that in the mid-Klamath River watershed, human-made off-channel ponds are effective at creating diverse thermal refuge habitats that likely benefit cold-water fishes. These thermal refuges persist even during severe drought. However, beyond our study watershed, the geomorphic and hydrologic context of other riverscapes may lead to different results. Critically, the ponds described in this study have persistent sources of well-oxygenated groundwater that help create large volumes of cooler water, and these groundwater sources were investigated before pond excavation began (e.g. MKWC 2014). Ponds also require some level of continued human maintenance to ensure pond outflows stay connected to the rest of the river network (e.g. MKWC 2014). Use of these ponds as thermal refuge by salmonids and other cold-water species may be variable and influenced by other concurrent restoration efforts in the watershed. Thus, applying this restoration strategy to other river systems should be approached with appropriate consideration. Overall, as climate change and droughts increase the importance of access to thermal refuge habitats in riverscapes (e.g. Tassone et al. 2022), managing thermal regimes will be increasingly critical to the integrity of river ecosystems.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Temperature time series from all sensors included in the study, grouped by site.

Figure S2. Depth profiles of dissolved oxygen and temperature taken in each pond in 2023 in the daytime during the DO maxima.

Figure S3. Dissolved oxygen data recorded in each pond in July 2020.
Table S1. For each site with more than one sensor, this table shows the mean difference and standard deviation of daily differences between each pair of time series.

Table S2. Coefficient of variation (CV) for each individual creek and pond.

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