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ARTICLE

Thermal Regimes, Nonnative Trout, and Their Influences on Native Bull Trout in the Upper Klamath River Basin, Oregon

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Abstract

The occurrence of fish species may be strongly influenced by a stream's thermal regime (magnitude, frequency, variation, and timing). For instance, magnitude and frequency provide information about sublethal temperatures, variability in temperature can affect behavioral thermoregulation and bioenergetics, and timing of thermal events may cue life history events, such as spawning and migration. We explored the relationship between thermal regimes and the occurrences of native Bull Trout *Salvelinus confluentus* and nonnative Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* across 87 sites in the upper Klamath River basin, Oregon. Our objectives were to associate descriptors of the thermal regime with trout occurrence, predict the probability of Bull Trout occurrence, and estimate upper thermal tolerances of the trout species. We found that each species was associated with a different suite of thermal regime descriptors. Bull Trout were present at sites that were cooler, had fewer high-temperature events, had less variability, and took longer to warm. Brook Trout were also observed at cooler sites with fewer high-temperature events, but the sites were more variable and Brook Trout occurrence was not associated with a timing descriptor. In contrast, Brown Trout were present at sites that were warmer and reached higher temperatures faster, but they were not associated with frequency or variability descriptors. Among the descriptors considered, magnitude (specifically June degree-days) was the most important in predicting the probability of Bull Trout occurrence, and model predictions were strengthened by including Brook Trout occurrence. Last, all three trout species exhibited contrasting patterns of tolerating longer exposures to lower temperatures. Tolerance limits for Bull Trout were lower than those for Brook Trout and Brown Trout, with contrasts especially evident for thermal maxima. Our results confirm the value of exploring a suite of thermal regime descriptors for understanding the distribution and occurrence of fishes. Moreover, these descriptors and their relationships to fish should be considered with future changes in land use, water use, or climate.

Water temperature is an important driver of physiological processes, ultimately manifesting its influence in the patterns of occurrence and distribution of aquatic organisms (Gillooly et al. 2001). This is particularly true for coldwater species, such as salmonids, that have relatively narrow thermal tolerances (McCullough et al. 2009). Most field-based studies of the

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relationship between temperature and salmonid occurrence have focused on only one or two summary descriptors of temperature. For example, the broader distribution of salmonids has been explained by mean or maximum summer temperatures (e.g., Eaton et al. 1995; Dunham et al. 2003b; Isaak et al. 2015), but it is unlikely that a single descriptor of temperature is the sole driver behind the observed patterns. In other words, mean or maximum temperature can explain much of the variability in fish distributions but these simple descriptors of temperature cannot account for the multiple ways in which temperature actually influences fish (Hughes and Grand 2000; McCullough et al. 2009). Accordingly, it may be more useful to consider a broader range of temperature descriptors that account for the magnitude, frequency, variability, and timing of thermal events across space and time—more generally referred to as thermal regimes (Poole et al. 2004; Caissie 2006; Arismendi et al. 2013).

Field-based studies that consider a more complete range of descriptors of thermal regimes for predicting the occurrence of salmonids are just beginning to emerge. Recent work (Butryn et al. 2013) found that coupling the magnitude of temperature with the number of days above a given temperature (i.e., frequency) improved the accuracy in predicting the presence of native Brook Trout *Salvelinus fontinalis* (see also Falke et al. 2013). Similarly, work on nonnative Brook Trout invasion indicated that consideration of summer mean temperatures and winter degree-days improved the prediction of species presence (Benjamin et al. 2007). Other studies have considered how fish respond to the simultaneous effects of the magnitude and duration of thermal exposure, showing that higher-magnitude exposures are likely tolerated for shorter durations (Wehrly et al. 2007). Results of these studies collectively point to the importance of considering a more complete range of thermal descriptors for predicting patterns of fish occurrence.

In addition to the influence of water temperature, the occurrence of salmonids can be influenced by the presence of other salmonids (Taniguchi et al. 1998; Dunham et al. 2002; Wenger et al. 2011a) as well as physical conditions within streams (Fausch et al. 1994; Benjamin and Baxter 2012). For instance, native Brook Trout in eastern North America are often displaced by nonnative Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*, whereas in western North America, nonnative Brook Trout and Brown Trout often displace the native trout, including Cutthroat Trout *O. clarkii* and Bull Trout *Salvelinus confluentus* (Dunham et al. 2002; Fausch 2008). Interactions between native and nonnative salmonids can be strongly influenced by water temperature when nonnative trout inhabit and are competitively superior in warmer temperatures relative to the native trout (Taniguchi et al. 1998; Taniguchi and Nakano 2000).

Bull Trout offer an ideal case study for exploring the use of thermal regimes to predict occurrence because Bull Trout are strongly tied to cold water temperatures (Selong et al. 2001). Moreover, in the presence of nonnative salmonids, Bull Trout can be restricted to higher-elevation, colder reaches (Paul and Post 2001; Rieman et al. 2006; Isaak et al. 2015), possibly due to a competitive advantage of nonnative trout in warmer water (McMahon et al. 2007). Previous studies on the distribution and occurrence of Bull Trout have largely been focused on physical habitat or geomorphic features (Watson and Hillman 1997; Baxter et al. 1999; Ripley et al. 2005). Although it is clear that temperature is critical for Bull Trout and is a major management concern, relatively few studies have used direct measures or predictions of water temperature to explain the variable presence of Bull Trout at a landscape extent (Al-Chokhachy et al. 2013), and those studies that did so only used a single metric (Dunham et al. 2003a; Jones et al. 2014; Isaak et al. 2015; but see Howell et al. 2010). To our knowledge, no previous studies have explored the use of multiple descriptors of thermal regimes to explain the occurrence of Bull Trout.

In this study, we used 2 years of continuously measured temperature data to calculate a suite of thermal regime descriptors in a river basin that is inhabited by native Bull Trout as well as nonnative Brook Trout and Brown Trout. Specifically, our objectives were to (1) define the thermal regimes (descriptors of thermal magnitude, frequency, variability, and timing) associated with the presence of the different trout species; (2) provide a more generalized model of Bull Trout occurrence in relation to the best descriptors of thermal regime, nonnative trout occurrence, and environmental variables; and (3) estimate the upper thermal tolerances of the three trout species under natural conditions.

METHODS

Study Area

The upper Klamath River basin is the southernmost limit of the Bull Trout's range and provides a diverse hydrologic template (Gannett et al. 2007). The basin drains mountainous terrain that is largely underlain by permeable volcanic rock, which contributes to substantial fluxes of groundwater influencing lakes, streams, and other water bodies. Elevations in the basin range from roughly 1,250 m to more than 2,700 m. Climate varies accordingly: winters are cold (minimum air temperatures are commonly below 0°C) and summers are warm, with temperatures typically exceeding 15°C at higher elevations and 20°C at lower elevations. On average, annual precipitation is about 35 cm at lower elevations and more than 165 cm at higher elevations, with snow representing most of the precipitation in the latter (Nolin and Daly 2006). Native salmonid fishes in the upper Klamath River basin include Bull Trout and Rainbow Trout. Populations of anadromous Chinook Salmon, Coho Salmon *O. kisutch*, and steelhead (anadromous Rainbow Trout) were once present, but all are currently extirpated due to the lack of passage over downstream dams (Hamilton et al. 2005). Nonnative salmonids in streams of the upper Klamath River basin include Brook Trout and Brown Trout.

Stream Temperature Sampling

Field sampling was focused entirely on quantifying the spatial and temporal variation in stream temperature. Our sampling frame included all streams with designated critical habitat for Bull Trout in the upper Klamath River basin (USFWS 2010; Figure 1), encompassing habitats within three major subbasins: (1) tributaries entering the basin from the north and west, including the Wood River and smaller streams draining the eastern flank of the Cascade Mountain Range; (2) tributaries to the Sycan River in the northeast portion of the basin; and (3) tributaries to the Sprague River. Bull Trout were also historically present in the Williamson River according to collections made by E. D. Cope in 1879 (Gilbert 1897), but this major river basin is not classified as critical habitat for Bull Trout at present. Within the sampling frame, study sites were drawn from a set of points distributed from a generalized random tessellation stratified design (Larsen et al. 2001; Stevens and Olson 2004). This was done to ensure that we sampled a range of variability in thermal regimes and other potential predictors and to avoid bias in subjective site location (i.e., based on previous surveys or ease of access).

With sample locations identified, we deployed temperature loggers (HOBO Water Temperature Pro v2 Data Loggers, U22-001; Onset Computer Co., Pocasset, Massachusetts) at 87 sites via the methods described by Dunham et al. (2005). Temperature was recorded every hour at 66 sites over two consecutive years (from June or July 2010 to October 2012) and at 21 sites over one consecutive year (from June or July 2010 to October 2011; or from October 2011 to October 2012). To our knowledge, thermographs during the two study years were not overly warm or cold, but instead were average. Temperature loggers were placed in deep pools that were well mixed to ensure that the loggers would remain

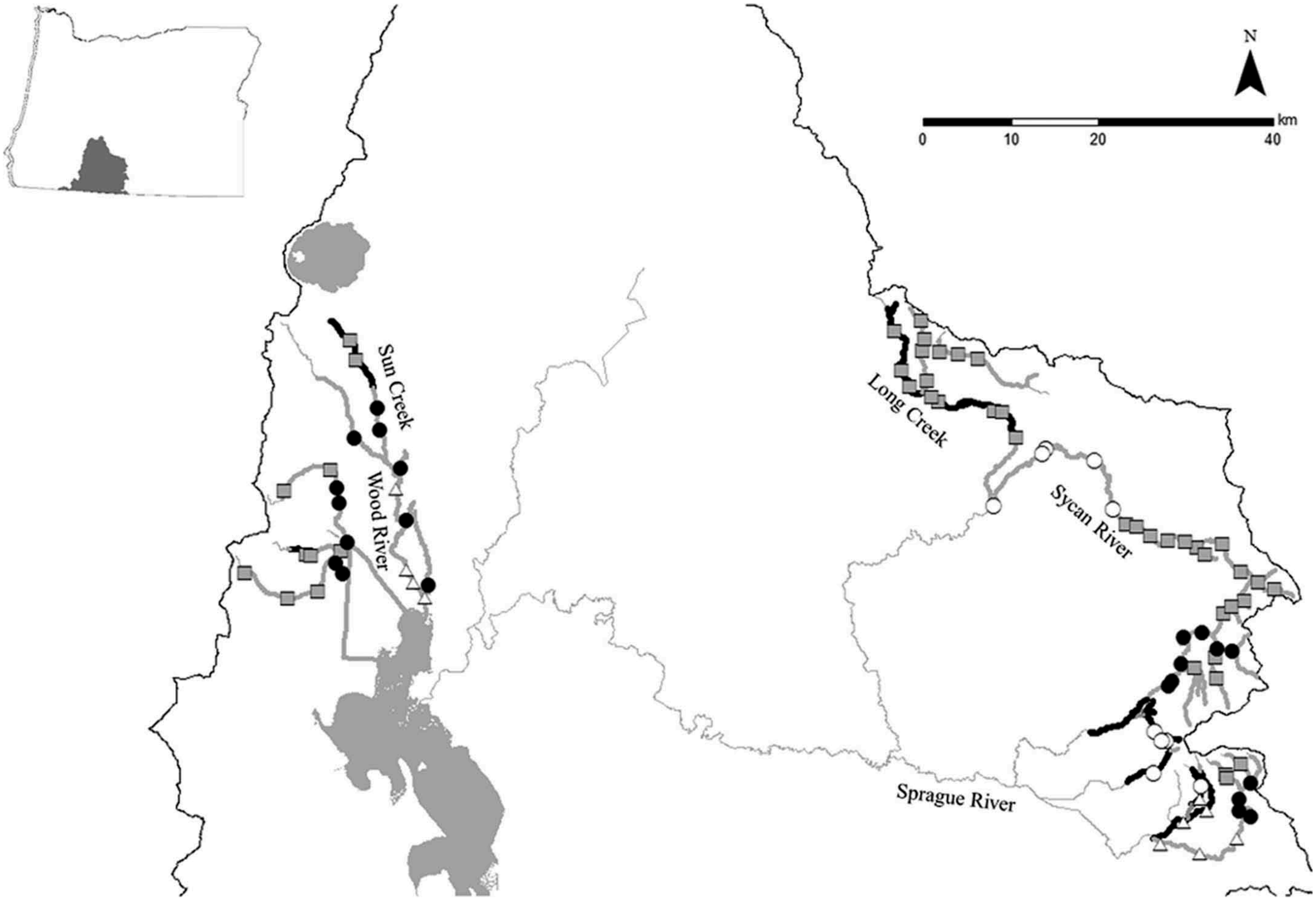

FIGURE 1. Upper Klamath River watersheds in Oregon, with symbols representing locations where temperature was measured and where thermal regimes were quantified; Bull Trout critical habitat is denoted with bold lines. If a symbol overlays a bold gray line, then Bull Trout were absent; if a symbol overlays a bold black line, then Bull Trout were present (see Methods, Stream Temperature Sampling, for more details). Open circles represent locations where neither Brook Trout nor Brown Trout were present; gray squares represent locations where Brook Trout were present; open triangles denote locations where Brown Trout were present; and black circles denote locations where both Brook Trout and Brown Trout were present.

underwater for the duration of the study and provide accurate measurements. Prior to deployment, temperature loggers were calibrated in cold (0.0°C) and warm (31.0°C) water baths to correct for bias (accuracy of ±0.2°C relative to a National Institute of Standards and Technology-certified digital thermometer). Upon removal of the temperature loggers, temperature data were inspected to remove—and if possible correct for—potential discrepancies (Dunham et al. 2005).

Spatial Covariates

Because trout occurrence can be influenced by local habitat and watershed characteristics in addition to temperature, we included a small subset of additional explanatory variables that could be estimated from spatial data (ArcGIS version 10.1; ESRI, Redlands, California). We initially considered five variables: elevation (m), gradient, mean annual discharge (m^3/s), catchment area (km^2), and Strahler stream order. All variables were derived from a 10-m-resolution digital elevation model and a stream segment layer in the National Hydrography Database Plus (http://www.horizon-systems.com/nhdplus/). If two variables were highly correlated with each other ($r > 0.70$), we omitted one variable. Catchment area and stream order were excluded on this basis because they were highly correlated with mean annual discharge and with each other. Thus, we fitted models with up to three habitat variables (elevation, gradient, and mean annual discharge; described below).

Fish Occurrence

Lack of available resources precluded formal sampling of fish in association with our sampling of stream temperatures, so we relied on existing local information to determine the presence of salmonids at sampled locations. We identified the occurrences of Bull Trout, Brook Trout, and Brown Trout by using three complementary approaches. First, the occurrence of Bull Trout was determined from pre-existing data compiled by the U.S. Fish and Wildlife Service (USFWS; USFWS 2010). Specifically, Bull Trout were classified as present if they were documented in a stream reach within the last four generations (i.e., listed as "occupied") and if the habitat within a stream reach was classified as "spawning and rearing." Otherwise, Bull Trout were classified as absent. Second, the presence of Brook Trout and Brown Trout was based on previous surveys (Dambacher et al. 1992; Ziller 1992; Buktenica et al. 2013) and professional judgement of local biologists from the Oregon Department of Fish and Wildlife, USFWS, U.S. Forest Service, and National Park Service. The latter was determined by having local biologists outline on a map the distribution of Brook Trout and Brown Trout without restrictions to specific life stages or seasonal use. We assumed that these distributions represented multiple life stages that had been present for a sufficient duration to interact with and potentially impact Bull Trout. In one stream (Sun Creek; $n = 4$ sites), nonnative trout were eradicated to restore a remnant Bull Trout population (Buktenica et al. 2013), which could confound our attempts to link the distributions of these species to ambient environmental conditions. Thus, we used pre-eradication conditions for Brook Trout and Brown Trout present at the two lower-elevation (<1,400 m) Sun Creek sites and for Brook Trout and Bull Trout present at the two higher-elevation sites. Third, if discrepancies occurred among expert opinions, we verified occurrence with hook-and-line sampling in September 2010 or with snorkel surveys in August 2011 ($n = 19$).

The lack of fish occurrence data during the time that temperature was recorded is not unique to this study (e.g., Al-Chokhachy et al. 2013; Isaak et al. 2015). Matched fish and temperature data are obviously preferable because studies that explicitly address capture or sighting probabilities and detectability (e.g., Thurow et al. 2006) or that use methods with a very high probability of detection (Wilcox et al. 2016) can provide a more unbiased perspective. However, the reliance on existing information and expert opinion to identify the presence of trout has been used successfully and has shaped some of our current thinking of the relationship between trout occurrence and temperature (Dunham et al. 2003a; Wenger et al. 2011a; Isaak et al. 2015).

Data Analyses

Thermal regimes and trout occurrence.—We calculated a suite of temperature metrics that described the magnitude, frequency, variability, and timing of thermal events at our study sites (Arismendi et al. 2013). All metrics were calculated using hourly data collected from April 1 through September 30 in 2011 and 2012. We collected temperature data year-round, but visual inspection of summary statistics did not show any differences between sites with and without trout during winter months (October 1–March 31; Supplementary Figure S.1 available in the online version of this article), potentially because their energy use was similar across a range of thermal regimes during those months (Hansen and Rahel 2015). In addition, some sites were compromised by freezing. Thus, we removed winter temperature data from the analyses. Magnitude metrics included the mean temperature, maximum temperature, maximum weekly maximum temperature (MWMT), maximum weekly average temperature (MWAT), and total monthly degree-days for April–September. Frequency metrics included the total number of days exceeding 16, 18, and 20°C, respectively, at each site. These temperature thresholds cover a range of biological criteria applied by the state of Oregon for water quality compliance (Oregon administrative rules; arcweb.sos.state.or.us/pages/rules/oars_300/oar_340/340_041.html). Variability descriptors included the mean and maximum daily variance and range. Timing descriptors included the cumulative temperature distribution (CTD), defined as the date when each site reached the 25th, 50th, or 75th percentile of its total degree-days. Descriptors were calculated for each site ($n = 87$) and then were averaged over the study period.

Modeling of Bull Trout occurrence.—We were primarily interested in predicting the occurrence of Bull Trout, and we fitted models that included temperature descriptors, environmental variables, and indicator variables for the presence of nonnative trout (Brook Trout or Brown Trout). This was done in three steps, similar to methods described by Wenger et al. (2011a, 2011b). First, we generated a correlation matrix to evaluate collinearity among descriptors within each thermal regime descriptor (magnitude, frequency, variability, and timing). As expected, variables within each descriptor were strongly correlated (Pearson's product-moment correlation coefficient $r > 0.80$) for most pairwise comparisons, whereas correlations varied across descriptors. When collinearity of predictor variables is an issue, potential approaches are to (1) choose one variable from each group, (2) create linear combinations of variables, or (3) use ordination methods, such as principal components analysis (Zuur et al. 2009). We chose the first approach, as it allowed us to focus on descriptors that were easily calculated from hourly temperature data and that might be more directly related to management criteria (e.g., Oregon water quality compliance standards).

Our second step was to compare the model fit of the temperature descriptors within each thermal regime descriptor (magnitude, frequency, variability, and timing). We fitted hierarchical logistic regression models with each descriptor plus a random effect for each of the three sampled subbasins within the upper Klamath River basin (Figure 1) to evaluate the association between individual temperature descriptors and the presence of Bull Trout. The best thermal regime descriptor was then selected by using Akaike's information criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002).

Third, we fitted global models with the best thermal regime descriptor, indicator variables for the presence of nonnative trout (Brook Trout or Brown Trout), and environmental variables (elevation, gradient, and mean annual discharge). Prior to fitting models, we standardized the predictor variables by subtracting by the mean and dividing by 2 SD to improve model convergence (Gelman and Hill 2007). Initially, models were fitted without a random effect for subbasin. Visual inspection of deviance residual plots suggested evidence of spatial autocorrelation owing to the presence of nonrandom spatial patterns. We calculated Moran's I-value, which is a measure of spatial autocorrelation based on Euclidean distances among sites, and again found evidence of spatial autocorrelation ($P > 0.05$). To account for the hierarchical structure of our data, which could have caused the observed spatial autocorrelation, we added subbasin as a random effect. This appeared to improve the fit of our models based on re-evaluation of residual plots and Moran's I. For the best thermal regime descriptor, the global model and all possible model subsets were ranked by AIC$_c$ score, and the most plausible model (i.e., that with the lowest AIC$_c$ score) and all models with a cumulative average Akaike weight (w_i) of 0.95 or less were retained for inclusion in the 95% confidence set (Burnham and Anderson 2002). Model performance was evaluated by calculating the area under the curve (AUC) of the receiver operating characteristic plot and prediction accuracy at the 0.5 level by using the ROCR package in R. These descriptors indicated how well the model performed in predicting Bull Trout presence/absence at our study sites (i.e., misclassification rate).

Finally, because more than one temperature descriptor may be important for predicting trout occurrence, we evaluated models with the best-supported thermal regime descriptor. We used a two-step process wherein we (1) fitted a global model with the best temperature metric in each thermal regime from step 2 above (i.e., the four best temperature predictors) and two trout indicator variables, considered all possible subsets of this model, and ranked models based on the AIC$_c$ score; and (2) added the three environmental variables to the most plausible model (i.e., the model with the lowest AIC$_c$ score), evaluated all possible subsets of that model, and selected the best model. We used this two-step approach when evaluating models with multiple temperature metrics to improve model convergence. In addition, we estimated the importance of each metric by summing the w_i of each model in the confidence set containing that metric (Burnham and Anderson 2002). The purpose of this modeling exercise was to evaluate whether including multiple temperature metrics improved our ability to predict Bull Trout occurrence.

Upper thermal tolerance limits.—We estimated upper thermal tolerance limits of Bull Trout, Brook Trout, and Brown Trout for chronic and acute exposures under natural conditions in the upper Klamath River basin via the methods of Wehrly et al. (2007). Briefly, we calculated the average daily mean and average daily maximum temperatures at each site for 10 exposure periods (1, 3, 7, 14, 21, 28, 35, 42, 49, 56, and 63 d). The average daily mean and maximum were calculated for each exposure period by using a moving average between April 1 and September 30, and the highest moving average value was selected within each exposure period. The upper thermal tolerance limit for the average daily mean and maximum was estimated as the warmest 10% of sites, or the 90th-percentile value, for each exposure period where each trout species was present. Next, we used nonlinear least-squares regression to fit an exponential function to the exposure period and the corresponding 90th-percentile temperature. Separate regressions were fitted for each species and each metric (i.e., average daily mean and average daily maximum), which allowed for comparisons with other studies (Selong et al. 2001; Wehrly et al. 2007). We compared the upper thermal tolerance limits for the three species by calculating bootstrapped 90% confidence intervals around the pairwise differences between the sample quantiles. If a confidence interval did not contain zero, we inferred that the upper thermal tolerance limits for the respective species differed. We repeated these calculations for each exposure period.

RESULTS

Thermal Regimes and Trout Occurrence

Warm thermal events were greater in magnitude, frequency, and variability and earlier in timing at sites where Bull Trout were absent than at sites where Bull Trout were present (Figure 2; Table S.1). For magnitude, the average (±SE) maximum temperature was less at sites where Bull Trout were present (14.86 ± 0.76°C) than at sites where Bull Trout were absent (17.63 ± 0.51°C). Similar results were observed for MWMT and MWAT. Monthly degree-days were consistently cooler at sites where Bull Trout were present than at sites where they were absent, with the greatest difference occurring in June and July. The frequency of days with temperatures exceeding 16, 18, and 20°C was lower at sites where Bull Trout were present. For variability, we observed a narrower range and lower variance at sites occupied by Bull Trout compared to sites where Bull Trout were absent. The timing descriptor (CTD) suggested that sites where Bull Trout were absent heated up more quickly than sites that contained Bull Trout. For example, sites without Bull Trout reached the 50th-percentile CTD 4 d earlier than sites where Bull Trout were present.

Similar to the results for Bull Trout, sites with Brook Trout were associated with cooler temperatures and fewer warm events that occurred later in the year relative to sites without Brook Trout (Figure 2; Table S.1). However, Brook Trout were present at sites that were more variable in temperature than sites without Brook Trout, and their presence did not appear to be associated with the timing descriptor. In contrast to Bull Trout, Brown Trout were present at sites that were warmer and that heated up faster (timing descriptor) compared to sites without Brown Trout. However, temperature variability and the number of days that exceeded 16, 18, and 20°C were similar between sites with and without Brown Trout. Brown Trout were not present in the Sycan River subbasin, and this may have skewed the results.

Modeling of Bull Trout Occurrence

Based on our model predictions, the best-supported temperature metric for Bull Trout in the upper Klamath River basin was June degree-days, a measure of magnitude in the thermal regime (Table 1). The best-approximating model (AIC_c = 62; w_i = 0.29) included June degree-days (estimate ± SE = –8.24 ± 1.75), the occurrence of Brook Trout (–4.03 ± 1.39), and elevation (–5.49 ± 2.54). Based on this model, Bull Trout in the upper Klamath River basin can occupy warmer sites when Brook Trout are absent compared to sites where Brook Trout are present (Figure 3). The AUC of this model was 95%, suggesting high predictive performance. The classification accuracy at the 0.5 level was 97% for predicting Bull Trout absence and did not increase when Brook Trout or elevation were added to the model. In contrast, the classification accuracy for predicting Bull Trout presence was greatly improved by the inclusion of Brook Trout (53%) or both Brook Trout and elevation (76%) compared to the model that only contained June degree-days (12%). For frequency, variability, and timing descriptors, the best-supported metrics were the number of days over 16°C, maximum variation, and the date of the 75th percentile of the CTD, respectively. However, the best models with these metrics had higher AIC_c scores (>70), lower AUCs (<82%), and lower classification probabilities (e.g., ≤41% for predicting Bull Trout presence) compared to the best model for the magnitude descriptor.

When we evaluated models with multiple thermal regime descriptors, the best-approximating model (AIC_c = 67; w_i = 0.19) when considering only temperature metrics and nonnative trout indicator variables included June degree-days and Brook Trout presence (Table 2). In addition, the June degree-days variable was present in every model in the confidence set and was ranked as the most important metric (cumulative w_i = 0.94). The date of the 75th percentile of CTD, number of days over 16°C, and maximum variation were also present in models in the confidence set, but those metrics had little support (cumulative $w_i \leq 0.27$). The best model after adding the environmental variables was the same as the model described above (June degree-days, Brook Trout occurrence, and elevation).

Upper Thermal Tolerance Limits

The magnitude and duration of thermal exposures associated with the presence of trout were inversely related. Estimated thermal tolerance limits based on average daily mean and average daily maximum temperatures showed similar patterns for Bull Trout, Brook Trout, and Brown Trout (Figure 4a, b). The upper thermal tolerance limits for average daily maximum temperatures were lower for Bull Trout than for Brook Trout and Brown Trout across all exposure periods (1–63 d). For example, the 1-d average daily maximum tolerance limit was 21.3°C for Bull Trout, 23.2°C for Brook Trout, and 25.0°C for Brown Trout. Average daily maximum tolerance limits for Brook Trout and Brown Trout did not differ for any of the exposure periods (i.e., the 90% confidence intervals around the pairwise differences between the sample quantiles contained zero; Table S.2). Similarly, average daily mean tolerance limits were lower for Bull Trout (16.9°C) than for Brook Trout (19.9°C) and Brown Trout (19.4°C), but none of the differences was significant for any of the exposure periods.

DISCUSSION

Our study highlights the importance of exploring a suite of descriptors of thermal regimes to understand the distribution and occurrence of fishes. In the upper Klamath River basin, we observed differences in the number and type of thermal regime descriptors associated with species occurrence. For instance, Bull Trout occurrence was related to all four descriptors considered (magnitude, frequency, variability, and timing), whereas Brook Trout occurrence was related to three descriptors (magnitude, frequency, and variability), and Brown Trout

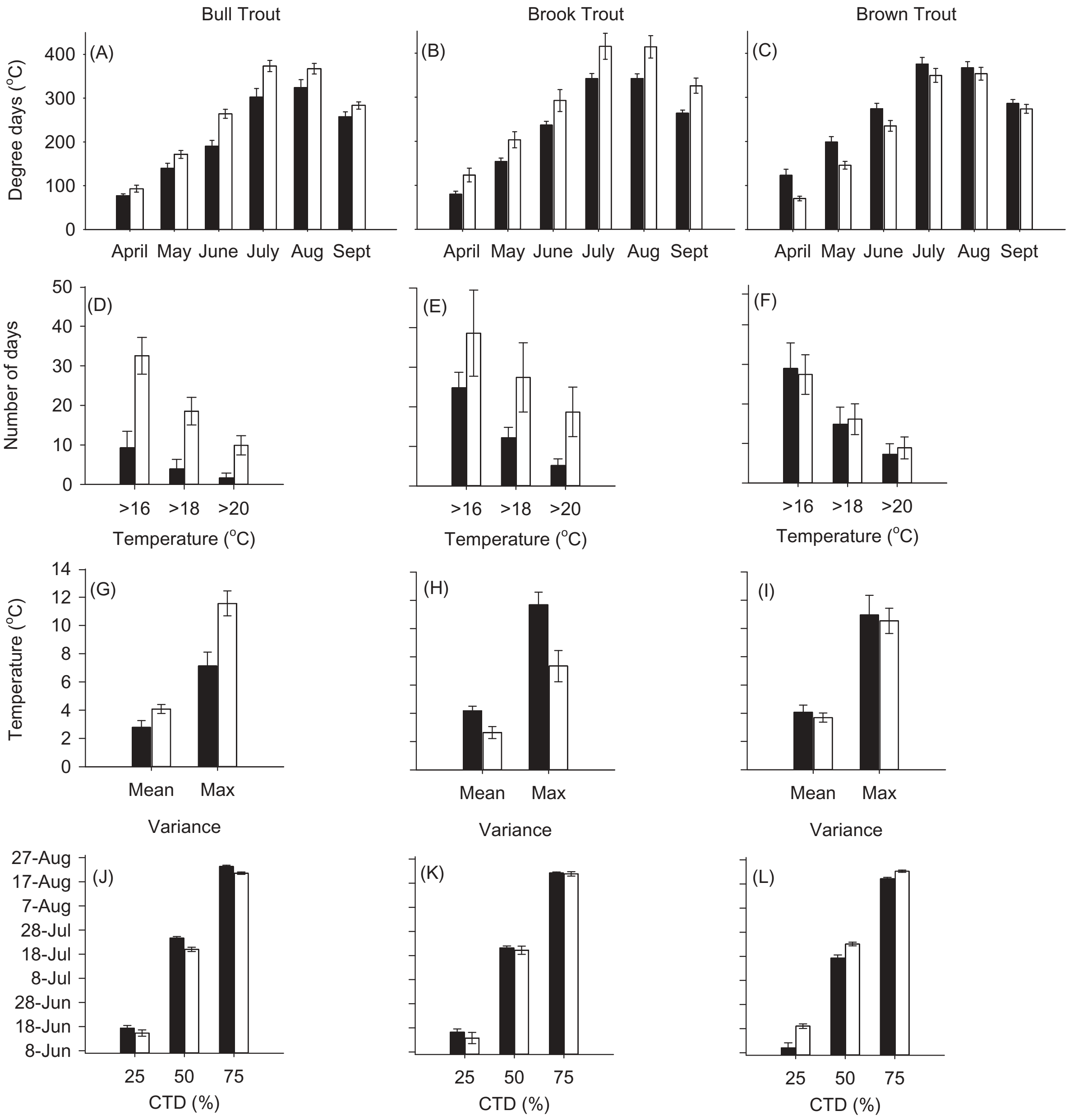

FIGURE 2. Mean values (±SE) of thermal regime descriptors for sites in the upper Klamath River basin: **(A), (B), (C)** degree-days; **(D), (E), (F)** number of days above 16, 18, and 20°C; **(G), (H), (I)** mean variance and maximum (max) variance; and **(J), (K), (L)** the date of the 25th, 50th, and 75th percentiles of the cumulative temperature distribution (CTD). Panels depict data for sites where Bull Trout (A, D, G, J), Brook Trout (B, E, H, K), or Brown Trout (C, F, I, L) were present (shaded bars) or absent (open bars). All metrics were calculated using data from the period April 1–September 30 and then were averaged across the study years (2011 and 2012). Note that Brown Trout were not present in the Sycan River subbasin.

occurrence was related to two (magnitude and timing). Overall, magnitude was the most important thermal regime descriptor for all species, although the trout species responded differently to the suite of descriptors we used to describe magnitude. For Bull Trout occurrence, we found June degree-days to be the best descriptor. The probability of occurrence for Bull Trout was further reduced in the presence of nonnative trout, particularly Brook Trout. However, measures of magnitude alone may not be sufficient to explain trout occurrence. For example, by coupling magnitude with duration, our results suggest that trout can tolerate a wide range of temperatures, but as expected, the fish appear to tolerate longer exposures to lower temperatures.

Each descriptor of the thermal regime can have important implications for fishes. For instance, magnitude and frequency provide information about the chronic and acute sublethal temperatures experienced by a fish (Boughton

TABLE 1. Coefficient estimate, SE, *P*-value, and Akaike's information criterion adjusted for small sample size (AIC_c) for individual metrics within each thermal regime descriptor predicting the occurrence of Bull Trout in the upper Klamath River basin. The best predictor within each thermal regime descriptor (shown in bold italics) was selected based on the lowest AIC_c score (MWMT = maximum weekly maximum temperature; MWAT = maximum weekly average temperature; CTD = cumulative temperature distribution; DD = degree-days).

Descriptor	Metric	Estimate	SE	*P*	AIC_c
Magnitude (°C)	Maximum	–2.62	0.99	0.0081	82.6
	MWMT	–2.47	0.96	0.0103	83.4
	MWAT	–1.45	0.78	0.0608	87.8
	Apr DD	–0.64	0.65	0.3259	91.1
	May DD	–1.07	0.66	0.1060	89.2
	Jun DD	***–2.82***	***0.97***	***0.0036***	***78.9***
	Jul DD	–2.16	0.88	0.0146	84.0
	Aug DD	–1.15	0.71	0.1030	89.1
	Sep DD	–0.99	0.69	0.1557	89.8
Variability (°C)	Mean range	–1.73	0.82	0.0351	87.4
	Maximum range	–2.98	1.05	0.0048	81.9
	Mean variance	–2.12	0.94	0.0239	86.0
	Maximum variance	***–3.59***	***1.28***	***0.0051***	***80.6***
Frequency (*n*)	***Days >16°C***	***–2.45***	***1.08***	***0.0238***	***84.0***
	Days >18°C	–2.25	1.23	0.0684	86.2
	Days >20°C	–2.30	1.65	0.1635	87.8
Timing	CTD 25%	0.44	0.58	0.4465	91.6
	CTD 50%	1.74	0.75	0.0205	85.2
	CTD 75%	***1.64***	***0.64***	***0.0106***	***84.4***

et al. 2007; McCullough et al. 2009); variability in temperature can affect behavioral thermoregulation and bioenergetics (Hughes and Grand 2000); and the timing of thermal events is an important cue for life history events, such as spawning and migration (Benjamin et al. 2014), as well as synchrony among fish and their prey (Harper and Peckarsky 2006; Rosenberger et al. 2011). We observed that Bull Trout in the upper Klamath River basin occurred at colder sites with less daily variation, whereas nonnative Brown Trout occurred at warmer sites and nonnative Brook Trout occurred at sites with intermediate temperatures and greater daily variation. These patterns are consistent with those observed during other studies conducted within the native range of Bull Trout (Dunham et al. 2003a) as well as in the native ranges of Brook Trout (Butryn et al. 2013) and Brown Trout (Hari et al. 2006). Moreover, Bull Trout and Brook Trout were more likely to be present in streams where warmer temperatures occurred less often (frequency), whereas Brown Trout were present in streams that heated up faster, regardless of the frequency of temperatures above 16, 18, or 20°C. Similar results were observed for Brook Trout in their native range, where they were more likely to be present in cooler streams with fewer high-temperature events (>18°C) that occurred for short time periods (Butryn et al. 2013). We are unaware of studies that have compared timing and frequency—let alone all the thermal regime descriptors—in relation to the occurrences of Bull Trout and Brown Trout.

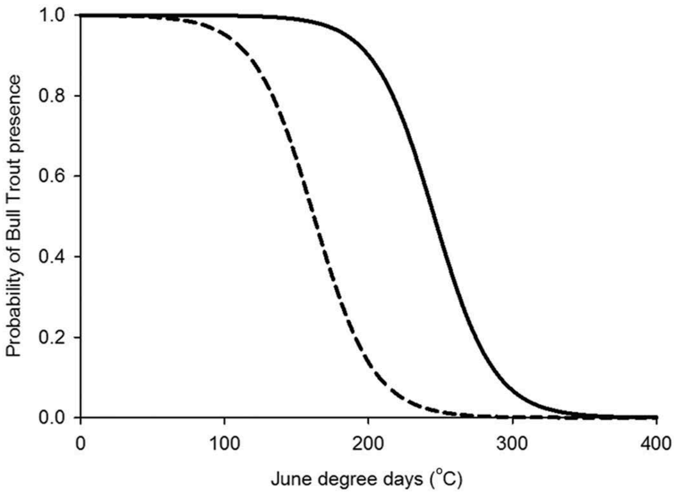

FIGURE 3. Probability of Bull Trout occurrence at sites in the upper Klamath River basin as a function of June degree-days (°C) and the presence (solid line) or absence (dashed line) of nonnative Brook Trout.

TABLE 2. The 95% confidence set of candidate models with multiple thermal regime descriptors to explain the occurrence of Bull Trout in the upper Klamath River basin. For each model, the number of parameters (K), –2 log-likelihood (–2log$L$), Akaike's information criterion adjusted for small sample size (AIC$_c$), the difference in AIC$_c$ between the given model and the best-performing model (ΔAIC$_c$), and Akaike weight (w_i) are shown (CTD = cumulative temperature distribution; Jun DD = June degree-days).

Model	K	–2log$L$	AIC$_c$	ΔAIC$_c$	w_i
Jun DD, Brook Trout	4	–29.0	66.5	0.0	0.19
Jun DD, Brook Trout, Brown Trout	5	–28.3	67.3	0.9	0.13
Jun DD, Brook Trout, CTD 75%	5	–28.5	67.6	1.2	0.11
Jun DD, Brook Trout, Brown Trout, CTD 75%	6	–27.4	67.9	1.5	0.09
Jun DD, Brook Trout, Maximum variance	5	–28.7	68.2	1.7	0.08
Jun DD, Brook Trout, Days >16°C	5	–29.0	68.7	2.2	0.06
Jun DD, Brook Trout, Brown Trout, Days >16°C	6	–28.2	69.4	2.9	0.05
Jun DD, Brook Trout, CTD 75%, Days >16°C	6	–28.2	69.4	2.9	0.05
Jun DD, Brook Trout, Brown Trout, Maximum variance	6	–28.3	69.6	3.2	0.04
Jun DD, Brook Trout, CTD 75%, Maximum variance	6	–28.3	69.7	3.2	0.04
Jun DD, Brook Trout, Brown Trout, CTD 75%, Days >16°C	7	–27.4	70.1	3.7	0.03
Jun DD, Brook Trout, Brown Trout, CTD 75%, Maximum variance	7	–27.4	70.2	3.8	0.03
Jun DD, Brook Trout, Maximum variance, Days >16°C	6	–28.7	70.5	4.0	0.03
Jun DD, Brook Trout, CTD 75%, Maximum variance, Days >16°C	7	–27.9	71.2	4.7	0.02
Jun DD, Brook Trout, Brown Trout, Maximum variance, Days >16°C	7	–28.1	71.7	5.2	0.01

Our modeling results suggested that magnitude was the best thermal regime descriptor for predicting Bull Trout occurrence—specifically, June degree-days, a metric that is not typically used to describe magnitude in relation to trout occurrence or distribution. The mean or maximum August water temperature is more frequently used (Dunham et al. 2003a; Jones et al. 2014; Isaak et al. 2015). The lack of importance for August temperature in the present study may be because the upper Klamath River basin is at the southern extent of the Bull Trout's range, thus heating up rapidly during June and reaching maximum temperature in July. In contrast, most streams within the range of Bull Trout are at high elevations and have a snowmelt hydrology that occurs later in the year (Rieman et al. 2007), which could delay the timing and rate of heating in those streams. Nevertheless, degree-days can also integrate the rate of heating along with magnitude (Neuheimer and Taggart 2007), which may make degree-days more appropriate than a monthly mean or maximum temperature as a measure for estimating Bull Trout occurrence. Moreover, degree-days are highly correlated with the development time of egg and juvenile life stages, thus further supporting the reliability of degree-days for predicting fish occurrence (Benjamin et al. 2007). A disadvantage of degree-days is that this variable cannot identify whether critical thermal maxima are exceeded (e.g., lethal or sublethal thresholds; MuCullough et al. 2009), but it is easy enough to consider thermal maxima and degree-days together (Benjamin et al. 2007). Regardless of the mechanism that makes June degree-days more appropriate in our model, the results suggest that a suite of metrics describing the thermal regime should be considered in future studies, including climate change projections (Arismendi et al. 2013).

We found that the magnitude of temperatures tolerated by Bull Trout varied as a function of exposure duration but that these values were lower than values reported in a laboratory study of thermal tolerance (Selong et al. 2001). Selong et al. (2001) found that 46% of Bull Trout exposed to a constant temperature of 21°C survived exposures of 60 d, whereas our field-based evaluation indicated that sites experiencing a daily maximum of 21°C for more than a single day did not support Bull Trout. With respect to cooler temperatures, our results indicated that under field conditions, Bull Trout can tolerate mean temperatures of 14°C and maximum temperatures of 17.5°C for up to 30 d. On average, our study streams that contained Bull Trout had mean temperatures less than 11°C and maximum temperatures less than 15°C, similar to predictions made by Dunham et al. (2003a), suggesting that Bull Trout frequently avoid areas with warmer temperatures and are often associated with colder temperatures than might be the case for maximizing growth in the laboratory (13.2°C; Selong et al. 2001). Laboratory studies provide an excellent means of controlling thermal exposure, but they typically represent a limited range of conditions (e.g., unlimited rations and constant water temperatures; Selong et al. 2001), whereas field-based studies lack such control due to the wide range of factors that can interact with temperature to influence fish responses. Overall, we would expect that coldwater fishes, such as the trout evaluated here, should be associated with colder temperatures in the field owing to factors such as food limitation (Mesa et al. 2013), species interactions (as considered herein), reproductive requirements (Eckmann et al., in press), or limited access to cold water (Howell et al. 2010).

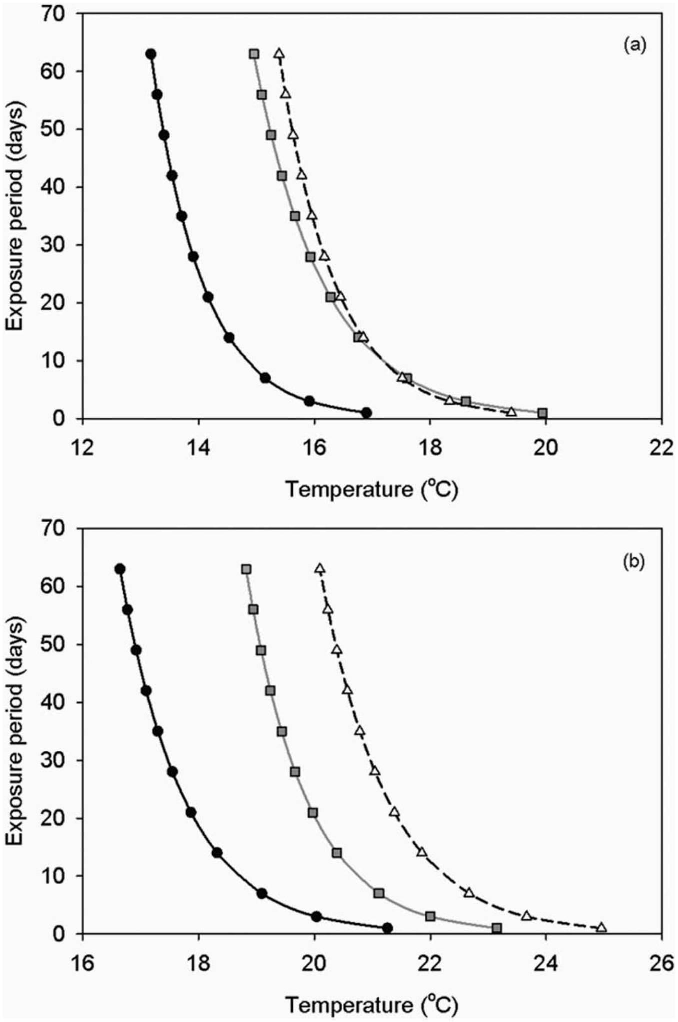

FIGURE 4. Estimated thermal tolerances of Bull Trout (circles and solid black line), Brook Trout (squares and gray line), and Brown Trout (triangles and dashed line) based on **(a)** average mean temperature and **(b)** average maximum temperature for 10 exposure periods (1, 3, 7, 14, 21, 28, 35, 42, 49, 56, and 63 d).

Although variability, frequency, and timing were not included in the best-approximating model, at least one metric within each of these descriptors was statistically related to Bull Trout occurrence. Bull Trout were less likely to occur in reaches with too many days exceeding 16, 18, or 20°C, which is consistent with other studies (Dunham et al. 2003a). Moreover, frequency, when coupled with magnitude, was the only thermal regime descriptor that was included as part of the confidence set. In the upper Klamath River basin, Bull Trout can tolerate maximum temperatures exceeding 16, 18, and 20°C for approximately 63, 15, and 3 d, respectively. Similarly, Bull Trout were found to occupy warm water (MWAT range = 18–25°C) for extended periods, but it was unclear whether those individuals had free access to colder locations (Howell et al. 2010). Based on the AIC_c values, the variability descriptor was important and could signify the presence of groundwater, but it was less accurate than the magnitude descriptor in predicting Bull Trout presence. Greater temperature variability was positively related to the survival and growth of Brook Trout, which may be attributable to a balance between optimal temperatures for feeding and assimilation (Xu et al. 2010). A similar explanation has been proposed for Bull Trout in Ross Lake, Washington (Eckmann et al., in press). Last, for timing, the difference between sites that contained Bull Trout and sites that lacked Bull Trout was 2–4 d, which we do not believe to be biologically significant.

Our results demonstrated an overlap of ranges for Bull Trout and nonnative trout, most prominently between Bull Trout and Brook Trout. This is not surprising since the optimal temperatures for Bull Trout growth (11–15°C; Selong et al. 2001) overlap more with those of Brook Trout (12–19°C; Hokanson et al. 1973) than with those of Brown Trout (13–19°C; Elliot and Elliot 2010). Based on this criterion, further spread of the nonnative trout is still possible in some reaches of our study area but would be limited by physiological constraints from the coldest temperatures we observed (see also Benjamin et al. 2007). In other words, Bull Trout may have thermal refuges from future invasions by Brook Trout and Brown Trout (Wenger et al. 2011a; Isaak et al. 2015). Moreover, Bull Trout were predicted to be present in warmer reaches when Brook Trout were absent, suggesting the displacement of Bull Trout by Brook Trout. Hence, the persistence of Bull Trout may depend on the management of nonnative trout. In one case in the upper Klamath River basin, the eradication of Brook Trout and the installation of barriers to prevent upstream invasion have proven successful in restoring Bull Trout (Sun Creek; Buktenica et al. 2013). Although eradication can be a viable option in some settings, conservation of native species such as Bull Trout is best accomplished via a full exploration of alternatives (Dunham et al. 2002; Fausch et al. 2009). For Bull Trout in some parts of the upper Klamath River basin, coexistence with nonnative Brook Trout may be an option (see also Dunham et al. 2003a). This would require management actions to improve conditions that favor Bull Trout over Brook Trout. For example, coexistence may be more likely if management actions can allow currently nonmigratory populations of Bull Trout to re-express migratory life histories (e.g., by enhancing connectivity or the quality of migratory destinations and maintaining temperatures that are suitable for Bull Trout but less suitable for Brook Trout [<13°C]). In contrast to Brook Trout, we found that Bull Trout and Brown Trout rarely occurred in sympatry ($n = 3$), and where they did co-occur, the water temperatures were at the upper limit preferred by Bull Trout (>14°C). Thus, Bull Trout conservation efforts may be less effective in stream reaches where Brown Trout exist.

There was little difference in the temperatures occupied by Brook Trout and Brown Trout and consequently no difference in their upper thermal tolerance limits for mean temperatures, consistent with the observations of Wehrly et al. (2007). However, we did find that Brown Trout had a higher tolerance for maximum temperatures than did Brook Trout. Our results suggested that the upper thermal tolerance limit for Brook Trout and Brown Trout is lower in the upper Klamath River basin than in the Wisconsin and Michigan streams studied by Wehrly et al. (2007), most likely due to differences in scale and sample size between the two studies. We were focused on 87 sites in three small subbasins, whereas the Wehrly et al. (2007) study encompassed nearly 300 sites in streams across two states. Moreover, we focused on sites within the potential range of Bull Trout in the upper Klamath River basin. If our study had been more broadly distributed across the upper Klamath River basin, different patterns of thermal tolerance and thermal regime descriptors for nonnative Brook Trout and Brown Trout might have emerged.

Though many aspects of our present findings were consistent with previous work, we were able to identify a more complete suite of thermal regime descriptors that could explain the presence of native and nonnative trout. This is important not only for providing additional insights into how these fishes respond to temperature, but also for supporting an examination of how temperature itself will respond to future changes in land use, water use, or climate. For example, recent work shows that the thermal regime descriptors used in this study can respond differently to climate change (Arismendi et al. 2013), and recognizing these changes can be useful for understanding species persistence and vulnerability. Moreover, temperature alterations owing to climate change may proceed more slowly than previously assumed (Isaak et al. 2016), potentially suggesting that projected contractions in Bull Trout distribution may be less dire than previously indicated (Rieman et al. 2007). Given that we now have an unprecedented capability to collect and analyze high-resolution information on year-round thermal regimes, which is of obvious importance to understanding fish biology (Poole et al. 2004; Butryn et al. 2013) and environmental change (Arismendi et al. 2013; Olden and Naiman 2010), we recommend that such efforts be more routinely and rigorously incorporated into future studies.

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