NRC Research Press

ARTICLE

Maximum stream temperature and the occurrence, abundance, and behavior of steelhead trout (*Oncorhynchus mykiss*) in a southern California stream

Matthew R. Sloat and Ann-Marie K. Osterback

Abstract: To determine individual and population responses of steelhead trout (*Oncorhynchus mykiss*) to stream temperature, we sampled summer stream temperature and juvenile steelhead occurrence, abundance, and behavior in a small stream near the species' southern limit. Maximum annual stream temperature (22.3–33.1 °C) exerted a strong threshold effect on steelhead occurrence. Steelhead persisted through summer in all pools that did not exceed 30 °C, but the probability of persistence rapidly decreased to zero at warmer sites. Below the threshold for fish persistence, thermal effects on steelhead abundance were inconsistent, with temperature receiving strong support for inclusion in models of fish abundance at the beginning of summer but weak support for inclusion in models of end-of-summer abundance and summer fish loss. Thermal refugia that would allow steelhead to behaviorally thermoregulate were rare. In response to elevated stream temperatures, steelhead reduced foraging and agonistic activity, presumably to minimize energetic costs. In anticipation of the effects of global climate trends on stream temperature, management actions that limit or reduce stream heating will be critical for conservation of steelhead populations in habitats approaching thermal tolerance thresholds.

Résumé : Afin de déterminer les réponses d'individus et de populations de truite arc-en-ciel (*Oncorhynchus mykiss*) à la température du cours d'eau, nous avons mesuré la température estivale de l'eau et observé la présence, l'abondance et le comportement de truites juvéniles dans un petit cours d'eau situé près de la limite sud de l'aire de répartition de l'espèce. La température annuelle maximum de l'eau (22,3–33,1 °C) exerçait un fort effet de seuil sur la présence de truites arc-en-ciel. Des truites persistaient tout l'été dans les fosses dont la température ne dépassait pas les 30 °C, alors que la probabilité de persistance chutait rapidement à zéro dans les sites plus chauds. Sous le seuil de persistance, les effets de la température sur l'abondance des truites arc-en-ciel n'étaient pas uniformes, les observations appuyant fortement l'intégration de la température aux modèles d'abondance du poisson au début de l'été, mais non aux modèles d'abondance à la fin de l'été ou de perte de poissons durant l'été. Les refuges thermiques qui auraient permis la thermorégulation comportementale des truites arc-en-ciel étaient rares. En réponse aux températures d'eau élevées, les truites réduisaient leurs activités agonistiques et d'alimentation afin, vraisemblablement, de minimiser leurs coûts énergétiques. Au vu des effets anticipés des changements climatiques planétaires sur la température des cours d'eau, des mesures d'aménagement qui limitent ou réduisent leur réchauffement seront essentielles à la conservation des populations de truites arc-en-ciel dans les habitats dont les conditions s'approchent des seuils de tolérance thermique. [Traduit par la Rédaction]

Introduction

Contemporary and projected effects of global climate change include a warming of stream ecosystems (Mohseni et al. 1999; van Vliet et al. 2011; Isaak et al. 2011). Alterations to stream thermal regimes may have fundamental consequences for the persistence of fish populations because of the direct effect of temperature on the physiological processes of ectotherms (e.g., Hokanson et al. 1977; Myrick and Cech 2000). Stream temperature influences fish physiology and bioenergetics through effects on routine and maximum metabolic rates, swimming efficiency, and food absorption and conversion efficiency (Wurtsbaugh and Davis 1977; Myrick and Cech 2000; Rodnick et al. 2004), with associated effects on growth rate (Hokanson et al. 1977; Boughton et al. 2007). Stream temperature also alters behaviors such as foraging and social interaction and can cause corresponding changes in microhabitat selection (Smith and Li 1983; Nielsen et al. 1994; Ebersole et al. 2001).

Physiological and behavioral responses of individuals to temperature are also reflected in larger-scale patterns of fish abundance and distribution across stream networks (Hughes and Grand 2000; Dunham et al. 2003a; Boxall et al. 2008). For example, relationships between temperature and fish abundance may result from temperature-mediated changes in reach or channel-unit carrying capacity that scale with per capita metabolic demand (Li et al. 1994; Hughes and Grand 2000). At the watershed scale, elevated temperatures near species' thermal tolerances may constrain fish populations to relatively cool headwaters or reaches where hyporheic exchange results in localized cooling of stream temperature (Dunham et al. 2003a; Boxall et al. 2008).

The effects of temperature can be especially pronounced near the lower-latitudinal distribution boundary of thermally sensitive

M.R. Sloat* and A.-M.K. Osterback.† Stillwater Sciences, 2855 Telegraph Avenue, Suite 400, Berkeley, CA 94705, USA.
Corresponding author: Matthew R. Sloat (e-mail: matthew.sloat@oregonstate.edu).
*Present address: Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331, USA.
†Present address: Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, and Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 110 Shaffer Road, CA 95060, USA.

species, where populations may experience more extreme ecological conditions than at higher latitudes. Indeed, a contraction towards higher latitudes in the range of many taxa suggests that low-latitude populations may be especially vulnerable to effects of climate warming (Parmesan and Yohe 2003; Root et al. 2003).

In California, steelhead trout (*Oncorhynchus mykiss*) approach the southern margin of their historical range and have experienced substantial reductions in distribution and abundance (Busby et al. 1996). Although urbanization and loss of migration opportunities have been prominent factors in the extirpation of southern California steelhead populations, prompting their listing as endangered under the US Endangered Species Act (ESA) (Busby et al. 1996), a recent northward range contraction also suggests the possibility that regional warming is contributing to the decline (Boughton et al. 2005). Even in watersheds with little anthropogenic disturbance, the semi-arid climate of southern California produces low dry-season stream discharge and summer stream temperatures that commonly approach reported stressful or lethal limits for steelhead (e.g., ≥25 °C) (Myrick and Cech 2000). Consequently, southern steelhead populations may be particularly vulnerable to increases in stream temperatures because ambient conditions are currently near the species' limits for thermal tolerance.

The goal of this paper was to determine individual and population responses of steelhead to stream temperature near the species' southern limit. To determine the importance of stream temperatures to steelhead in their southern range, we sampled summer stream temperatures and juvenile fish populations in Santa Paula Creek, California. We conducted our research at a variety of spatial scales to assess the effects of temperature on (*i*) fish persistence at the watershed scale, (*ii*) variation in fish abundance among individual channel units, and (*iii*) behavior and microhabitat choice of individual fish within channel units.

Materials and methods

Study site

Santa Paula Creek is an historically important producer of steelhead in the Santa Clara River basin (Stoecker and Kelley 2005), draining the Western Transverse Ranges, Ventura County, California (34°N, 119°W). The semi-arid climate of the region produces hot, dry summers and moderate winters punctuated by episodic rainfall. The area receives 90% of its rainfall from November through April (mean annual precipitation < 50 cm). Stream flows are flashy, responding rapidly to intense winter rainfall, especially during El Niño – Southern Oscillation (ENSO) episodes (Schonher and Nicholson 1989). Dry-season discharge ranges between 0.02 and 0.06 m³·s⁻¹, while winter peak flows commonly exceed 150 m³·s⁻¹ (USGS gage 11113500). The summer wetted channel averages about 3 m wide and alternates between shallow riffles and pools (mean depth ~0.5 m) over gravel, cobble, and boulder substrate. As streamflows diminish during the summer dry season, riffles separating pool habitats become very shallow or intermittent.

We conducted the study within a 5 km reach that was bounded at the lower end by the confluence with Sisar Creek, a fish-bearing tributary of Santa Paula Creek entering 10.5 km upstream from the stream's mouth (elevation ~340 m). Near the confluence of these streams, natural tar and sulphur seeps reduce summer water quality. Juvenile steelhead are rare downstream of this point, occurring in <5% of pool habitats (M. Sloat and A.-M. Osterback, unpublished data). The upstream extent of our study reach (elevation ~500 m) consisted of a ~10 m falls that marks the historical limit to steelhead anadromy. The study area is mostly contained within Los Padres National Forest, with hillslope vegetation consisting of chaparral–scrub and mixed evergreen and deciduous forest. Limited agricultural (~10% of the total watershed area) and residential (<1% of total area) land use occurs in the study area.

Riparian vegetation is dominated by white alder (*Alnus rhombifolia*), with a mix of black cottonwood (*Populus trichocarpa*), western sycamore (*Platanus racemosa*), Fremont cottonwood (*Populus fremontii*), willow species (*Salix* sp.), and mule fat (*Baccharis salicifolia*) also present. Steelhead are the only fish species present in most of the study reach, with arroyo chub (*Gila orcuttii*), Santa Ana sucker (*Catostomus santaanae*), and threespine stickleback (*Gasterosteus aculeatus*) occurring at low abundances in the downstream-most study pools.

Stream temperature measurement

In 2007 and 2009, we documented summer stream temperatures using a combination of instantaneous measurements with a hand-held YSI-85 thermometer (accuracy ±0.1 °C; YSI Inc., Yellow Springs, Ohio) and continuous temperature monitoring with a series of temperature data loggers (Onset Tidbit, accuracy ±0.2 °C; Onset Computer Corp., Pocasset, Massachusetts). In May of each year, instantaneous measurements of maximum daily stream temperature were collected in well-mixed areas of the thalweg with a YSI-85 thermometer and mapped at ≤1 °C intervals throughout the study reach on high-resolution satellite imagery (scale = 1:1274). All measurements were taken during a 2.5 h interval between 1400 and 1630, when diel stream temperatures peaked and temperature fluctuation was <1 °C (confirmed with continuously recording temperature data loggers). The resulting maps represented snapshots of the longitudinal pattern of temperature maxima throughout the study stream at the beginning of the summer dry season at a resolution of ≤1 °C.

The temperature mapping process revealed discontinuities in longitudinal stream heating resulting from cool hyporheic inputs at topographic nick points (sensu Boxall et al. 2008). Nick points are the transition zones between less topographically confined valley segments and confined canyon segments, and their effects on stream temperature within the study area were similar in each study year. In contrast with a typical pattern of gradual downstream increases in temperature, thermal conditions in the study area were highly variable, with maximum daily stream temperatures cooling by as much as 11 °C at nick points marking the transition from less to more topographically confined valley segments. We used the temperature mapping process to guide sample site selection for deployment of a series of calibrated temperature loggers that measured summer stream temperature from late May to early November of 2007 and 2009.

In 2007, 10 temperature logger sites were selected to bracket the upper and lower boundaries of confined and unconfined valley segments. In 2009, we employed a more extensive network of 38 temperature logger sites. To allow sampling of a full range of temperatures in the study stream while maintaining randomness in site selection, we performed a stratified random selection of pools based on stream temperature maxima observed in 2007 (range = 22–34 °C). We selected three to four study pools within each 1 °C temperature bin between 22 and 34 °C. In both years, we programmed temperature loggers to record at 15 min intervals, installed them in well-mixed areas of the thalweg, and shielded the data recorders from direct insolation with perforated opaque plastic sleeves.

To assess temperature variation within individual pools, we used a handheld YSI-85 thermometer with a sensor probe attached to a 1.5 m pole to systematically search study pools for deviations from thalweg temperatures. Because preliminary sampling indicated that temperature variation within pools was greatest during the warmest period of the day, we restricted our sampling to occur from 1400 to 1630. After recording the thalweg temperature, we slowly swept the thermometer probe over the entire study pool at a depth approximately 5 cm from the stream substrate to identify areas that deviated by >1 °C from the thalweg temperature. Except for thalweg temperature measurements, we limited our sampling to a depth within 5 cm of the stream sub-

strate because we expected potential cool-water sources, such as hyporheic upwelling or thermal stratification, to be most detectable near the bottom of study pools (Nielsen et al. 1994; Matthews and Berg 1997). We made all temperature measurements from the stream bank to avoid potential mixing of thermal patches.

Fish occurrence and behavior

In 2007, we documented fish presence in 29 pools at the beginning (May) and end (November) of the summer dry season using a combination of streamside observation, snorkeling, and electrofishing. We selected sample sites to span the range of stream temperature maxima observed in May and first made streamside observations by slowly walking upstream along the streambank and scanning selected pool habitats for juvenile steelhead. We were confident that we could correctly identify juvenile steelhead from the streambank because of excellent water clarity and because preliminary electrofishing surveys indicated that steelhead were the only species present in the majority (>90%) of study pools (M. Sloat and A.-M. Osterback, unpublished data). If we did not observe juvenile steelhead from the streambank, we snorkeled the habitat by entering the downstream end of the study pool and systematically searching for fish. If we did not observe juvenile steelhead while snorkeling, we returned the following morning and sampled the habitat using multiple passes with a backpack electrofisher. This stepwise sampling approach reduced potential injury to ESA-listed steelhead by minimizing the use of electrofishing (Nielsen 1998), while confirming presence or absence of steelhead in each study pool.

In 2009, we followed a similar stepwise protocol to document fish occurrence in 38 pools, but did not include streamside observations because we had the additional objective of estimating fish abundance. Fish sampling in 2009 occurred in the same pools that received temperature loggers. Within each study pool, we conducted four-pass snorkel dives in May, September, and November 2009. To complete each pass, a single snorkeler entered the downstream end of the study pool and systematically searched the pool to count all fish. Snorkelers estimated fish size to the nearest 25 mm length bin and recorded data underwater on plastic slates attached to their sleeves. All snorkeling was completed during daylight between 0900 and 1700, with individual passes separated by 15 to 30 min to allow study pools to return to presampling levels of water clarity. We used handheld lights and searched substrate crevices and undercut banks for concealed fish. Because of potential fish displacement during a freshet occurring between the September and November 2009 sampling events, we only include the May and September information in our analysis of 2009 fish distribution and abundance.

To characterize physical conditions in each pool sampled in 2009, we measured wetted width at three equally spaced orthogonal transects (mean = 3.0 m, range = 1.7–5.6 m), total habitat length (mean = 5.1 m, range = 3.4–8.4 m), and maximum pool depth (mean = 0.65 m, range = 0.41–0.94 m). We visually estimated the percent pool area with available cover in the form of unembedded cobble and boulder, aquatic vegetation, turbulence (i.e., "bubble curtains"), or undercut banks (mean = 52%, range = 30%–85%). We also recorded the longitudinal position of each study unit (m above downstream study reach boundary) using georeferenced digital satellite imagery (scale = 1:1274).

To document thermal habitat selection within pools, we recorded fish focal positions in 24 individual pools on 1–3 September 2009. We made all observations between 1400 and 1600 during the diel peak in stream temperature. Observers carefully approached the stream and noted the position and focal depth of undisturbed fish. After a 3–5 min period of observation to confirm that fish were stationary and to identify focal position and depth using features on the streambed as visual reference points, the observer measured stream temperature to the nearest 0.1 °C at

the fish's position and at five randomly selected points within the habitat unit using a YSI-85 temperature probe. At randomly selected points, we measured temperature across the full range of water depth and chose the coolest observed temperature to represent the available temperature at that point.

To document potential changes in fish behavior associated with stream temperature, we used underwater videography to record the behavior of individual steelhead exposed to a range of diurnal temperature fluctuations. We selected 14 pool habitats and recorded fish behavior in two to four pools per day from 1 to 4 September 2009. The videography system consisted of remote underwater cameras connected to video monitors and DVD recorders via 30.5 m cables. We positioned the underwater cameras near the center of each pool 12 to 18 h prior to recording behavior and hid them within natural substrate. We placed video monitors and recorders in sheltered locations on the streambank to avoid disturbing focal animals. Recordings were made in each pool for a period of 5 min every 1.5 hours between 0600 and 1500, resulting in a total of six recordings per pool that spanned a 9 h period covering the full range of daily temperature extremes. Cameras were left in place until completion of the last recording of each day and then removed and transferred to pools selected for sampling on the following day.

Because food abundance may alter the behavioral response of individuals to stream temperature, food additions were made to half of the pools to control for diel variation in the density of naturally drifting invertebrate prey. The addition of food to half of the pools allowed us to make qualitative comparisons between the behavioral response of fish to temperature under conditions with an abundant food supply (i.e., with food addition) and under ambient conditions (i.e., without food addition). Food additions consisted of frozen meal worm larvae (*Tenebrio molitor*) added to pools at a uniform rate of 0.24 g·h^{-1} using automated belt feeders placed at the head of seven of the pools (Boss and Richardson 2002; Boughton et al. 2007). Meal worms were used because of their resemblance to naturally drifting aquatic invertebrates and because a pilot study indicated that fish immediately recognized them as prey. To associate fish behavior with stream temperature, we used temperature data loggers to measure temperature within each pool and matched instantaneous stream temperature measurements with the time of each behavioral recording.

To quantify steelhead behavior from the video recordings, we used instantaneous sampling (Martin and Bateson 1993) to categorize the activity of a single focal animal from each pool at 10 s intervals during each 5 min recording. Each of the six recordings per pool, therefore, resulted in 30 instantaneous measurements of fish behavior, for a total of 180 observations per fish. Behavioral categories included feeding (interception of prey item from water column or benthos), agonism (territorial display towards conspecific, chasing, or fleeing from conspecific), holding (maintenance of focal position within water column by swimming without apparent directional movement), and sheltering (concealment within stream substrate or other cover).

Data analysis

We performed all statistical analyses using SAS version 9.1 (SAS 2006). To relate the persistence of juvenile steelhead in study pools to summer temperature maxima in 2007 and 2009, we used multiple logistic regression (Allison 1999), with study year and maximum summer temperature as independent variables. We defined fish persistence within a pool as the presence of fish during both the beginning- and end-of-summer sampling events within a given year. Although we did not restrict movement from the study pools between sampling events, riffles separating pool habitats become very shallow or intermittent during early summer. Since the end-of-summer sampling occurred prior to any increases in streamflow during both study years, the opportunity for fish movement between pools was assumed to be minimal, so

that fish observed within a study pool had experienced the thermal regime of that pool. By convention, we considered habitats having a ≥0.50 probability of fish persistence, as predicted by logistic regression, to be thermally suitable for occupancy by steelhead (e.g., Dunham et al. 2003b).

Maximum summer stream temperatures were summarized as the instantaneous stream temperature maxima occurring between 1 July and 15 September of each year. We focused on instantaneous maximum stream temperature, a measure of acute thermal stress, because temperatures in Santa Paula Creek exceed previously reported stressful or lethal limits for steelhead (i.e., >25 °C; Myrick and Cech 2000) and because observed stream temperature maxima were highly correlated with similar measures of temperature such as maximum weekly average temperature ($r > 0.99$, $P < 0.001$) and summer mean temperatures ($r = 0.85$, $P < 0.001$), and thus alternative temperature metrics would be statistically redundant in the models we used. Maximum stream temperatures in pools in 2007 were obtained through a combination of direct measurement with temperature data loggers and interpolation between data logger sites. Interpolation of maximum stream temperature was based on linear regressions of instantaneous measurements of May maximum temperatures obtained at all sites with a YSI-85 thermometer against summer maximum temperatures measured at ten sites with continuously recording thermographs (2007 summer maximum temperature = 1.21 × May 2007 maximum temperature + 0.16; $F_{[1,10]} = 68.07$, $P < 0.001$, $R^2 = 0.90$). Interpolations were not made outside the range of stream temperature maxima measured directly by data loggers. In 2009, we used temperature loggers to record maximum instantaneous temperatures at all 38 study sites, but five loggers were not recovered. At these five sites, maximum temperatures were interpolated in the same manner as described for 2007 (2009 summer maximum temperature = 1.39 × May 2009 maximum temperature − 7.87; $F_{[1,33]} = 532.54$, $P < 0.001$, $R^2 = 0.95$.)

We determined the importance of temperature relative to other habitat variables for predicting the 2009 abundance of age-1+ steelhead (defined as all fish ≥ age 1) by constructing linear regression models with May age-1+ steelhead density, September age-1+ steelhead density, and summer loss rate as dependent variables. We characterized summer fish loss from study units by calculating a k factor (ln(May density) – ln(September density); Varley and Gradwell 1960; Elliott 1994; Einum 2005), which includes combined effects of fish mortality and emigration between early and late summer sampling. We restricted our analysis of fish abundance and fish loss rates to age-1+ steelhead because a portion of the age-0 steelhead population was too small to detect during our May 2009 survey. We determined fish age classes by scale analysis from a sample of steelhead collected by electrofishing in May and September, respectively. Length thresholds separating age-0 from age-1+ steelhead were 75 mm in May and 125 mm in September.

To estimate age-1+ steelhead abundance for each study unit, we used the bounded counts estimator (Robson and Whitlock 1964; Routledge 1982):

$$\tilde{y}_B = d_{[m]} + (d_{[m]} - d_{[m-1]})$$

where $\tilde{y}_B$ is the estimated number of fish, $d_{[m]}$ is the maximum fish count on any of n dives, and $d_{[m-1]}$ is the second highest fish count.

We included maximum daily stream temperature, pool depth, percent cover, and longitudinal stream position (m above the bottom of the study reach) as independent variables in all analyses of fish abundance. Pool depth and stream cover are known to influence survival of stream fish (e.g., Power 1984; Harvey et al. 2005) and were hypothesized to be potentially important predictors of summer habitat quality in the study stream. We included longitudinal stream position of the experimental units because previous studies have shown that stream position can influence the

distribution and abundance of juvenile salmonids (e.g., Harvey 1998; Harvey et al. 2005). We included initial log-transformed age-1+ steelhead density in the analysis of summer fish loss after testing for density dependence following recommendations by Varley and Gradwell (1968) and because of previous findings of density-dependent survival in stream salmonids (e.g., Keeley 2001; Einum 2005; Sogard et al. 2009).

We evaluated the relative likelihood of each set of candidate models of fish abundance using Akaike's information criterion adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002). Model selection using AIC$_c$ provides a means of selecting the most parsimonious model from the set of candidate models, given the data (Burnham and Anderson 2002). The model with the smallest AIC$_c$ value is regarded as the most plausible, given the data, and models within two AIC$_c$ units of the model with the lowest AIC$_c$ value were considered to be equally supported by the data. We also assessed the relative importance of each independent variable using Akaike weights (w_i), which describe the weight of evidence that a model is the best-approximating model, given the data and set of candidate models. To determine the weight of support for inclusion of a particular variable, we summed Akaike weights for all models that included a given independent variable (Burnham and Anderson 2002).

To analyze behavioral data, we constructed activity budgets based on the number of observations per behavioral category within each 5 min recording. Activity budgets describe the amount of time focal animals perform each of a set of predefined behaviors (Martin and Bateson 1993). To help summarize behavioral trends in relation to stream temperature, we grouped observations occurring at similar temperatures within each feeding treatment into 1 °C bins and averaged activity budgets across fish. We then plotted mean activity within each behavioral category (as a percentage of total activity) against stream temperature and fit nonlinear least-squares regressions to the data. The goal of this analysis was to help visualize population-average behavioral trends in relation to temperature rather than generating precise parameter estimates.

Results

Fish persistence in relation to temperature

Stream temperature maxima in study pools ranged from 22.6 to 33.1 °C in 2007 and from 22.3 to 29.7 °C in 2009. Deviations from thalweg temperature > 1 °C occurred in only 4 of the 48 pools instrumented with temperature loggers in 2007 and 2009, indicating that pools were well mixed and micro-scale thermal refugia were rare. Maximum stream temperature was not correlated with stream position ($r = -0.16$, $P = 0.36$), nor was this variable correlated with other stream habitat variables that we measured (habitat area: $r = -0.15$, $P = 0.36$; pool depth: $r = 0.15$, $P = 0.36$; cover: $r = 0.20$, $P = 0.23$). Stream temperature maxima occurred in September 2007 and July 2009, preceding our late-summer fish sampling in each year. In both 2007 and 2009, fish persisted over the dry season in all study pools where summer temperature maxima remained ≤30 °C, but the probability of persistence declined rapidly at warmer temperatures, falling below 50% when temperatures reached 31.5 °C (logistic regression: likelihood ratio $\chi^2 = 45.93$, df, = 1, $P < 0.001$; Fig. 1). There was no effect of study year on the relationship between maximum stream temperature and fish occurrence (logistic regression: Wald's $\chi^2 < 0.001$, $P = 0.998$), and this variable was dropped from the final regression model.

Temporal change in 2009 fish abundance and potential effects of temperature

For fish abundance at the beginning of the summer dry season, a positive relationship with stream position and a negative relationship with May stream temperature maxima provided the best-approximating model ($F_{[1,37]} = 16.43$, $P < 0.001$, $R^2 = 0.48$) of age-1+

Fig. 1. Persistence of juvenile steelhead in relation to maximum annual stream temperature. The right *y* axis shows the percentage of sites where juvenile steelhead were observed in 2007 (solid circles; *n* = 29) and 2009 (shaded circles; *n* = 38). Data points correspond to 1 °C bins and are offset to display data for both study years. The left *y* axis shows the predicted probability of fish presence in relation to maximum annual stream temperature based on a logistic regression model (solid line).
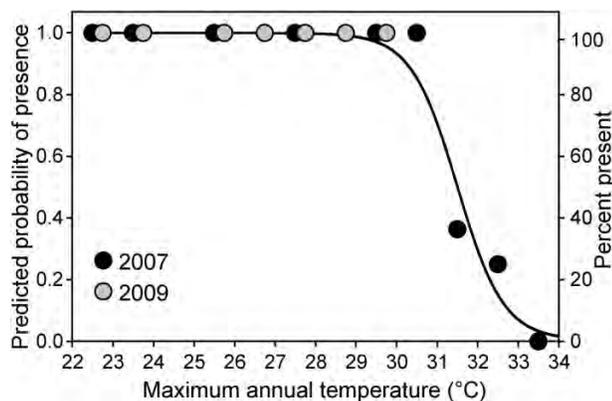
steelhead abundance among the 15 possible combinations of the four independent variables stream position, May stream temperature maxima, pool depth, and percent cover (Table 1; Fig. 2). Summation of Akaike weights revealed strong support for inclusion of both stream position ($\Sigma w_i > 0.99$) and May temperature maxima ($\Sigma w_i = 0.79$) and relatively weak support for inclusion of pool depth ($\Sigma w_i = 0.26$) and percent cover ($\Sigma w_i = 0.22$) in the best-approximating model.

At the end of the summer dry season, positive relationships with stream position and pool depth provided the best-approximating model for September 2009 age-1+ steelhead abundance ($F_{[1,37]} = 16.309$, $P < 0.001$, $R^2 = 0.48$) when we considered all 15 model combinations of the four independent variables stream position, summer temperature maxima, pool depth, and percent cover (Table 1; Fig. 3). Akaike weights indicated strong support for both stream position ($\Sigma w_i = 0.99$) and pool depth ($\Sigma w_i = 0.85$), but relatively weak support for summer temperature maxima ($\Sigma w_i = 0.23$) and percent cover ($\Sigma w_i = 0.23$) for inclusion in the best-approximating model.

From May to September 2009, the mean density of age-1+ steelhead declined by 0.11 fish·m^{-2} (95% confidence interval (CI): 0.06–0.15) from an average of 0.28 fish·m^{-2} (range: 0.05–0.64) in May to 0.17 fish·m^{-2} in September (range: 0.04–0.46) (paired *t* test: *t* = 4.511, df = 37, *P* < 0.001). Fish loss rate during the 2009 summer dry season was best approximated by a model including a positive effect (i.e., increased fish loss) of initial age-1+ fish density and negative effects of both stream position and pool depth ($F_{[3,37]} = 13.328$, $P < 0.001$, $R^2 = 0.54$) when we considered all 31 model combinations of the five independent variables stream position, summer temperature maxima, pool depth, percent cover, and initial age-1+ fish density (Table 1). Initial log-transformed age-1+ fish density provided the best single-factor model of summer fish loss ($F_{[1,37]} = 15.464$, $P < 0.001$, $R^2 = 0.30$) and had the strongest possible support for inclusion in the best-approximating model ($\Sigma w_i > 0.99$), but both stream position ($\Sigma w_i = 0.99$) and pool depth ($\Sigma w_i = 0.94$) also received strong support. Summer temperature maxima alone had a weak positive effect on summer fish loss ($F_{[1,37]} = 4.540$, $P = 0.040$, $R^2 = 0.11$) but had little support for inclusion in the best-approximating model ($\Sigma w_i = 0.24$). Percent cover was unrelated to summer fish loss ($F_{[1,37]} = 3.042$, $P = 0.090$) and had little support for inclusion in the best-approximating model ($\Sigma w_i = 0.21$).

Because of evidence for inclusion of stream position in the best-approximating models of fish abundance and summer fish loss,

we examined correlations between stream position and other habitat variables that may have influenced fish abundance. However, exploration of the data a posteriori produced no significant correlations between stream position and wetted habitat area, pool volume, cover availability, pool depth, or maximum stream temperature (*P* > 0.05 for all variables).

Fish microhabitat selection and behavior

On the dates that we measured thermal conditions at fish focal positions in September 2009, stream temperature maxima exceeded 29 °C, approaching the warmest stream temperatures measured that year (i.e., 29.7 °C). Temperatures at fish focal positions in 24 study pools ranged from 20.3 to 28.2 °C, compared with a range of available stream temperature from 20.3 to 29.2 °C. The majority of these pools were well mixed and homogenous in temperature, providing little opportunity for selection of thermal habitat. However, we observed variability in available temperature in four pools that stratified vertically, and in these pools fish occupied the coldest temperatures measured. The mean difference between temperatures at fish focal positions and available temperature was small (mean = –0.4 °C, 95% CI: –0.8–0.0). Because opportunities to behaviorally thermoregulate were rare, when all 24 sampled pools were considered, temperatures at fish focal positions did not vary significantly from available thermal habitat (Kolgomorov–Smirnoff test; *D* = 0.1583, *P* = 0.659; Fig. 4).

During instantaneous sampling of steelhead behavior, stream temperatures ranged from 17.9 to 29.0 °C. Steelhead behavior included holding, feeding, and agonistic behavior. Individual fish typically maintained a consistent focal position to which they returned after brief forays to intercept food or interact with conspecifics. We did not observe any fish to switch from holding within the water column to sheltering within stream substrate. Temperature appeared to affect both the percent time spent feeding and in agonistic interactions (Fig. 5). The addition of food increased feeding rates at temperatures below approximately 24–25 °C, but feeding rates in pools with and without food additions began to converge and approach zero as temperatures increased to 29 °C (Fig. 5). The trends in feeding activity both in pools with and without food addition were best fit by second-order polynomial regressions (with food addition: $R^2 = 0.86$, $P < 0.001$; without food addition: $R^2 = 0.78$, $P < 0.001$; Fig. 5). The addition of food did not have clear effects on agonistic behavior, which peaked at intermediate temperatures. Similar to feeding activity, agonistic activity decreased towards zero both in pools with and without food additions as stream temperatures exceeded 24–25 °C (Fig. 5). Trends in agonistic activity across the range of observed temperatures were best fit by second-order polynomial regressions (with food addition: $R^2 = 0.59$, $P = 0.012$; without food addition: $R^2 = 0.45$, $P = 0.049$; Fig. 5).

Discussion

At the watershed scale, maximum stream temperature was strongly associated with the persistence of juvenile steelhead over the summer dry season. Because the observed thermal threshold for steelhead persistence was very steep, interannual variation in stream temperatures resulted in large differences in the extent of available summer rearing habitat for steelhead between study years. For example, cooler maximum stream temperatures in 2009 resulted in a 43% increase in the extent of the study reach that was thermally suitable for juvenile steelhead occupancy (i.e., having a probability of persistence ≥0.50) compared with 2007. These results suggest that relatively small increases in maximum stream temperatures resulting from anthropogenic or natural disturbances can have large consequences for steelhead production in southern California populations.

Our estimated temperature threshold for steelhead persistence (31.5 °C) is only slightly higher than reported from previous field studies of more northerly populations. Both Li et al. (1994) and

Table 1. Best-approximating models representing relationships among age-1+ steelhead abundance, summer fish loss, and physical characteristics of habitats in Santa Paula Creek as measured by AIC_c.

Response variable	Independent variables	Δ_i	R^2	w_i
May fish density	Stream position (+), maximum temperature (–)	0.00	0.50	0.46
	Stream position (+), minimum temperature (–), pool depth (+)	2.19	0.51	0.15
	Stream position (+), maximum temperature (–), percent cover (+)	2.48	0.51	0.13
September fish density	Stream position (+), maximum depth (+)	0.00	0.48	0.51
	Stream position (+), maximum depth (+), maximum temperature (–)	2.46	0.48	0.15
	Stream position (+), maximum depth (+), percent cover (+)	2.48	0.49	0.15
Summer fish loss	Initial fish density (+), maximum depth (–), stream position (–)	0.00	0.54	0.45
	Initial fish density (+), maximum depth (–), stream position (–), percent cover (–)	2.66	0.55	0.11
	Initial fish density (+), maximum depth (–), stream position (–), maximum temperature (+)	2.66	0.55	0.11

Note: Δ_i indicates the difference in AIC_c between models. No models were within two AIC_c units of the best-approximating model, but the top three models for each response variable are included for comparison. w_i indicates the Aikaike weights for the candidate models. Independent variables are listed in order of weight of support for inclusion in the best-approximating models. In models of summer fish loss, a positive effect indicates that a variable was associated with increased fish loss.

Fig. 2. Best-approximating model of age-1+ steelhead density in May 2009 within habitats of Santa Paula Creek from a set of candidate models that included all combinations of stream cover, habitat depth, maximum daily stream temperature in May, and the position of the units in the 5 km study reach.
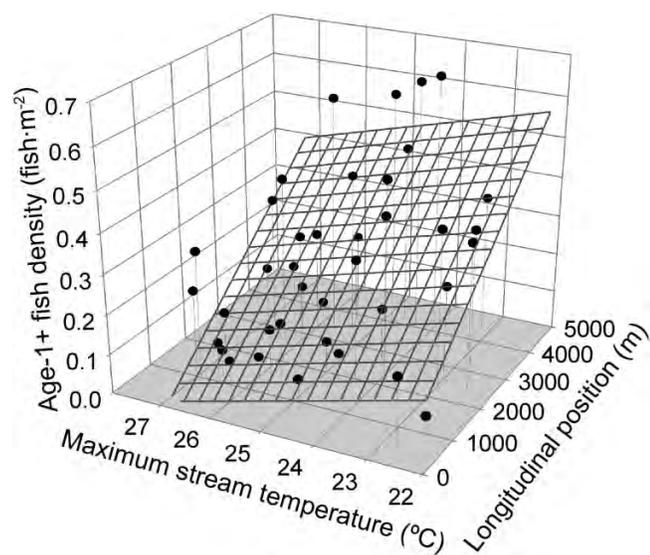
Fig. 3. Best-approximating model of age-1+ steelhead density in September 2009 within habitats of Santa Paula Creek from a set of candidate models that included all combinations of stream cover, habitat depth, maximum daily stream temperature in May, and the position of the units in the 5 km study reach.
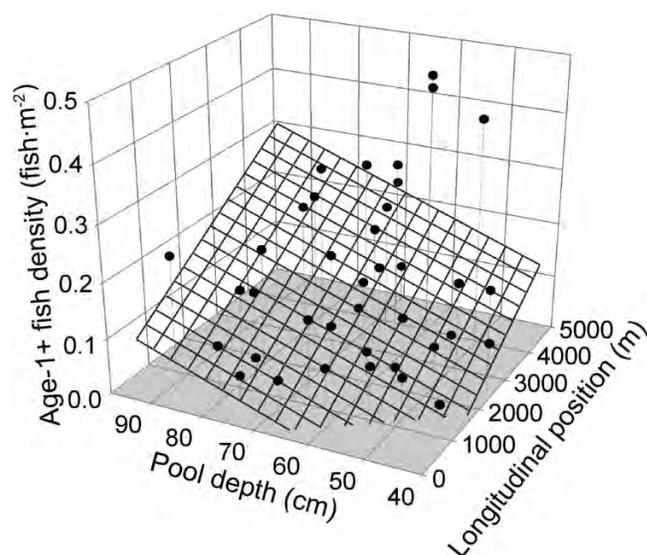
Rodnick et al. (2004) observed rainbow trout at sites with maximum stream temperatures up to 30 °C in small streams in eastern Oregon. Zoellick (1999) found that rainbow trout survived short-term exposure to stream temperatures as high as 29 °C in southwestern Idaho streams, and Werner et al. (2005) observed juvenile steelhead at sites reaching 28.6 °C in tributaries to the Navarro River, California.

Our results are also consistent with laboratory estimates of thermal tolerance for the species. For example, Myrick and Cech (2000) reported critical thermal maxima (CTM) from 30 to 32 °C for Eagle Lake and Mt. Shasta strains of rainbow trout acclimated to high temperatures (i.e., 20–25 °C). The results of Myrick and Cech (2000) are very similar to other published CTM values for rainbow trout, which fall between 29 and 31 °C when fish are acclimated at temperatures ≥19 °C (Lee and Rinne 1980; Currie et al. 1998; Rodnick et al. 2004) (Table 2).

The relatively short duration of fish exposure to extreme temperatures under a naturally fluctuating thermal regime probably accounts for the concordance of our results and previous findings with laboratory-derived CTM values, which are based on acute responses to increasing temperatures rather than chronic exposure. A second factor that may help explain the consistency of our field results with CTM estimates is the rarity of other fish species in Santa Paula Creek. Steelhead are the only fish present in >90% of the study reach and are numerically dominant in the few pools where other fish species occurred. In systems where steelhead are sympatric with other fish, temperature-dependent competition can reduce steelhead condition and abundance at warmer temperatures (e.g., Reeves et al. 1987; Reese and Harvey 2002). The lack of interspecific competition in Santa Paula Creek may allow steelhead to realize a thermal niche approaching potential niche limits estimated from laboratory studies such as those by Myrick and Cech (2000). Competitive exclusion of steelhead from warm habitats may explain lower observed thermal thresholds for steelhead occurrence in stream systems with more diverse fish communities (e.g., Eaton et al. 1995; Thompson et al. 2012).

Because southern steelhead populations often occur in streams with warm water temperatures, it is tempting to speculate that they have adapted higher thermal tolerances than more northerly populations. However, previous research provides little evidence for local adaptation of thermal tolerance within *O. mykiss* (Table 2). Although CTM values vary among studies, most of this variation reflects differences in the temperature at which fish were accli-

Fig. 4. Estimated probability densities of maximum daily temperature at fish focal positions (solid line) and available temperature (dashed line) based on observations in 24 study pools in Santa Paula Creek. The shaded region represents the standard error of the difference between the density curves for fish focal position temperature and available temperature.
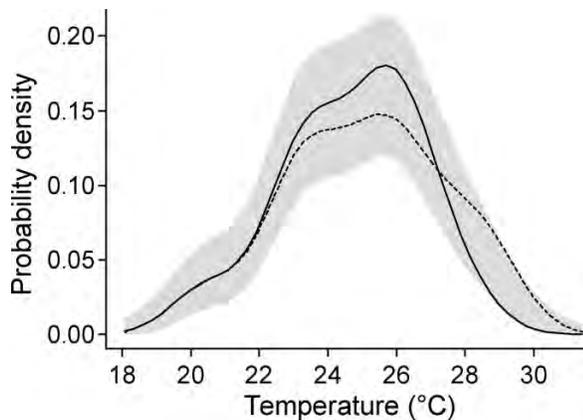
mated prior to CTM trials (Fig. 6). Fish acclimated at higher temperatures have greater thermal resistance to elevated temperatures (e.g., Lee and Rinne 1980; Currie et al. 1998; Myrick and Cech 2000). These results suggest that physiological mechanisms underlying CTM in *O. mykiss* are highly conserved and point to strong environmental rather than genetic effects on thermal tolerance. If southern populations of steelhead are adapted to warmer thermal regimes, we suggest that they are more likely to demonstrate differences from northern populations in physiological reaction norms (e.g., growth performance) under sublethal temperature ranges, as seen in other teleosts (Yamahira and Conover 2002; Baumann and Conover 2011).

While the logistic relationship between maximum stream temperature and fish persistence suggests a strong threshold effect for fish occurrence at the watershed scale, below this threshold the influence of temperature on variation in fish abundance among individual habitat units was less clear. Previous research documented negative correlations between rainbow trout abundance and maximum stream temperatures (e.g., Li et al. 1994; Ebersole et al. 2001; Zoellick 2004). Negative relationships between temperature and fish abundance may result from temperature-mediated reductions in habitat carrying capacity as a function of increased fish metabolic demands (Li et al. 1994), increased mortality or emigration of fish with lower status or condition (Hughes and Grand 2000), or as a result of temperature-mediated competition with other stream fish (Reeves et al. 1987; Li et al. 1994; Reese and Harvey 2002). Consistent with previous findings, we observed a negative effect of maximum stream temperature on steelhead density in May 2009 when daily stream temperature maxima had already approached stressful levels. We expected the negative influence of stream temperature on fish abundance to strengthen over the summer of 2009 as stream temperatures continued to increase, approaching maximum values of nearly 30 °C. Contrary to our expectations, however, stream temperature alone was a weak predictor of end-of-summer abundance and had little support for inclusion in the best-approximating models of either September 2009 fish density or summer fish loss.

Why was fish abundance responsive to stream temperature at the beginning of the summer, but not over the warmest portion of the year? We suggest that variation in fish abundance at the beginning of the summer is more likely to reflect the results of thermal habitat selection because stream flows may still facilitate fish movement from warmer sites to sites with cooler tempera-

Fig. 5. Mean activity (±1 SE) of steelhead in relation to instantaneous stream temperature in pools with (shaded circles) and without (open circles) food addition. Split symbols indicate overlapping data points for pools with and without food addition. (*a*) Agonistic activity is represented by best-fit lines from second-order polynomial regressions. The solid and dashed lines denote pools with and without food addition, respectively. (*b*) Feeding activity is represented by best-fit lines from second-order polynomial regressions. The solid and dashed lines denote pools with, and without food addition, respectively.
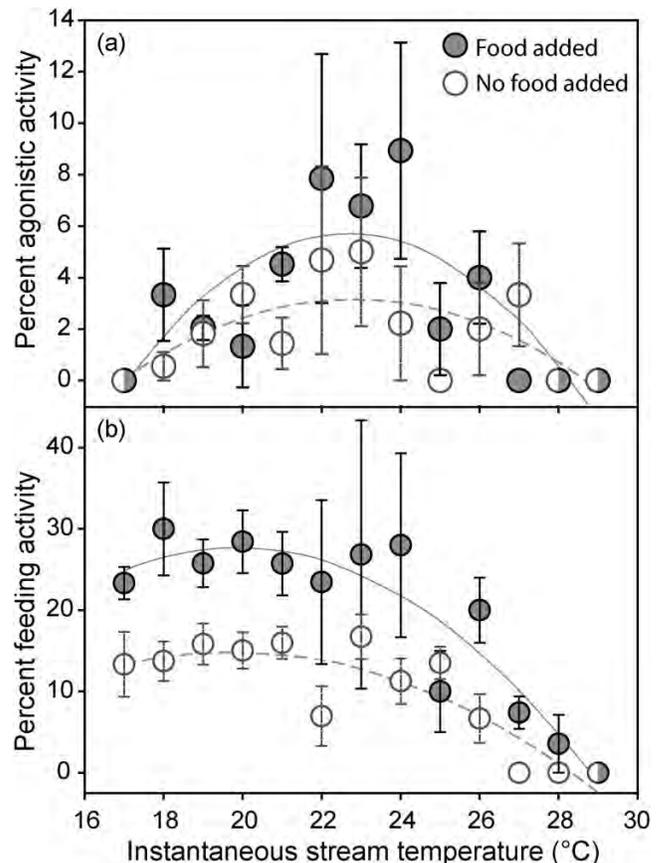
tures. As streamflow diminished over the summer, riffles separating pool habitats became very shallow or intermittent, especially in warm, hydrologically losing stream reaches in unconfined valley segments. Opportunities for thermal habitat selection via movement between pools, therefore, probably decrease with summertime decreases in streamflow. Habitat selection for relatively cool pools at the beginning of the summer may elevate local fish densities above the level that can be supported later during the ecological crunch (sensu Wiens 1977) of the dry season when reductions in streamflow and food availability increase intraspecific competition. This hypothesis is supported by the relatively high densities of age-1+ steelhead observed in May 2009, which averaged 0.28 fish·m⁻². Mean late-summer densities of age-1+ steelhead in pools of small streams typically fall below the range of 0.10–0.20 fish·m⁻² (e.g., Everest et al. 1988; Roper et al. 1994; Reedy 1995). In Santa Paula Creek, the abundance of age-1+ steelhead declined in 21 of the 22 study pools where age-1+ steelhead densities exceeded 0.20 fish·m⁻² in May. By comparison, fish abundance decreased in only 5 of 16 pools where age-1+ steelhead densities were below 0.20 fish·m⁻² in May. The effects of intraspecific competition may further be exacerbated in habitats cool enough to promote summertime fish growth, since larger fish have higher energetic requirements. For example, self-thinning relationships

Table 2. Comparison of mean critical thermal maxima for various wild and domesticated strains of *Oncorhynchus mykiss* acclimated at temperatures from 9.8 to 25 °C.

Acclimation temperature (°C)	Critical thermal maximum (°C)	O. mykiss strain	Source
9.8	27.6	Benner Springs, Pennsylvania: domestic	Carline and Machung 2001
9.8	28.1	Unspecified, Pennsylvania: wild	Carline and Machung 2001
10	27.6	Eagle Lake, California: wild	Myrick and Cech 2000
10	27.7	Mt. Shasta, California: domestic	Myrick and Cech 2000
10	28.0	Crystal Lake, Missouri: domestic	Currie et al. 1998
10	28.5	Williams Creek, Arizona: domestic	Lee and Rinne 1980
11	27.5	American River, California: domestic	Myrick and Cech 2005
14	28.4	Mt. Shasta, California: domestic	Myrick and Cech 2000
14	28.6	Eagle Lake, California: wild	Myrick and Cech 2000
14	29.4	Interior Columbia, Oregon: wild	Rodnick et al. 2004
15	28.4	American River, California: domestic	Myrick and Cech 2005
15	29.1	Crystal Lake, Missouri: domestic	Currie et al. 1998
19	29.6	American River, California: domestic	Myrick and Cech 2005
19	29.7	Mt. Shasta, California: domestic	Myrick and Cech 2000
19	30.1	Eagle Lake, California: wild	Myrick and Cech 2000
20	29.4	Williams Creek, Arizona: domestic	Lee and Rinne 1980
20	29.8	Crystal Lake, Missouri: domestic	Currie et al. 1998
22	30.7	Mt. Shasta, California: domestic	Myrick and Cech 2000
22	31.0	Eagle Lake, California: wild	Myrick and Cech 2000
25	31.5	Mt. Shasta, California: domestic	Myrick and Cech 2000
25	32.0	Eagle Lake, California: wild	Myrick and Cech 2000

Fig. 6. Critical thermal maxima (CTM) of *O. mykiss* acclimated to different temperatures. The association between CTM and acclimation temperature is represented by a linear best-fit line and 95% confidence interval ($R^2 = 0.90$, $P < 0.001$). Data are from sources in Table 2.
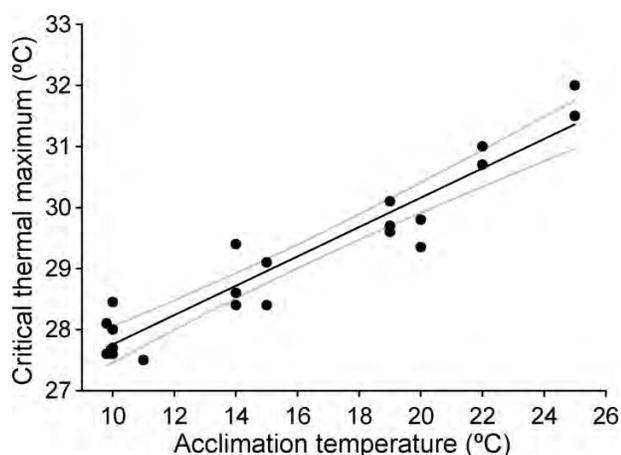
between fish density and fish mass are well established for salmonid populations (Grant 1993; Bohlin et al. 1994; Dunham and Vinyard 1997), and slopes of the thinning coefficient can be particularly steep for fish greater than 140–150 mm (Rincón and Lobón-Cerviá 2002), a size threshold exceeded by 60% of the age-1+ steelhead we observed in September.

In contrast with the inconsistent effects of stream temperature, stream position was included in all of the best-approximating models of fish abundance and fish loss. Longitudinal trends in stream fish demographics are typically correlated with downstream increases in discharge, temperature, and associated effects on secondary production (Harvey 1998; Harvey et al. 2005). However, we observed strong longitudinal patterns of fish abundance despite insignificant correlations between stream position and other measured habitat features of maximum depth, instream cover, and stream temperature. Although we did not measure spatial variation in stream discharge, the absence of longitudinal trends in wetted surface area and pool volume suggest that while

groundwater flux and hyporheic exchange were locally variable, there was no net downstream loss of surface flow that would negatively affect fish abundance. The influence of stream position in models of fish abundance indicates that spatial patterning of resources is important but unaccounted for using the common, site-specific features of habitat quality we measured.

Conditions necessary for creating micro-scale thermal refugia were rare in Santa Paula Creek, a situation similar to observations in other southern California steelhead streams (Spina 2007; but see Matthews and Berg 1997). Nielsen et al. (1994) demonstrated that isolated bodies of cold water in stream pools persist only where mixing is severely limited. Structural features such as large wood jams and gravel bars that were important for limiting mixing in the study of Nielsen et al. (1994) are largely absent in Santa Paula Creek. Although we observed point sources of cooler subsurface waters at topographic nick points, the volume of cool water influx and the turbulence of surface flow caused sufficient mixing to cool the entire stream. Consequently, variation in availability of thermal habitat occurred among pools and reaches, rather than within pools. Vertically stratified pools were present but uncommon, and the majority of pool habitats were well-mixed and thermally homogeneous. Furthermore, in those pools with vertical stratification, cooler microhabitats near the bottom of pools still exceeded 25 °C, a threshold that has been identified as stressful or, under prolonged exposure, lethal for the species (Cherry et al. 1977; Hokanson et al. 1977). Therefore, within individual pools, fish had little choice but to endure exposure to high ambient temperatures.

In response to elevated stream temperatures, steelhead appeared to alter their behavior to reduce energetic costs associated with foraging and agonistic interactions. Previous research across a lower range of stream temperatures (8–21 °C) found that increases in temperature promoted an increase in the time and energy that juvenile steelhead spent foraging, presumably to support temperature-mediated increases in metabolic demands (Smith and Li 1983). However, observations made by Nielsen et al. (1994) under warmer conditions are consistent with our findings that both foraging and agonistic activity in steelhead decline sharply around 24–25 °C. This reduction in activity is also consistent with the laboratory results of Myrick and Cech (2000), who found that food consumption, growth, food conversion, and

72

Can. J. Fish. Aquat. Sci. Vol. 70, 2013

routine metabolic rate decreased at 25 °C in rainbow trout fed ad libitum. In our study, elevated temperatures reduced fish activity in pools with and without food additions, suggesting that increased food production is not likely to sufficiently offset the energetic cost of activity at temperatures approaching tolerance limits.

This study has several implications for conservation and restoration of southern California steelhead populations. The consistency of our field observations with laboratory studies documenting the effects of temperature on the physiological performance of a variety of *O. mykiss* strains suggests that southern populations of steelhead are probably as sensitive to elevated stream temperatures as more northerly populations. These results emphasize the importance of maintaining or restoring suitably cool thermal regimes in streams currently or historically occupied by southern steelhead populations. Conservation actions that limit stream heating will be especially important given evidence for contemporary (Kaushal et al. 2010; Isaak et al. 2011) and projected increases in stream temperatures due to climate change (Mohseni et al. 1999; van Vliet et al. 2011). The threshold effect of temperature on steelhead persistence indicates that in regions where ambient conditions already approach critical thermal limits, relatively small increases in maximum stream temperatures may substantially reduce the extent of suitable summer rearing habitat. Conversely, management actions that reduce stream heating even slightly may result in large benefits for steelhead populations. Lastly, we observed considerable heterogeneity in stream temperatures among habitats in a stream with minimal anthropogenic disturbance. An improved understanding of the biophysical processes influencing the spatial distribution of suitable thermal habitat would benefit conservation of southern steelhead populations.

Acknowledgements

References

Allison, P.D. 1999. Logistic regression using the SAS system. SAS Institute, Cary, North Carolina.

Baumann, H., and Conover, D.O. 2011. Adaptation to climate change: contrasting patterns of thermal-reaction-norm evolution in Pacific versus Atlantic silversides. Proc. R. Soc. B Biol. Sci. **278**: 2265–2273. doi:10.1098/rspb.2010.2479.

Bohlin, T., Dellefors, C., Faremo, U., and Johlander, A. 1994. The energetic equivalence hypothesis and the relation between population density and body size in stream-living salmonids. Am. Nat. **143**: 478–493. doi:10.1086/285614.

Boss, S.M., and Richardson, J.S. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. Can. J. Fish. Aquat. Sci. **59**: 1044–1053. doi:10.1139/f02-079.

Boughton, D.A., Fish, H., Pipal, K., Goin, J., Watson, F., Casagrande, J., Casagrande, J., and Stoecker, M. 2005. Contraction of the southern range limit for anadromous *Oncorhynchus mykiss*. NOAA Tech. Memo. NMFS-SWFSC-**380**.

Boughton, D.A., Gibson, M., Yedor, R., and Kelley, E. 2007. Stream temperature and the potential growth and survival of juvenile *Oncorhynchus mykiss* in a southern California creek. Fresh. Biol. **52**: 1353–1364. doi:10.1111/j.1365-2427.2007.01772.x.

Boxall, G.D., Giannico, G.R., and Li, H.W. 2008. Landscape topography and the distribution of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in a high desert stream. Environ. Biol. Fishes, **82**: 71–84.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag Inc., New York.

Busby, P.J., Wainwright, T.C., Bryant, G.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W., and Lagomarsino, I.V. 1996. Status review of west coast steelhead. NOAA Tech. Memo. NMFS-NWFSC-**27**.

Carline, R.F., and Machung, J.F. 2001. Critical thermal maxima of wild and domestic strains of trout. Trans. Am. Fish. Soc. **130**: 1211–1216. doi:10.1577/1548-8659(2001)130<1211:CTMOWA>2.0.CO;2.

Cherry, D.S., Dickson, K.L., Cairns, J., Jr., and Stauffer, J.R. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J. Fish. Res. Board Can. **34**: 239–246. doi:10.1139/f77-035.

Currie, R.J., Bennett, W.A., and Beitinger, T.L. 1998. Critical thermal minima and maxima of three freshwater game-fish species acclimated to constant temperatures. Environ. Biol. Fish. **51**: 187–200. doi:10.1023/A:1007447417546.

Dunham, J.B., and Vinyard, G.L. 1997. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. Can. J. Fish. Aquat. Sci. **54**: 1025–1030. doi:10.1139/f97-012.

Dunham, J.B., Schroeter, R., and Rieman, B.E. 2003a. Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. N. Am. J. Fish. Manag. **23**: 1042–1049. doi:10.1577/02-029.

Dunham, J.B., Rieman, B.E., and Chandler, G. 2003b. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. Trans. Am. Fish. Soc. **23**: 894–904.

Eaton, J.G., McCormick, J.H., Goodno, B.E., O'Brien, D.G., Stefany, H.G., Hondzo, M., and Scheller, R.M. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries, **20**: 10–18.

Ebersole, J.L., Liss, W.J., and Frissell, C.A. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecol. Freshw. Fish. **10**: 1–10. doi:10.1034/j.1600-0633.2001.100101.x.

Einum, S. 2005. Salmonid population dynamics: stability under weak density dependence? Oikos, **110**: 630–633.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.

Everest, F.H., Reeves, G.H., and Sedell, J.R. 1988. Changes in habitat and populations of steelhead trout, coho salmon, and chinook salmon in Fish Creek, Oregon, 1983–1987, as related to habitat improvement. Annual Report. Prepared by US Forest Service for Bonneville Power Administration, Portland, Oregon.

Grant, J.W.A. 1993. Self-thinning in stream-dwelling salmonids. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. **118**: 99–102.

Harvey, B.C. 1998. Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. Can. J. Fish. Aquat. Sci. **55**: 1902–1908. doi:10.1139/f98-083.

Harvey, B.C., White, J.L., and Nakamoto, R.J. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. Can. J. Fish. Aquat. Sci. **62**: 650–658. doi:10.1139/f04-225.

Hokanson, K.E.F., Kleiner, C.F., and Thorslund, T.W. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. **34**: 639–648. doi:10.1139/f77-100.

Hughes, N.F., and Grand, T.C. 2000. Physiological ecology meets the ideal free distribution: predicting the distribution of size-structured fish populations across temperature gradients. Environ. Biol. Fishes, **59**: 285–298.

Isaak, D.J., Wollrab, S., Horan, D., and Chandler, G. 2011. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. Clim. Change. **113**: 499–524.

Kaushal, S.S., Likens, G.E., Jaworski, N.A., Pace, M.L., Sides, A.M., Seekell, D., Belt, K.T., Secor, D.H., and Wingate, R.L. 2010. Rising stream and river temperatures in the United States. Front. Ecol. Environ. **8**: 461–466. doi:10.1890/090037.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology, **82**: 1247–1259.

Lee, R.M., and Rinne, J.N. 1980. Critical thermal maxima of five trout species in the southwestern United States. Trans. Am. Fish. Soc. **109**: 632–635. doi:10.1577/1548-8659(1980)109<632:CTMOFT>2.0.CO;2.

Li, H.W., Lamberti, G.A., Pearsons, T.N., Tait, C.K., Li, J.L., and Buckhouse, J.C. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day basin, Oregon. Trans. Am. Fish. Soc. **123**: 627–640. doi:10.1577/1548-8659(1994)123<0627:CEORDA>2.3.CO;2.

Martin, P.R., and Bateson, P. 1993. Measuring behaviour: an introductory guide, 2nd ed. Cambridge University Press, Cambridge.

Matthews, K.R., and Berg, N.H. 1997. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. J. Fish. Biol. **50**: 50–67. doi:10.1111/j.1095-8649.1997.tb01339.x.

Mohseni, O., Erickson, T.R., and Stefan, H.G. 1999. Sensitivity of stream temperatures in the United States to air temperatures projected under a global warming scenario. Water Resour. Res. **35**(12): 3723–3733. doi:10.1029/1999WR900193.

Myrick, C.A., and Cech, J.J., Jr. 2000. Temperature influences on California rain-

bow trout physiological performance. Fish Physiol. Biochem. **22**: 245–254. doi:10.1023/A:1007805322097.

Myrick, C.A., and Cech, J.J., Jr. 2005. Effects of temperature on the growth, food consumption, and thermal tolerance of age-0 Nimbus-strain steelhead. N. Am. J. Aqua. **67**: 324–330. doi:10.1577/A04-050.1.

Nielsen, J.L. 1998. Scientific sampling effects: electrofishing California's endangered fish populations. Fisheries, **23**: 6–12. doi:10.1577/1548-8446(1998)023<0006:SSEECE>2.0.CO;2.

Nielsen, J.L., Lisle, T.E., and Ozaki, V. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Trans. Am. Fish. Soc. **123**: 613–626. doi:10.1577/1548-8659(1994)123<0613:TSPATU>2.3.CO;2.

Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, **421**: 37–42. doi:10.1038/nature01286. PMID:12511946.

Power, M.E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology, **65**: 523–528. doi:10.2307/1941414.

Reedy, G.D. 1995. Summer abundance and distribution of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) in the Middle Fork Smith River, California. Master's thesis, Humboldt State University, Arcata, California.

Reese, C.D., and Harvey, B.C. 2002. Temperature-dependent interactions between juvenile steelhead and Sacramento pikeminnow in laboratory streams. Trans. Am. Fish. Soc. **131**: 599–606. doi:10.1577/1548-8659(2002)131<0599:TDIBJS>2.0.CO;2.

Reeves, G.H., Everest, F.H., and Hall, J.D. 1987. Interactions between the redside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Can. J. Fish. Aquat. Sci. **44**: 1603–1613. doi:10.1139/f87-194.

Rincón, P.A., and Lobón-Cerviá, J. 2002. Nonlinear self-thinning in a stream-resident population of brown trout (*Salmo trutta*). Ecology, **83**: 1808–1816. doi:10.1890/0012-9658(2002)083[1808:NSTIAS]2.0.CO;2.

Robson, D.S., and Whitlock, J.H. 1964. Estimation of a truncation point. Biometrika, **51**: 33–39.

Rodnick, K.J., Gamperl, A.K., Lizars, K.R., Bennett, M.T., Rausch, R.N., and Keeley, E.R. 2004. Thermal tolerance and metabolic physiology among redband trout populations in southeastern Oregon. J. Fish. Biol. **64**: 310–335. doi:10.1111/j.0022-1112.2004.00292.x.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. Nature, **421**: 57–60. doi:10.1038/nature01333. PMID:12511952.

Roper, B.R., Scarnecchia, D.L., and La Marr, T.J. 1994. Summer distribution of and habitat use by Chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Trans. Am. Fish Soc. **123**: 298–308. doi:10.1577/1548-8659(1994)123<0298:SDOAHU>2.3.CO;2.

Routledge, R.D. 1982. The method of bounded counts: when does it work? J. Wildl. Manag. **46**: 757–761. doi:10.2307/3808569.

SAS. 2006. SAS OnlineDoc. Version 9.1. SAS Inc., Cary, North Carolina.

Schonher, T., and Nicholson, S.E. 1989. The relationship between California rainfall and ENSO events. J. Clim. **2**: 1258–1269. doi:10.1175/1520-0442(1989)002<1258:TRBCRA>2.0.CO;2.

Smith, J.J., and Li, H.W. 1983. Energetic factors influencing foraging tactics in juvenile steelhead trout, *Salmo gairdneri*. *In* Predators and prey in fishes. *Edited by* D.G. Lindquist, G.S. Helfman, and J.A. Ward. Dr. W. Junk Publishers, The Hague, the Netherlands. pp. 173–180.

Sogard, S.M., Williams, T.H., and Fish, H. 2009. Seasonal patterns of abundance, growth, and site fidelity of juvenile steelhead in a small coastal California stream. Trans. Am. Fish. Soc. **138**: 549–563. doi:10.1577/T08-172.1.

Spina, A.P. 2007. Thermal ecology of juvenile steelhead in a warm-water environment. Environ. Biol. Fishes, **80**: 23–34.

Stoecker, M., and Kelley, E. 2005. Santa Clara River steelhead trout: assessment and recovery opportunities [online]. Prepared for The Nature Conservancy and The Santa Clara River Trustee Council. Available from http://www.stoeckerecological.com.

Thompson, L.C., Voss, J.L., Larsen, R.E., Tietje, W.D., Cooper, R.A., and Moyle, P.B. 2012. Southern steelhead, hard woody debris, and temperature in a California central coast watershed. Trans. Am. Fish. Soc. **141**: 275–284. doi:10.1080/00028487.2012.662200.

vanVliet, M.T.H., Ludwig, F., Zwolsman, J.J.G., Weedon, G.P., and Kabat, P. 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. Water Resour. Res. **47**: W02544. doi:10.1029/2010WR009198.

Varley, G.C., and Gradwell, G.R. 1960. Key factors in population studies. J. Anim. Ecol. **29**: 399–401. doi:10.2307/2213.

Varley, G.C., and Gradwell, G.R. 1968. Population models for the winter moth. *In* Insect abundance. *Edited by* T.R.E. Southwood. Blackwell, Oxford and Edinburgh. pp. 132–142.

Werner, I., Smith, T.B., Feliciano, J., and Johnson, M.L. 2005. Heat shock proteins in juvenile steelhead reflect thermal conditions in the Navarro River watershed, California. Trans. Am. Fish. Soc. **134**: 399–410. doi:10.1577/T03-181.1.

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. **65**: 590–597.

Wurtsbaugh, W.A., and Davis, G.E. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. J. Fish. Biol. **11**: 87–98. doi:10.1111/j.1095-8649.1977.tb04101.x.

Yamahira, K., and Conover, D.O. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? Ecology, **83**: 1252–1262.

Zoellick, B.W. 1999. Stream temperatures and the elevational distribution of redband trout in southwestern Idaho. Great Basin Nat. **59**: 136–143.

Zoellick, B.W. 2004. Density and biomass of redband trout relative to stream shading and temperature in southwestern Idaho. West. N. Am. Nat. **64**: 18–26.