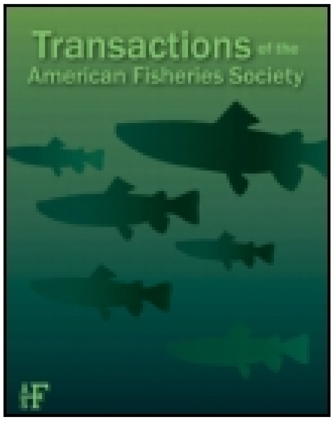

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Thermal Potential for Steelhead Life History Expression in a Southern California Alluvial River

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ARTICLE

Thermal Potential for Steelhead Life History Expression in a Southern California Alluvial River

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Abstract
Steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) near the southern limit of the species' range commonly use shallow alluvial rivers for migration, spawning, and rearing. These rivers have been widely modified for water management, and an enduring question is whether their rehabilitation would create summer nursery habitat for steelhead. We used process-based models to evaluate the thermal potential for steelhead nursery habitat in the Santa Ynez River, California, a regulated alluvial river that currently supports few steelhead. We assessed (1) how well a calibrated model of river heat fluxes predicted summer temperature patterns for a warm year and an average year; (2) whether those patterns created thermal potential for the rapid growth that is characteristic of steelhead nursery habitat; and (3) whether manipulation of flows from an upstream dam significantly altered thermal potential. In the heat flux model, the root mean square error for 15-min temperatures was 1.51°C, about three times greater than that of the larger, deeper Sacramento River in northern California. Generally, the Santa Ynez River was thermally suitable but stressful for juvenile steelhead. Flow augmentation reduced the number of thermally stressful days only near the dam, but it reduced the intensity of thermal stress throughout the river. Daytime movement of steelhead into natural, thermally stratified pools would reduce stress intensity by similar levels. In this region, *O. mykiss* commonly pursue an anadromous (steelhead) life history by entering nursery habitat early in their first or second summer and rapidly growing to attain a threshold size for anadromy by fall. In the average year, the river was thermally suitable for the first-summer pathway under high food availability and for the second-summer pathway under medium food availability. The warm year also supported the second-summer pathway under high food availability. Currently, the Santa Ynez River's capacity to support these pathways does not appear to be limited by summer temperature, thus indicating a need to identify other limiting factors.

Steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) in southern California near the southern limit of the species' native range historically migrated up wide, shallow alluvial rivers that drained arid mountain ranges (Figure 1). An enduring question is whether the summertime thermal patterns of these rivers constitute a fundamental control on

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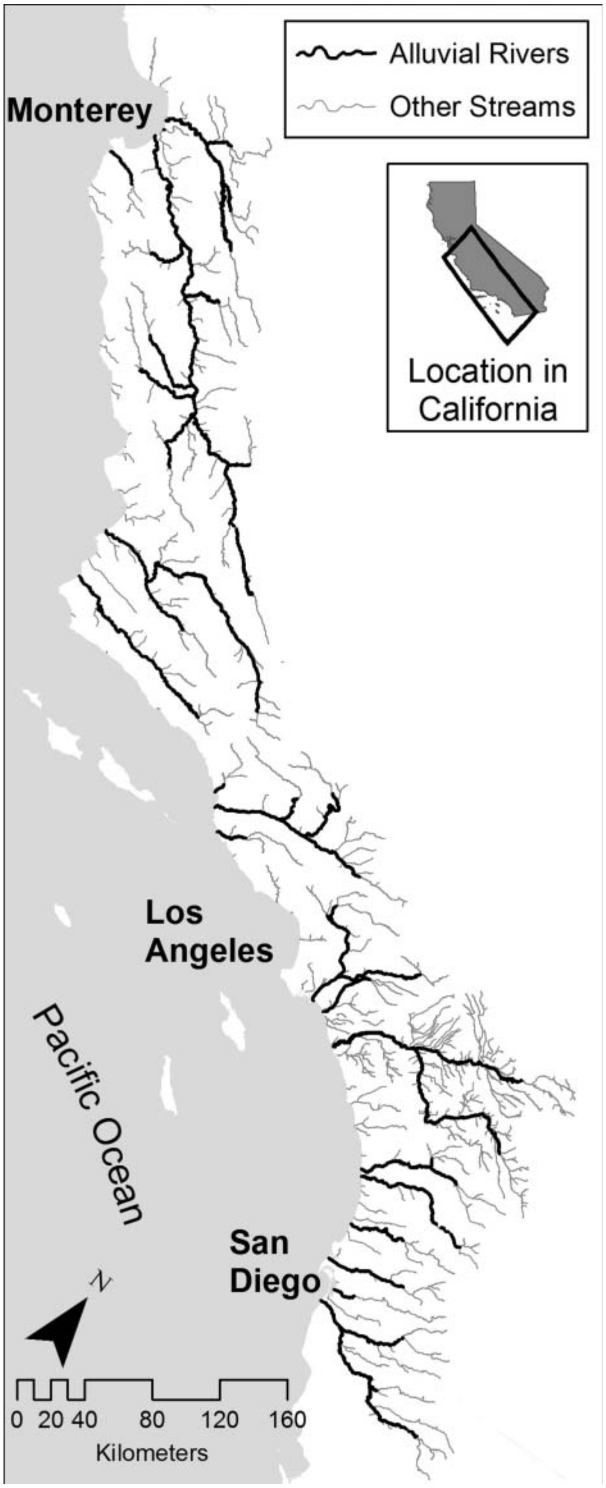

FIGURE 1. Coastal California alluvial rivers currently or formerly used by steelhead (anadromous *Oncorhynchus mykiss*) near the southern limit of the species' native range (Boughton et al. 2005). Steelhead historically used alluvial rivers as migration corridors to upland creek habitat and possibly as spawning and rearing habitat. The alluvial rivers that are highlighted here are channels with gradients less than 1% and upstream watershed areas greater than 500 km^2 within the shrub-dominated coastal mountain ranges south of Monterey Bay.

productivity and life history diversity of *O. mykiss* in this region. Southern California steelhead are currently scarce and considered highly endangered, in part due to widespread human impacts but also to challenging climatic conditions that may limit the rivers' suitability (Boughton et al. 2009). Better insight into thermal factors that limit steelhead has implications for recovery potential in the region and, more broadly, for the responses of other steelhead populations to the impacts of climate change on rivers (e.g., Mantua et al. 2010; Benjamin et al. 2013).

Steelhead are stressed by or excluded from water that is warmer than specific tolerance limits (Jobling 1981; Eaton et al. 1995; Werner et al. 2005; Kammerer and Heppell 2013a), which indirectly links their geographic distribution to summer climate via river temperature (Mohseni et al. 2003). Water temperature also sets an upper limit on the potential growth of juveniles (Wurtsbaugh and Davis 1977; Kammerer and Heppell 2013b, 2013a), with implications for the fitness and expression of anadromous and nonanadromous (resident) life histories (Mangel and Satterthwaite 2008; McMillan et al. 2012; Sogard et al. 2012; Benjamin et al. 2013). Numerous other ecological factors and human impacts also influence distribution, abundance, and life history expression in *O. mykiss* (Busby et al. 1996) but only within the bounds of a river's thermal potential for the species. Thus, if a given river habitat lacks the basic thermal potential to support the anadromous life history, then there is little scope for steelhead recovery, irrespective of other factors. We used this premise to assess the recovery potential of steelhead in an alluvial main-stem river in southern California.

Southern California *O. mykiss* populations historically expressed both anadromous (steelhead) and resident (Rainbow Trout) life histories. Anadromous life histories appear to depend on habitats that produce large smolts, which survive well in the ocean and are disproportionately represented in adult spawning migrations (Bond 2006). Such areas qualify as nursery habitat—defined as rearing habitats for which the contribution per unit area to the production of recruits to the adult population is greater than the contributions from other habitats where juveniles occur (Beck et al. 2001). Thus, steelhead nursery habitats constitute the subset of juvenile rearing habitats that generate high numbers of adult steelhead per unit area, and these nursery habitats are important for maintaining population size and persistence (Beck et al. 2001). Hayes et al. (2008) identified three pathways by which juvenile *O. mykiss* use nursery habitat in coastal California to achieve sizes that are suitable for anadromous life histories; each of the pathways involves the use of summer habitats that are capable of sustaining rapid growth (Figure 2). In the "first-summer" pathway, age-0 steelhead enter nursery habitat in early summer and grow rapidly. By fall, they reach a size that enables them to exhibit more typical growth during winter yet still successfully smolt the following spring at age 1. In the "second-summer" pathway and the much rarer "third-summer" pathway, age-0

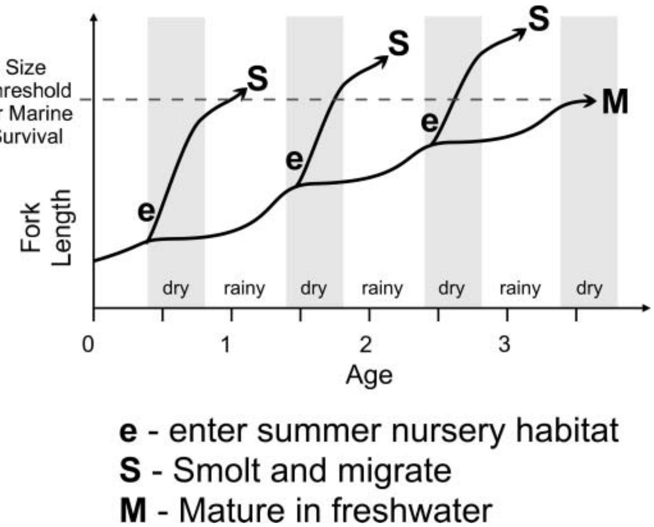

FIGURE 2. Conceptual model for *Oncorhynchus mykiss* life history pathways in stream systems of the California coast (adapted from Hayes et al. 2008; see also Bond 2006; Satterthwaite et al. 2009, 2012; and Beakes et al. 2010). Because marine survival is low for *O. mykiss* smaller than a certain size threshold (~150 mm FL), habitats only produce the anadromous life history form (steelhead) if the fish sustain rapid growth during the summer before smolting. Such habitats disproportionately contribute recruits to anadromous runs and thus fit the definition of steelhead nursery habitat (sensu Beck et al. 2001).

steelhead remain in upland creeks for 1 or 2 years, where they grow slowly until entering nursery habitat in their second or third summer and then smolting the following spring at age 2 or age 3. Some fish also follow a resident pathway, maturing in freshwater as Rainbow Trout (Hayes et al. 2012).

Growth potential is probably a central feature distinguishing steelhead nursery habitat from Rainbow Trout nursery habitat. This is because body size correlates strongly with fitness components, such as habitat-specific survival (Ward et al. 1989; Bond 2006; Evans et al. 2014; Thompson and Beauchamp 2014) and female fecundity (Shapovalov and Taft 1954), and such fitness components evolutionarily favor anadromy in some environments and freshwater residency in others (Satterthwaite et al. 2009, 2010). Thus, although life histories are partly under genetic control (Thrower and Joyce 2004; McPhee et al. 2007; Heath et al. 2008; Pearse et al. 2014), natural selection should favor a conditional life history strategy that uses body size as an internal cue for whether and when to switch from freshwater habitat to marine habitat (Mangel and Satterthwaite 2008; Satterthwaite et al. 2009; McMillan et al. 2012; Sloat et al. 2014). At the same time, the growth and body size necessary to cue the switch are expected to (1) differ for males and females (Sloat et al. 2014); (2) vary regionally as a function of local survival in both the marine and freshwater environments; and (3) depend on the maximum attainable body size (asymptotic body size) in the two environments (Satterthwaite et al. 2010). For simplicity, we focus here on female life histories under the assumption that limits on anadromous production are more closely tied to female fecundity than to male fecundity. For some salmonid species in some environments, very rapid growth and large attainable body sizes for females in freshwater appear to favor resident life histories (i.e., maturation in freshwater; Sloat et al. 2014). For *O. mykiss* in coastal California, the combination of survival schedules and very rapid growth that favors such a strategy has not yet been observed (Hayes et al. 2008). Instead, rapid growth appears to evolutionarily favor an anadromous life history, whereas moderate growth apparently favors a resident life history (Satterthwaite et al. 2009). Feeding experiments suggest that the physiological "decision" to forsake a nonanadromous path and switch to marine habitats is made in the fall—after the summer growth period and before outmigration the next spring (Beakes et al. 2010). Thus, to a first approximation, a habitat's potential to generate the anadromous life history in coastal California simplifies to the potential to support survival and rapid growth of juvenile female *O. mykiss* during summer. In the context of thermal potential addressed here, survival will fail if temperatures become lethally warm, and rapid growth will fail if water temperatures are either too warm or too cool for the growth rate required to trigger smoltification and the switch to marine habitats.

The best-studied steelhead nursery habitats in the region are coastal estuaries (Bond 2006), which form dry-season lagoons that produce abundant large smolts. Coastal climate and inputs of marine wrack and invertebrates provide the appropriate combination of temperature and feeding opportunity for rapid growth, but the total productivity of estuaries is limited by their small spatial extent. Upland creek habitat is more widespread and supports abundant juvenile *O. mykiss* (e.g., Boughton et al. 2009). However, the channels must be well shaded to stay cool enough for the species (Boughton et al. 2012), whereas dense shade appears to limit instream primary productivity, creating a food-limited environment and low growth potential in summer (Hayes et al. 2008; Rundio and Lindley 2008; Sogard et al. 2009). Coastal estuaries are usually steelhead nurseries and upland creeks are usually not, but the nursery role of a third common habitat, alluvial rivers, remains an open question.

Lowland alluvial rivers, defined here as streams with low gradients (<1%) and large upstream watersheds (>500 km^2), are numerous and widespread at the species' southern range limit in California (Figure 1); therefore, these systems could potentially produce large steelhead runs if they are capable of functioning as nursery habitat. In summer, alluvial rivers are wide, shallow, and sparsely shaded, making them vulnerable to heating but also typically allowing them to support substantial algal growth, which suggests a physical basis for a productive food web and the high feeding opportunities necessary for rapid growth of juvenile fish. Summer air temperatures in this region routinely exceed 30°C, but river temperatures are reduced to varying extents by cool onshore winds and fog from the ocean and by hydrological exchange with large aquifers. These physical influences on temperature are spatially heterogeneous (e.g., Alagona et al. 2012; Booth et al. 2013), and the degree to which they keep rivers in the thermal zone required for rapid growth—or even survival—of juvenile *O. mykiss* is unclear. Unfortunately, the potential role of lowland alluvial rivers as summer nursery habitat is ambiguous due to an incomplete historical record and the extensive negative impacts from water development, adjacent land uses, and nonnative species (Marchetti et al. 2004; Klose et al. 2012; Cooper et al. 2013).

We used process-based models of river temperature and fish response to evaluate whether a representative alluvial river in southern California has the thermal potential to support anadromous life history expression by the local population of *O. mykiss*. The Santa Ynez River serves as a useful case study because it has a historical record of occasional (and perhaps frequent) large steelhead runs (Alagona et al. 2012) and because the existing river and its human impacts are representative of many other rivers in the region (Kondolf et al. 2013). We focused our analysis on three questions: (1) Do summer temperature patterns in the main stem of the river create thermal potential for steelhead survival and a first-summer or second-summer life history strategy?; (2) How much does the manipulation of water releases from an upstream dam alter the thermal potential of the river?; and (3) How much do cold patches of water in thermally stratified pools increase the thermal potential of the river by reducing thermal stress on steelhead?

STUDY AREA

The Santa Ynez River flows west about 110 km from tributaries in the Transverse Ranges of California to the Pacific Ocean just north of Point Conception. The reach we modeled was the lower 65-km section below Bradbury Dam (Figure 3). Historical data suggest that steelhead runs once numbered in the tens of thousands in some years but were nearly nonexistent in other years (Alagona et al. 2012). Currently, anadromous *O. mykiss* are consistently rare despite the predominance of anadromous genotypes in the local population (Pearse et al. 2014, cf. Salsipuedes and Hilton creeks) and more than a decade of rehabilitation efforts (Robinson et al. 2009). Bradbury Dam impounds a large reservoir near the middle of the basin and blocks steelhead migration 70 km upstream of the

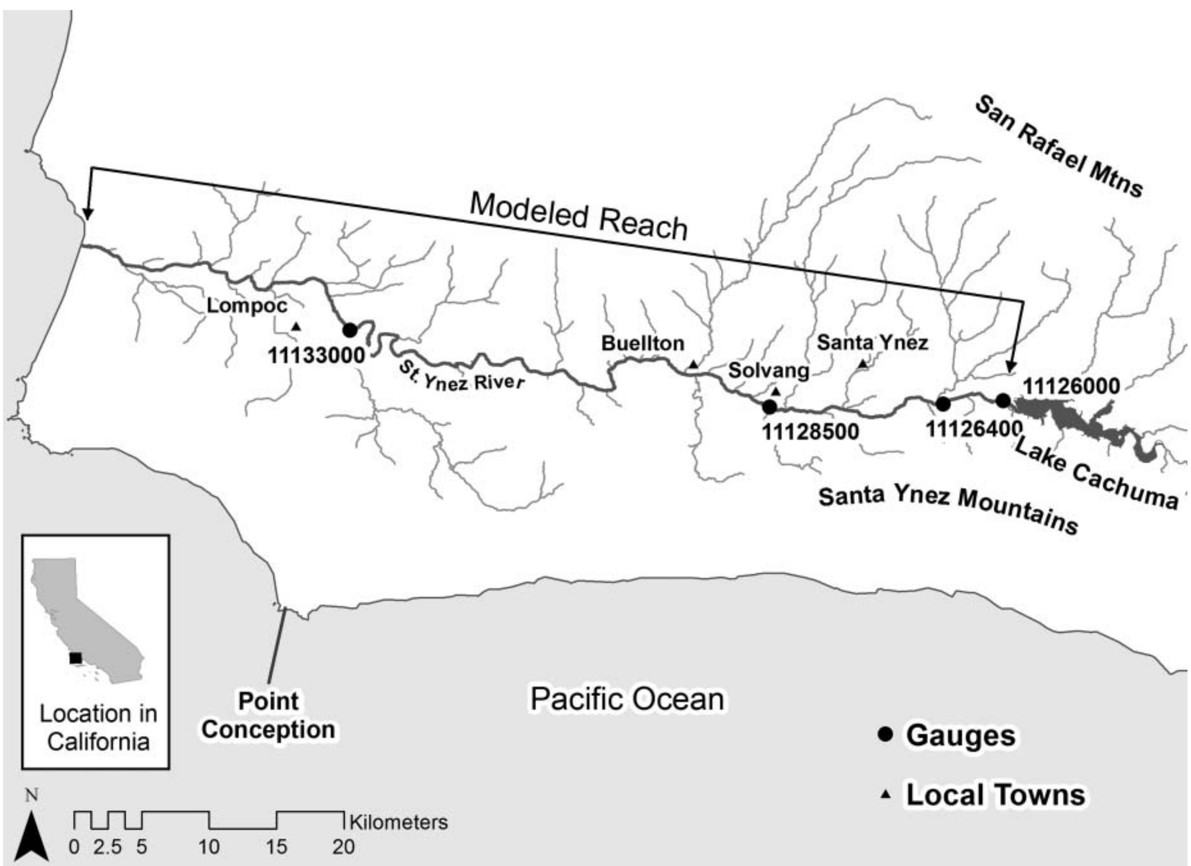

FIGURE 3. Map of the study area in the Santa Ynez River, showing landmarks and locations of stream gauges that recorded flow and temperature. U.S. Geological Survey (USGS) gauge 1112600 defined the upstream boundary conditions for the River Assessment for Forecasting Temperature model; USGS gauges 11126400, 11128500, and 11133000 were used to calibrate the parameters.

estuary; about two-thirds of the basin's spawning and rearing habitat are located upstream of the dam and are therefore inaccessible (Alagona et al. 2012). Genetically similar but nonanadromous *O. mykiss* occupy the stream network upstream of the dam (Clemento et al. 2009; Pearse et al. 2014). Summertime flows below the dam are managed for multiple objectives, including steelhead rearing and continuous replenishment of aquifers tapped by agriculture. Summer flows typically range between 0.3 and 1.0 m^3/s but may be temporarily ramped up as high as 4 m^3/s to replenish the downstream aquifers.

Between Bradbury Dam and the town of Solvang (Figure 3), the Santa Ynez River has a gravel bed with alternating pool–riffle sequences and a sparsely vegetated floodplain. The channel migrates laterally during infrequent flood events, thereby scouring pools, shaping gravel bars, and recruiting coarse woody debris via bank migration. Together, these processes produce physical habitat complexity that is characteristic of the habitats typically used by steelhead. This complexity includes a diversity of water depths and velocities; visual cover provided by instream wood, undercut banks, and overhanging vegetation; and gravel beds suitable for spawning. During years between floods, dense shrubby vegetation colonizes the active channel margins, and the riverbed develops thick algal mats. Further downstream from Solvang, the Santa Ynez River shifts to a sand-bedded channel with fewer pool–riffle sequences and more closely resembles a braided river. Important human impacts include managed flow regimes, high nitrogen loading from agricultural activities, and a profusion of exotic fish species. Juvenile and adult Largemouth Bass *Micropterus salmoides* are especially abundant, occurring in the tens of thousands throughout the lower river during summer (Robinson et al. 2009).

In summer, juvenile steelhead are common in a few small tributaries of the lower Santa Ynez River; in the river itself, however, they are rare and confined to small coldwater patches associated with thermally stratified pools or groundwater seeps (Robinson et al. 2009). Thermal stratification occurs at low flows, when water velocities are slow enough to allow poorly mixed layers of water at different temperatures to develop in well-shaded pools, or in areas where groundwater seeps up from the bed. Geomorphically, the river seems suitable for steelhead rearing, yet rearing is rare; therefore, the key questions (and the motivation for this study) are whether the lack of steelhead rearing can be attributed to thermal constraints and whether such constraints are more closely linked to dam releases or to prevailing weather.

METHODS

River temperature.—We estimated fine-grained temperature dynamics in the Santa Ynez River by using the River Assessment for Forecasting Temperature (RAFT) model (Pike et al. 2013). The RAFT model was previously developed for the Sacramento River, a large, cool California river with managed summer flows that typically range from 180 to 520 m^3/s—or about 200–1,500 times greater than typical summer flows in the Santa Ynez River. The much shallower Santa Ynez River provides a more challenging system to model because heat fluxes with the riverbed and atmosphere are potentially large relative to the thermal capacity of the river. Pike et al. (2013) described the RAFT model in detail; below, we summarize aspects that are relevant to the challenge of simulating thermal processes in the Santa Ynez River.

The RAFT model assimilates data on meteorology, flow, and river temperature to simulate hydrological and thermal processes at a temporal resolution of 15 min and a spatial resolution of 1 km. A one-dimensional hydrodynamic model simulates the advection and diffusion of heat longitudinally in the river, coupled to physical models of all upward and downward heat fluxes with the atmosphere and streambed, respectively. For the Sacramento River, RAFT accurately predicted (root mean square error [RMSE] $< 0.5°C$) the magnitude and timing of diel temperature fluctuations over entire summers, including thermal artifacts, such as the phase–antiphase pattern of downstream temperature below a dam releasing water of constant temperature (Pike et al. 2013). The model requires channel bathymetry as input, which in this study comprised topographic cross-sections spaced at ~50-m intervals, derived from aerial LiDAR and ground surveys of the Santa Ynez River. Other required input included gridded hourly meteorological data and a time series of measured hourly temperature and flow at the upstream boundary of the modeled reach (U.S. Geological Survey [USGS] gauge 1112600, about 5 km downstream of Bradbury Dam; see Figure 3).

The model runs in either a hindcast or forecast mode. Hindcasts simply assimilate temperature observations to spatiotemporally infer a past temperature field that is encompassed by the time span of the data. Forecasts predict future temperature time series based on constructed flow and temperature scenarios at the upstream boundary. We used hindcasts to calibrate RAFT and reconstruct temperature fields from the recent past, and we used forecasts to predict the effects of hypothetical water release scenarios.

Calibration of the model benefits from the assimilation of flow records that include both large and small flows, so we focused on two recent summers (2006 and 2010) with flows spanning a relatively broad range (0.3 to 5.0 m^3/s). Based on daily temperatures at the Lompoc gauge (USGS gauge 11133000), 2006 had the hottest summer of the last decade, with a mean summer water temperature of 21.41°C (range of summer means for the last decade = 19.46–21.41°C; calculated for June 1–October 1 of each year from 2003 to 2012). In contrast, 2010 had a nearly average summer, with a mean water temperature of 20.48°C (mean of summer means for the last decade = 20.56°C).

For each summer, the RAFT model was calibrated by adjusting several tunable parameters to achieve a best fit with 15-min water temperatures at three gauges downstream of

Bradbury Dam (USGS gauges 11126400, 11128500, and 11133000; Figure 3). Tunable parameters included the depth of the streambed (affecting the rate of bed heat conduction), the temperature of the deep groundwater reservoir (assumed to be constant over time), and coefficients for the rate of evaporative cooling relative to wind speed.

After calibration, we simulated alternative flow scenarios by using the same data used for hindcasts, altering only the flow. Seven scenarios of constant flow (0.14, 0.28, 0.71, 1.4, 2.8, 4.3, and 5.7 m^3/s [5, 10, 25, 50, 100, 150, and 200 ft^3/s]) were simulated for the dry season (May 1–October 1).

Thermal indicators of habitat suitability.—To evaluate how river temperature was likely to affect southern California steelhead, we developed a set of biological indicators. A review of the literature suggested that steelhead in various regions can persist in streams if short-term maximum temperatures remain below 30°C or perhaps 29°C (Zoellick 1999; Rodnick et al. 2004; Huff et al. 2005; Werner et al. 2005; Sloat and Osterback 2013), which is similar to laboratory estimates of the critical thermal maximum, a measure of short-term physiological tolerance for high temperature (Myrick and Cech 2004; Rodnick et al. 2004; Hasnain et al. 2013). However, at temperatures above 22–24°C, feeding and agonistic behaviors decline in frequency (Sloat and Osterback 2013), and the fish show signs of stress (Werner et al. 2005). Laboratory estimates of incipient lethal temperature (50% mortality after long exposure) vary across studies but average around 25°C. Steelhead start to concentrate in thermal refugia, if available, when temperatures exceed 21°C, and they almost completely retreat to refugia when temperatures are around 24°C (Nielsen et al. 1994; Ebersole et al. 2001; Baird and Krueger 2003; Sutton et al. 2007). Many southern California streams that support steelhead do not provide such refugia, and steelhead actively feed in the temperature range of 21–24°C, which is presumably stressful (Spina 2007; Sloat and Osterback 2013).

Based on this review, we define thermal indicators as follows. A day is "thermally suitable" if maximum daily temperature stays below 29°C *and* mean daily temperature stays below 25°C. However, a day is "thermally stressful" if temperature rises above 21°C at any time, with the daily stress intensity quantified as degree-hours above 21°C (i.e., for each day, $\Sigma[T_t - 21]\Delta t$).

Thermal growth potential.—We defined thermal growth potential as the maximum attainable growth of an individual fish, a function of the river's thermal regime and food availability. Thermal growth potential was estimated using the bioenergetics model for *O. mykiss* described by Railsback and Rose (1999), as modified by Satterthwaite et al. (2010) and Arriaza (2013). Individual growth arises from the difference between energy intake and energy expenditure (Rand et al. 1993; Railsback and Rose 1999; Satterthwaite et al. 2010), which are modeled as weight- and temperature-dependent functions for food consumption and respiration, respectively (see Arriaza [2013] for details). The functional form of the growth response to temperature is hump-shaped after Thornton and Lessem (1978) for coldwater species; the functional form was parameterized for California steelhead as in Railsback and Rose (1999). Expressions for maximum food intake and respiration costs in the basic model were modified by functions simulating the energy cost of activity and the difficulty of finding food in a wild habitat, in accordance with recommendations made by Andersen and Riis-Vestergaard (2004) and Bajer et al. (2004). Higher activity increases food consumption, but total energetic cost also increases. For simplicity, we assumed that fish choose a unique activity level that optimizes growth given all other parameters (Arriaza 2013). In the resulting model, the growth rate depends on fish size and food availability but generally peaks in the range of 15–17°C and becomes negative at temperatures above 22–24°C.

We applied the bioenergetics model to temperature output from RAFT scenarios in combination with assumptions about food availability. For *O. mykiss* in the Santa Ynez River (either in its current state or under hypothetical flow scenarios), the level of difficulty in finding food is unknown although presumably low, as judged from the great abundance of juvenile Largemouth Bass and other exotic fish in the river. For simplicity, we assumed that the difficulty of finding food over the summer was constant, and uncertainty was represented by simulating low, medium, and high food availability as drawn from parameter estimates for the same model when applied to two alluvial rivers in California's Central Valley over various years and seasons (Satterthwaite et al. 2010).

Nursery potential.—Growth potential was used to evaluate whether thermal patterns in the Santa Ynez River were sufficient to support either a first-summer or second-summer pathway to anadromy. Growth of age-0 and age-1 *O. mykiss* from June 1 to October 1 was simulated at daily time steps by using mean daily temperature from the RAFT scenarios. Weights of juveniles on June 1 were assumed to be 1.9 g for age-0 fish and 13.6 g for age-1 fish (D. Rundio, National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center, personal communication).

Thermal growth potential was judged to be sufficient for steelhead nursery habitat if fish had grown past a smolting criterion, defined as the minimum FL on October 1 associated with successful anadromy. In the spring, FLs greater than 150 mm are associated with successful anadromy (i.e., a high smolting rate and high marine survival; Ward et al. 1989; Bond 2006; Evans et al. 2014; Thompson and Beauchamp 2014). We examined two versions of the October 1 criterion to account for uncertainty. The "high" smolting criterion was an October 1 FL exceeding 150 mm, which makes the very conservative assumption that growth is negligible in the intervening winter. The "typical" smolting criterion was an October 1 FL greater than 100 mm; this criterion is more apt because it assumes that growth in the intervening winter is typical of upland creeks in the region, which would produce fish larger than the 150-mm threshold by the following spring (Satterthwaite et al. 2009).

Stratified pools.—To assess the extent to which thermally stratified pools might reduce thermal stress, we deployed vertical arrays of temperature loggers in five sections of the Santa Ynez River during summer 2011. Sites were chosen on the basis of accessibility and wide geographic distribution. Stratified pools have been observed in California rivers with large gravel bars, flow separation, extensive intergravel flow, groundwater seeps, and pools that are forced by large woody debris or boulders (Nielsen et al. 1994). Based largely on these findings, we selected pools within each section that possessed at least three geomorphic and hydrologic criteria indicating a high potential for stratification. We identified 16 such pools. In each pool, we positioned a fence post vertically at the deepest point (either by driving it into the substrate or placing it in a manufactured concrete base) and attached three Hobo pendant loggers (Onset Corporation) housed by gray plastic sunshields. One logger was placed 10 cm below the water's surface, another logger was placed against the streambed, and the third logger was deployed midway between the first two. The period of record was July 1–October 1, except for three loggers that were not deployed until the second week of July.

The pools were snorkel surveyed for the presence of steelhead in late summer (August 16–18). Standard methods (e.g., Boughton et al. 2009) were used for the survey, including visual assignment of fish to three general size-classes (<100, 100–200, or >200 mm FL). Such methods generally achieve per-fish observation probabilities around 0.70–0.85.

Complete data sets were recovered from 14 pools. In many cases, declining flows exposed the upper (surface) temperature logger; in the remaining cases, the records of the middle and surface loggers were nearly identical, so records from the middle logger were taken to represent the main flow. Pools were defined as stratified if they showed an absolute difference greater than 1°C between middle and bottom loggers for at least 5% of the period of record. Mean daily stress intensity was calculated for the middle and bottom logger positions in each pool.

RESULTS

Performance of the RAFT Model

Each RAFT hindcast produced 14,689 temperature predictions for the 153 d from midnight on May 1 to midnight on October 1. The RMSE of 15-min temperatures was 1.51°C in both years, with the RMSE of daily means being slightly smaller and the RMSE of daily maximums being slightly larger (Table 1). The RMSE broken down by USGS gauge and flow showed a negative relationship with flow but not consistently; the lower flows generally involved prediction error ranging from 1°C to 2°C. Thermal stress had an RMSE of 14.8 degree-hours in 2006 and 11.0 degree-hours in 2010, which were comparable in magnitude to the predicted daily stress itself (see below).

TABLE 1. Performance metrics for the River Assessment for Forecasting Temperature hindcasts estimated from three downstream temperature gauges in the Santa Ynez River, California (RMSE = root mean square error).

	RMSE		Bias	
Metric	2006	2010	2006	2010
15-min temperature (°C)	1.51	1.51	−0.04	0.30
Daily mean temperature (°C)	1.03	0.80	−0.04	0.30
Daily maximum temperature (°C)	1.70	2.00	−0.24	1.60

Mean biases in 15-min and daily temperatures were small (≤0.3°C; Table 1). The bias in maximum daily temperature was about five times larger than the bias in mean daily temperature for each year (Table 1). Bias as a function of flow tended to be hump-shaped, with a relatively small or negative bias at low and high flows and a positive bias at intermediate flows.

Thermal Suitability and Thermal Stress

The seven flow scenarios altered the mean daily river temperature relative to the temperature records of the recent past (Figure 4A, C). The lowest flow (0.14 m^3/s) raised temperature by as much as 1.25°C but only in the vicinity of Bradbury Dam; effects were less than 0.5°C further than 10 km from the dam and were negligible beyond 20 km from the dam. The highest flow (5.7 m^3/s) lowered temperature by as much as −2.6°C in 2006 and −1.6°C in 2010, with effects persisting further downstream (40–50 km); however, less extreme scenarios (1.4 m^3/s or less) always had negligible effects further than 20 km below the dam.

In contrast, the seven flow scenarios had larger and more extensive effects on mean maximum daily temperature (Figure 4B, D). The largest effects were close to the dam and ranged from +2.5°C to −4.6°C for the lowest and highest flow scenarios, respectively. However, effects ranging between about +0.8°C and −1.7°C persisted as far as 60 km from the dam, much further than the effects for mean daily temperature.

Based on the recent temperature data and based on the scenarios, no part of the river became thermally unsuitable for steelhead, with one small exception. In 2006, at the lowest flow (0.14 m^3/s), 3 km of the lower river became unsuitable for 1 d in late summer.

In general, nearly all summer days were thermally stressful throughout the entire river except for the area immediately below Bradbury Dam (Figure 5A, C). Higher water releases could expand this less-stressful zone downstream, but the highest release could only create a truly low-stress zone a few kilometers long just below the dam. However, dam releases had large effects on the intensity of stressful days, and these effects persisted much further downstream, especially for the three largest releases (Figure 5B, D).

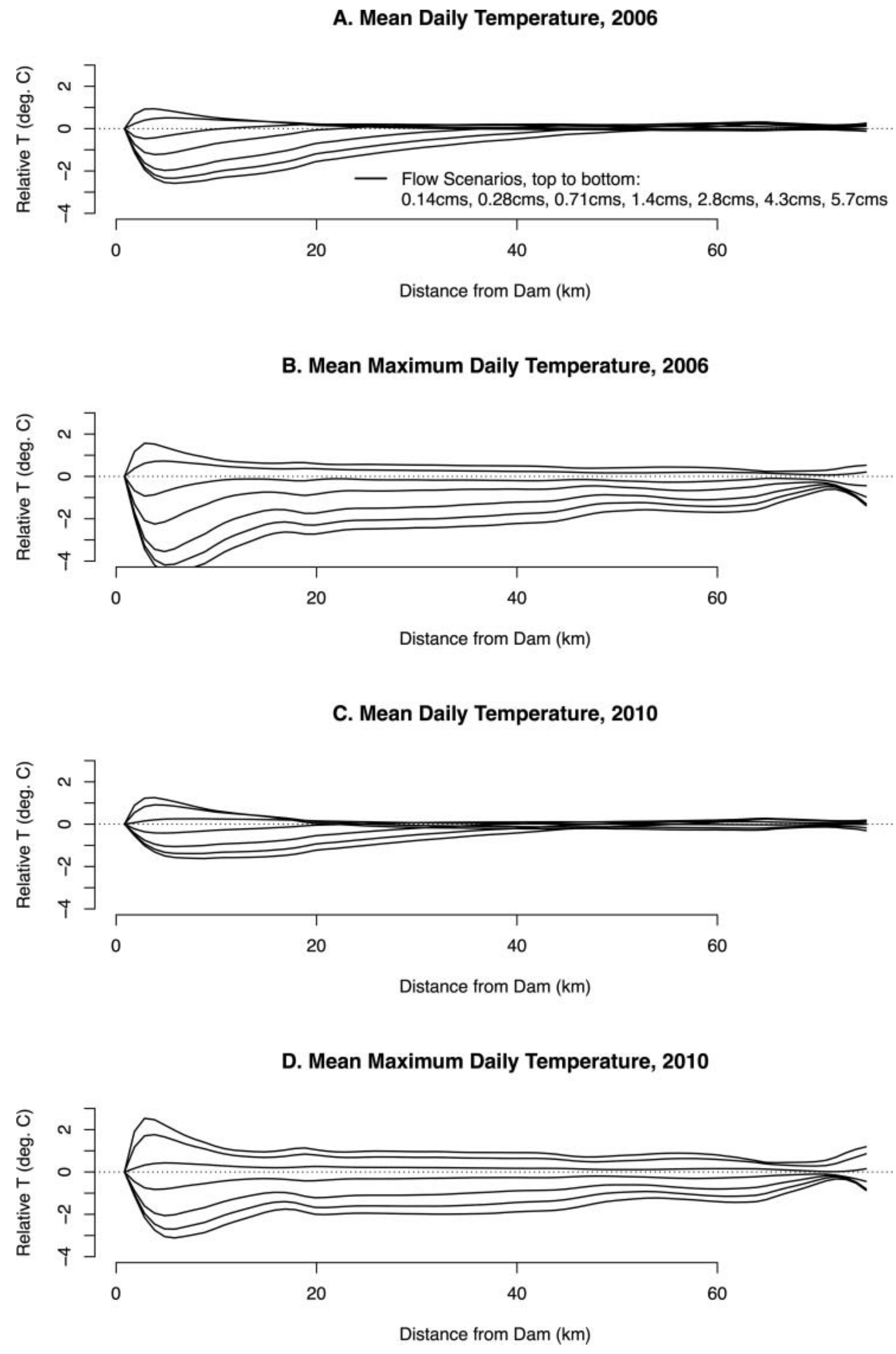

FIGURE 4. Effects of flow levels (simulated dam releases; cms = cubic meters per second) on temperatures (*T*) downstream of Bradbury Dam on the Santa Ynez River relative to the calibration scenario (hindcast temperature from actual flow releases occurring in 2006 and 2010). The mean of mean daily temperature and mean maximum daily temperature for the summer release season (May 1–October 1) are shown.

Nursery Potential

For clarity, nursery potential results from the various scenarios are reported in terms of relative final mass, calculated as the final mass of fish on October 1 divided by the corresponding final mass projected under the actual summer flows of 2006 and 2010.

Age-0 fish.—In 2010, the average year, medium to high food availability produced fish with masses greater than the

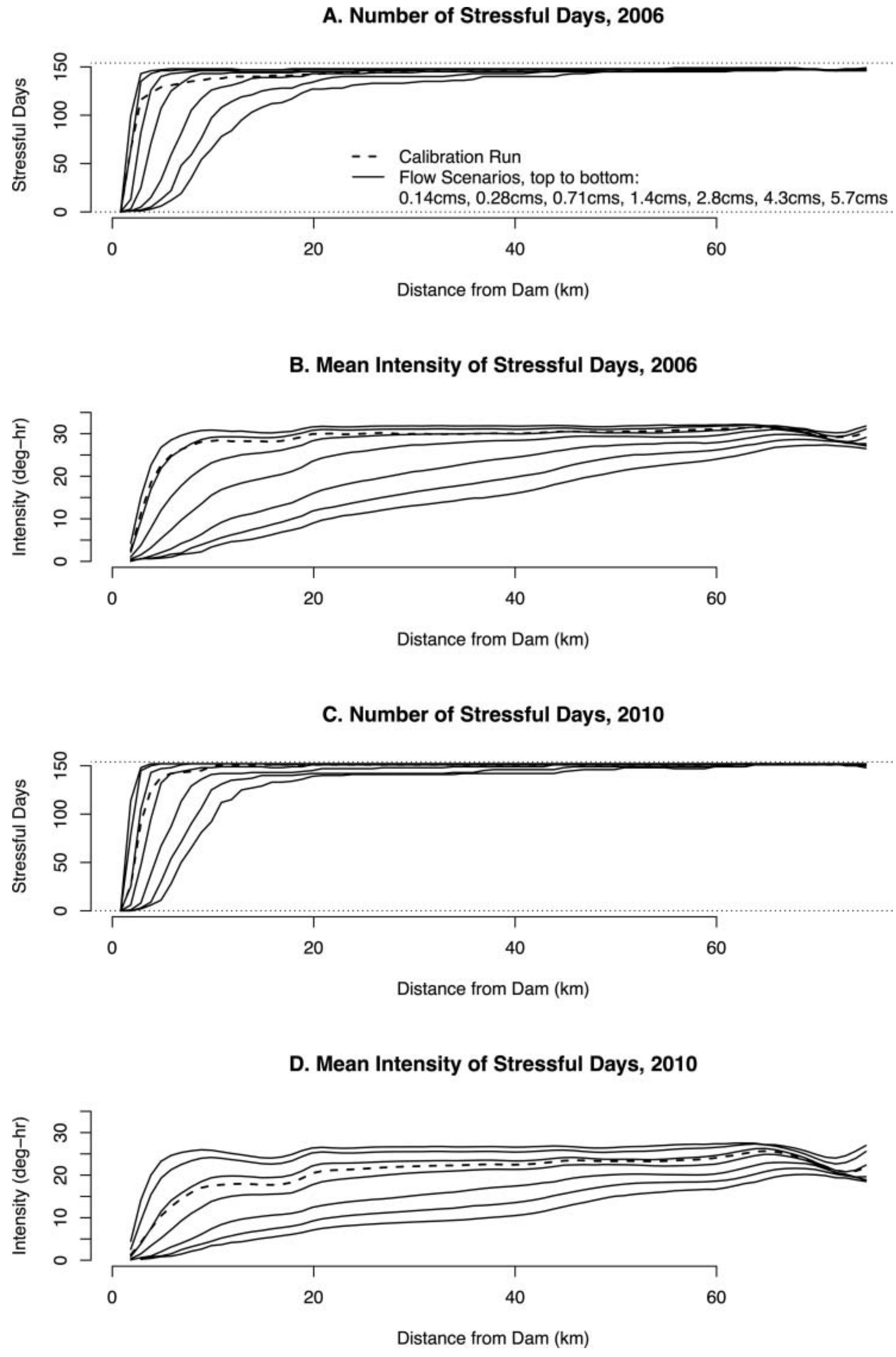

FIGURE 5. Number of days that were thermally stressful for steelhead and the mean stress intensity (degree-hours) under various simulated flow levels (cms = cubic meters per second) in the Santa Ynez River during the summer season (May 1–October 1).

typical smolting criterion throughout the entire river and regardless of flow scenario (Figure 6A, B). For other combinations (high food availability plus high smolting criterion; or low food availability plus typical smolting criterion), fish only reached smolting size near the dam (Figure 6A, C). The size of the potential nursery zone near the dam ranged from 3 to 20 km depending on the flow scenario examined (Figure 6A, C). If the high smolting criterion was used in combination with medium or low food availability, the first-summer pathway was not supported in any area of the river.

The year 2006, a hot year, had results similar to those for 2010 except that at intermediate food availability under the typical smolting criterion, the first-summer strategy was not supported throughout the entire river (Figure 6D). Instead, a nursery zone was present below the dam, and the size of the zone varied greatly (5–42 km) depending on the flow scenario. Very high flows (>4 m^3/s) were necessary to expand the nursery zone to a length greater than 20 km.

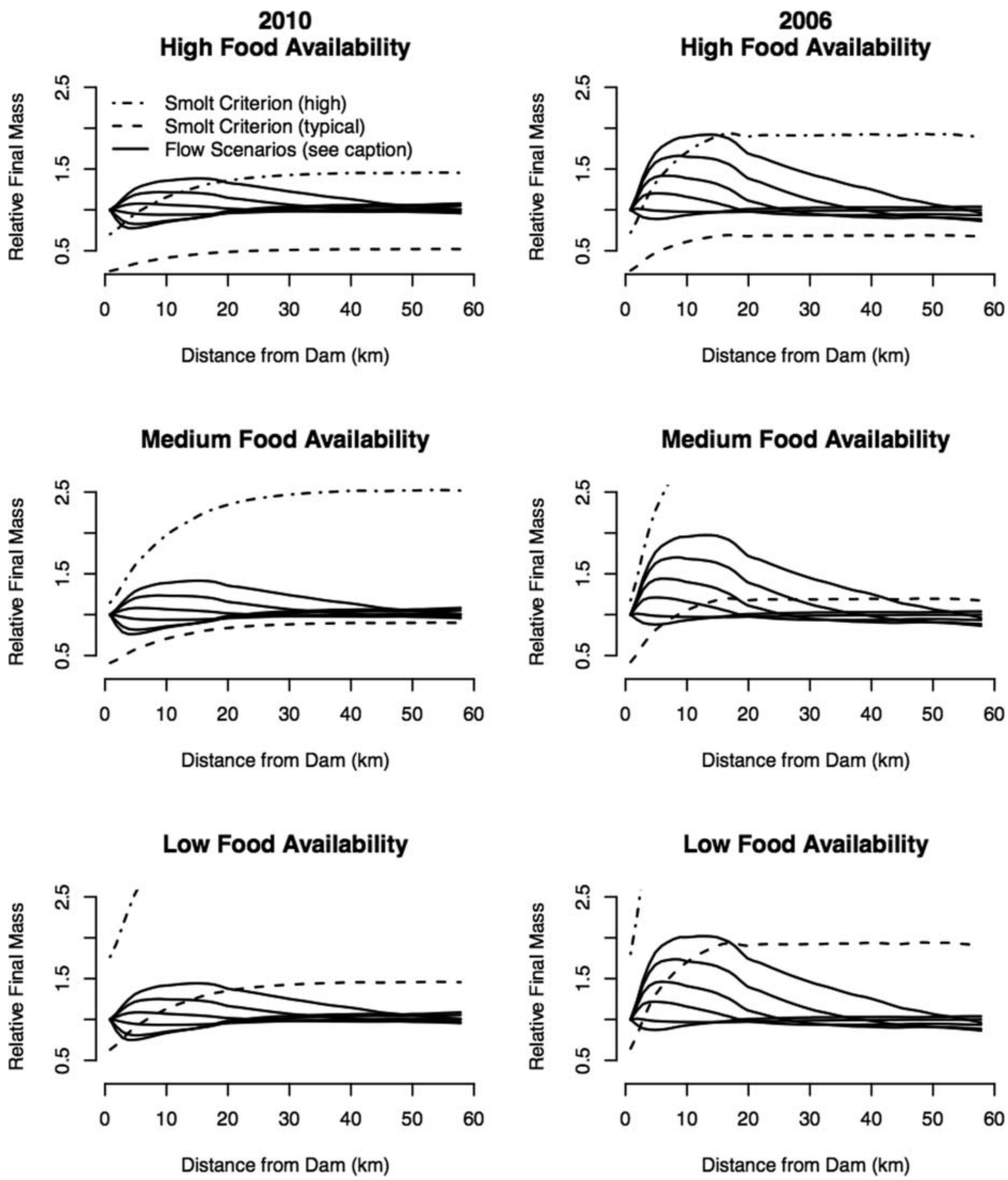

FIGURE 6. Relative final mass for age-0 steelhead on October 1 as modeled for various flow scenarios (solid lines), years (columns), and levels of food availability (rows) at locations downstream of Bradbury Dam on the Santa Ynez River. The "typical" smolt criterion describes the final mass on October 1 that is assumed necessary to trigger smolting and out-migration during the following spring, given typical winter growth conditions. The "high" smolt criterion conservatively assumes zero winter growth. Flow scenarios (lines from top to bottom) are 5.7, 4.3, 2.8, 1.4, 0.71, and 0.28 m^3/s.

Age-1 fish.—In 2010, the entire river could support the second-summer pathway under a typical smolting criterion, regardless of food availability (Figure 7A, C, E). Under the high smolting criterion, the area supporting the second-summer pathway was still the entire river if food availability was high (Figure 7A), but the area shrank to a flow-dependent zone near the dam if food availability was intermediate (Figure 7C). The year 2006 gave similar overall results except

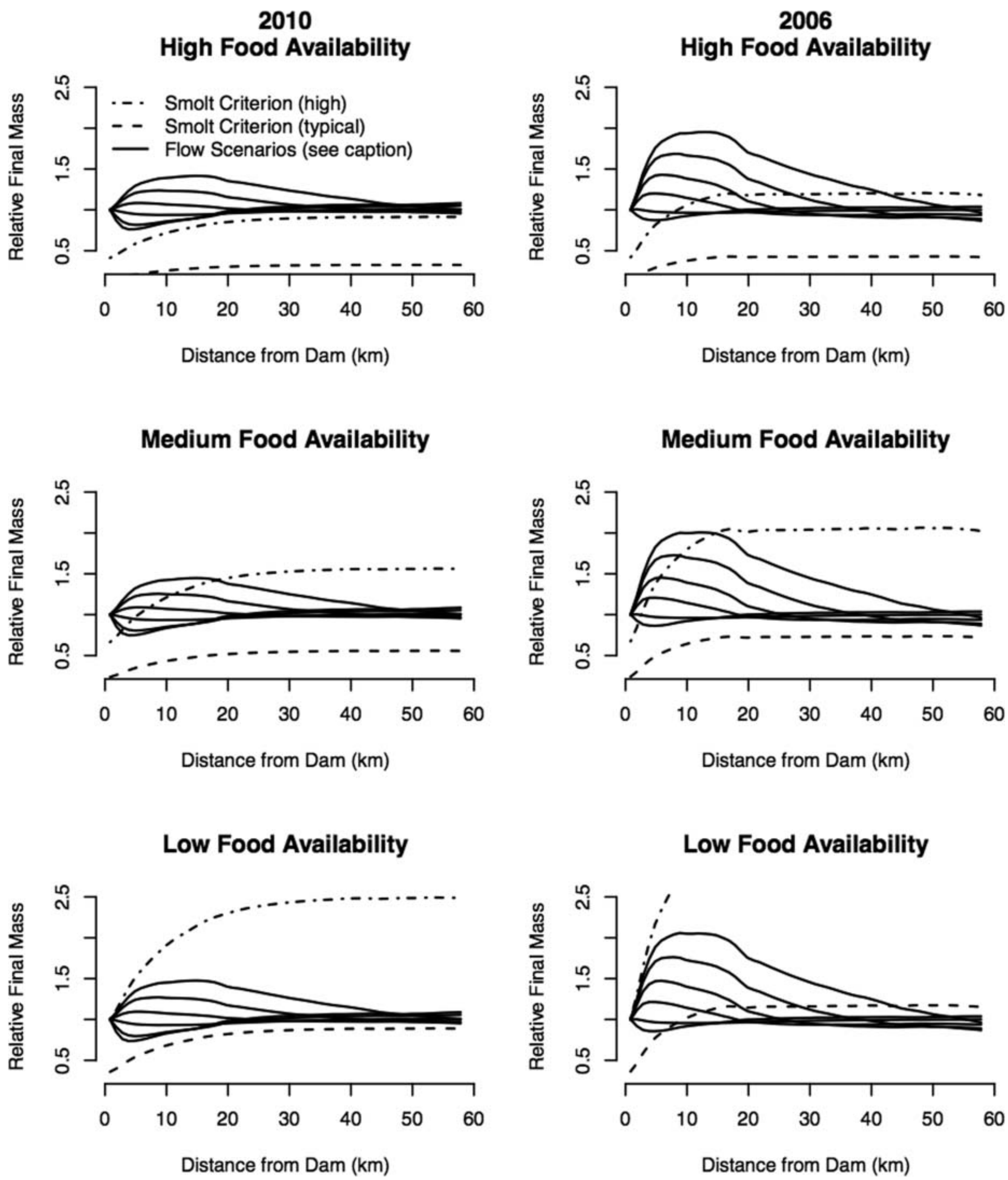

FIGURE 7. Relative final mass for age-1 steelhead on October 1 as modeled for various flow scenarios (solid lines), years (columns), and food availability (rows) at locations downstream of Bradbury Dam on the Santa Ynez River. The "typical" smolt criterion describes the final mass on October 1 that is assumed necessary to trigger smolting and out-migration during the following spring, given typical winter growth conditions. The "high" smolt criterion conservatively assumes zero winter growth. Flow scenarios (lines from top to bottom) are 5.7, 4.3, 2.8, 1.4, 0.71, and 0.28 m^3/s.

that reaches supporting a second-summer pathway shrank from the entire river to the zone below the dam for two scenarios: (1) high food availability plus the high smolting criterion (Figure 7B); and (2) low food availability plus the typical smolting criterion (Figure 7F). The size of the nursery zone generally ranged from 5 to 18 km depending on flow; however, for very high flows (>4 m^3/s), the zone could extend as far as 43 km downstream.

In no case did a flow scenario convert the entire river into potential nursery habitat—either the combination of year (meteorological conditions) and food availability produced riverwide nursery habitat or the flow scenarios created a nursery zone near the dam that disappeared downstream as the river reached thermal "quasi-equilibrium" with meteorological conditions. Only for flows greater than 4 m^3/s was the nursery zone ever longer than approximately 20 km.

Stratified Pools

Of the 14 pools that were successfully monitored, eight (~60%) were thermally stratified. Neither the bottom nor the main flow of any pool became thermally unsuitable for steelhead during the study, but water temperatures were often stressful. Mean daily stress intensity was consistently lower at the bottoms of stratified pools (Figure 8).

Only five of the pools were thermally stratified on the day of their fish survey; of these pools, three harbored juvenile *O. mykiss*, whereas only one of the nine unstratified pools harbored *O. mykiss* (one-tailed z-test: $P = 0.027$).

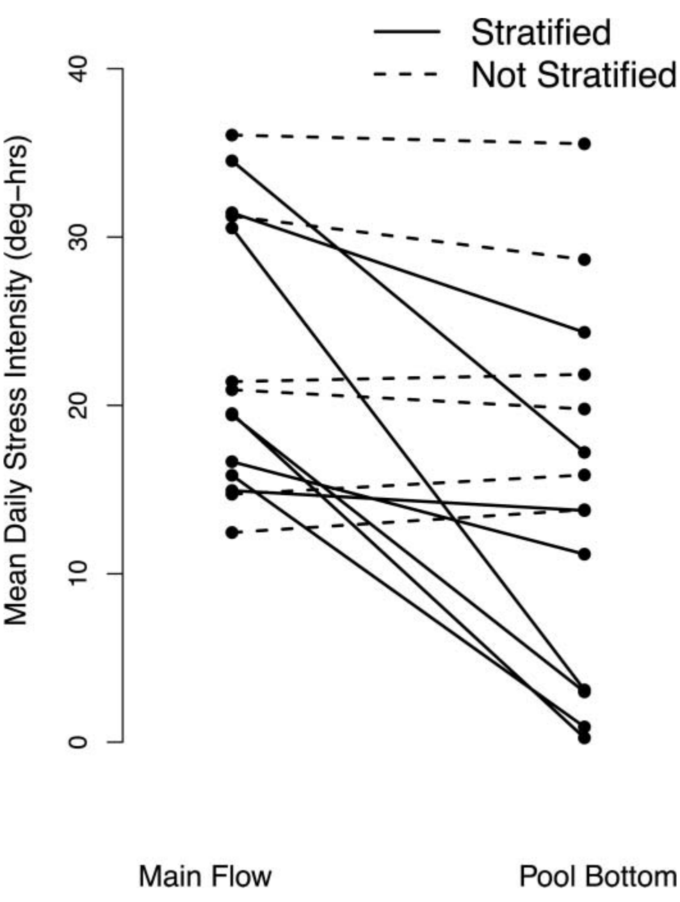

FIGURE 8. Mean daily intensity of thermal stress (degree-hours) for steelhead, as measured in the main flow and at the bottom of thermally stratified and unstratified pools in the Santa Ynez River during summer 2011.

DISCUSSION

Thermal Potential for Steelhead Life Histories

The simulations suggested that even during relatively hot summers, a coastal alluvial river in southern California was thermally suitable for juvenile steelhead. Nevertheless, nearly every summer day in both 2006 (the hot year) and 2010 (the average year) was thermally stressful throughout the Santa Ynez River, with stress intensity about 20% higher during 2006 than during 2010. Increasing the flow did not reduce the number of thermally stressful days except in an area just downstream of Bradbury Dam, but it did reduce the stress intensity throughout the entire river (Figure 5). Our data suggest that fish movement into stratified pools when temperatures exceed 21°C would tend to reduce stress intensity by an amount comparable to that achieved by increasing the flow (10–20 degree-hours/d; Figure 8). Presumably, this retreat to stratified pools would lower the rearing capacity for the river as a whole. However, juvenile steelhead appear to be able to use thermal refugia as a base from which to exploit the wider river during cool times of day (Brewitt and Danner 2014), so overall rearing capacity would be considerably larger than the pools themselves. Increasing the water releases from the dam might have additional benefits beyond stress reduction, such as increasing the river's capacity for first-summer life histories relative to second-summer life histories, thus supporting a greater life history diversity overall.

Predictions for potential steelhead nursery habitat can be summarized as follows. If the Santa Ynez River system supports typical winter growth, the second-summer pathway will be thermally available throughout the entire lower river but will be sensitive to climate if summer feeding opportunity is low. The first-summer pathway will also be thermally available but will become sensitive to climate when feeding opportunity is intermediate. In such situations, the pathways to anadromy can become thermally restricted to a tailwater zone below Bradbury Dam. On the other hand, if the river system produces neglible winter growth, then nursery habitat usually will be restricted to the tailwater or will be completely absent, depending on food availability.

In the simulations, flow scenarios did not determine whether the entire Santa Ynez River was nursery versus nonnursery habitat. Flow only altered the spatial extent of the tailwater zone when the river was otherwise physically unsuited to producing rapid growth of *O. mykiss*. Downstream of this zone, the river temperature became more equilibrated to local microclimate and riverbed conditions. Thus, temperature presumably became shaped much more by natural processes than by upstream dam releases and therefore was more similar to what would generally be considered an unimpaired thermal regime for this climate. In general, temperatures tended to stay above the range for maximum growth (15–17°C) but below the threshold for thermal exclusion (mean daily temperature <25°C, maximum temperature <29°C). Whether the river is thermally suitable for steelhead production (as opposed to producing *O. mykiss* that grow slowly and mature in freshwater) appears to depend more on annual weather than on flow, at least for the 2 years studied. This result accords with historical information for the late-19th and early 20th centuries, which suggests that annual runs of adult steelhead in the Santa Ynez River numbered in the thousands during some years and in the single digits during other years (Alagona et al. 2012).

Recent annual runs of steelhead in the Santa Ynez River have consistently stayed below approximately 10 fish since intensive monitoring began in the 1990s (Robinson et al. 2009). Our results suggest that water temperatures are not so high that they eliminate the potential for considerable smolt production; this indicates the existence of some other factor that keeps current steelhead production depressed relative to the production observed a century ago. Recent snorkel surveys conducted in the summer usually have found juvenile *O. mykiss* to be few and concentrated in stratified pools (Robinson et al. 2009), suggesting that very few fish currently pursue a first-summer or second-summer strategy in the lower main stem. The capacity for the second-summer pathway could also be limited by a lack of suitable upland creek habitat that can support successful spawning by anadromous *O. mykiss* and successful rearing of their progeny up to the second summer. Currently, most such habitat occurs upstream of the dam, where it is inaccessible to anadromous steelhead although commonly used by Rainbow Trout.

Exotic fish species almost certainly impact steelhead rearing in the Santa Ynez River. In particular, Largemouth Bass are quite abundant in the lower river (Robinson et al. 2009), occupy a thermal niche that broadly overlaps with the thermal niche of steelhead (Currie et al. 1998, 2004), and may both compete with and prey on juvenile steelhead (Hodgson et al. 1991; Christensen and Moore 2008, 2010; Braun and Walser 2011). Prior to the introduction of exotic fishes, southern California steelhead would have been the only medium-to-large bodied fish (>150 mm TL) feeding on invertebrates and other fishes in the Santa Ynez River and in nearby streams, where steelhead remain the only such fish and are observed to behave normally in water temperatures up to around 24°C (Spina 2007; Sloat and Osterback 2013). One explanation for the rarity of steelhead in the Santa Ynez River may be the competitive or predatory dominance of introduced fish (e.g., Largemouth Bass) that are adapted to the high end of the steelhead's thermal niche.

Shallow-River Heat Dynamics

Changing climate is generally expected to decrease summer flows relative to winter flows in western U.S. rivers that are occupied by Pacific salmonids; mechanisms include less water storage in deep soil, increased water demand by vegetation, greater surface evaporation, and especially the loss of snowpack (Mantua et al. 2010; Null et al. 2010). Although decreased summer flow affects heat fluxes by a variety of mechanisms, for simplicity these are often omitted from assessments (Mantua et al. 2010; Wenger et al. 2011; Benjamin et al. 2013). Instead, water temperature is assumed to track air temperature; this assumption relies on equilibrium assumptions that are only valid at relatively large flows and at a resolution of weekly (or coarser) average temperature (Bogan et al. 2003). Finer-grained temperature patterns, such as daily maximum temperature or degree-hours above some temperature threshold, are often biologically important but are poorly predicted by equilibrium assumptions. For example, Caissie et al. (2001) used statistical techniques to predict maximum daily creek temperature from air temperature and found that the empirical coefficient linking stream temperature and air temperature varied seasonally and was not independent of flow within seasons.

In general, subdaily temperature patterns should be sensitive to flow because for a given channel geometry and microclimate, flow establishes the scaling between heat fluxes and the thermal mass, or responsiveness, of the stream. Heat fluxes tend to scale to areas (surface area, streambed area, and cross-sectional area), whereas thermal mass, which describes the temperature response to a given flux, scales to water volume. In contrast to deep rivers, such as those fed by snowmelt, a wide, shallow river like the Santa Ynez River will have a cross-sectional area and volume that are quite small relative to horizontal surface areas; thus, longitudinal flux and thermal mass will be small relative to vertical energy fluxes. Longitudinal heat flux is reduced even further by slow water velocities in shallow rivers due to a greater effect of bed roughness. This situation would tend to decouple a shallow river from upstream conditions and raise the river's responsiveness to vertical heat exchange with the immediate riverbed and atmosphere. Since thermal mass acts as a sort of "smoother" on the temperature response, a RAFT hindcast for a shallow river such as the Santa Ynez River should involve greater error than a hindcast for a deeper river with a relatively high thermal mass; indeed, this is what we observed (RMSE = 1.5°C for the Santa Ynez River, whereas RMSE = 0.5°C for the Sacramento River; Pike et al. 2013).

Our results suggest that when the thermal mass of the water itself becomes small relative to vertical heat flux, the thermal mass of the riverbed becomes an important smoother of subdaily fluctuations. In the RAFT model, heat exchange between water and bed passively follows thermal gradients and thus reduces the temperature response to the diurnal fluctuations in atmospheric heat fluxes. When we conducted RAFT simulations with the streambed flux turned off (results not reported here), we found that this mechanism was essential to accurately hindcasting the temperatures of the lower Santa Ynez River. In our results, each doubling (or halving) of flow changed the maximum daily temperature by less than 1°C in most of the river (Figure 4), suggesting that a large amount of water must be released to add enough thermal mass to significantly augment what the riverbed already provides. In general, heat exchanges between rivers and their beds are often highly heterogeneous due to various mechanisms (Constantz 1998; Arscott et al. 2001; Arrigoni et al. 2008; Burkholder et al. 2008; Westhoff et al. 2010; Boughton et al. 2012). Anticipation of such heterogeneity may be important in identifying rivers with greater thermal resilience to the loss of summer flow, which is expected to result from climate change.

In our case study, changes in flow altered summer thermal habitat in the Santa Ynez River by two mechanisms: (1) the release of water that was out of thermal equilibrium with the local climate directly downstream of the dam; and (2) modulation of the mean depth—and thus thermal mass—of the entire river. Mechanism 1 produced a zone near the dam that functioned as a heat sink, with thermal properties that attenuated rapidly downstream, whereas mechanism 2 produced a heat buffer throughout the river. Steelhead indices that were sensitive to fine-grained fluctuations in temperature (e.g., stress intensity) responded to flow scenarios throughout the entire river (Figure 5). In contrast, the indices that integrated temperature effects over multiple days (e.g., potential growth) only responded strongly to flow scenarios within 20 km of Bradbury Dam (Figures 6, 7) or to extremely high-flow scenarios (>2.8 m^3/s [>100 ft^3/s]) that would probably not be characteristic of the river if the dam was absent. By decreasing upstream temperature, increasing mean depth, and raising water velocities, large enough summer releases from the dam might expand steelhead life history diversity in the Santa Ynez River, especially by enabling more steelhead to pursue a first-summer pathway, although it remains unclear whether this first-summer expression would be characteristic of the river in the absence of dams.

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