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Variation in thermal niche of a declining river-breeding frog: From counter-gradient responses to population distribution patterns

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Abstract

1. When dams or climate change alter the thermal regimes of rivers, conditions can shift outside optimal ranges for aquatic poikilothermic vertebrates. Plasticity in thermal performance and preference, however, may allow temperature-vulnerable fauna to persist under challenging conditions.
2. To determine the effects of thermal regime on *Rana boylii* (Ranidae), a threatened frog species endemic to rivers of California and Oregon, we quantified tadpole thermal preferences and performance in relation to thermal conditions. We monitored temperature and censused populations across a coastal to inland cline in six catchments where dams have altered thermal environments in close proximity to river reaches with natural conditions.
3. We found geographic variation in population distribution and abundance based on river size combined with water temperature. The large inland rivers that supported breeding frogs, although cooler in spring due to snowmelt, became warmer during the summer than occupied coastal sites. Inland populations were constrained to reaches where the average temperature over the warmest 30 days ranged from 17.6 to 24.2°C, higher than coastal rainfall-driven systems where averages ranged from 15.7 to 22.0°C. Frogs in rivers with hypolimnetic-release dams bred in colder waters than they did in free-flowing rivers.
4. Common-garden and field translocation experiments revealed local adaptations in larval growth and phenotypically plastic thermoregulatory behaviour. Tadpoles from all rivers had a positive linear growth response to temperature, but individuals from inland rivers displayed intrinsically higher growth rates. Consistent with a counter-gradient model of selection in which the response to temperature change is in the opposite direction of the change, individuals from cooler rivers selected warmer temperatures. When reared under common conditions, however, tadpoles showed similar temperature preferences regardless of source river.
5. Our results suggest a role for local growth rate adaptation in structuring the distribution of *Rana boylii*. Plastic thermoregulatory behaviour by tadpoles may explain how small populations are able to persist where dams release cold water. Management of edgewater habitats to increase the availability of warm microsites may ameliorate this impact.

KEYWORDS
climate sensitivity, common-garden experiment, declining amphibians, hypolimnetic releases, *Rana boylii*

1 | INTRODUCTION

Phenotypic plasticity in ecological, physiological and behavioural traits may allow species to persist in local environments in spite of changing conditions, and thus maintain widespread geographical distribution (Canale & Henry, 2010; Urban, Richardson & Freidenfelds, 2014). Freshwater species in particular display a high degree of phenotypic plasticity with regard to thermal adaptation (Alahuhta, Ecke, Johnson, Sass, & Heino, 2017; Magnuson & Destasio, 1997; Wittmann, Barnes, Jerde, Jones, & Lodge, 2017). Nonetheless, concern is mounting that riverine biodiversity is imperiled by extreme thermal change, either warming due to human-induced increases in air temperature and water extraction (Kaushal et al., 2010; Pyne & Poff, 2017; van Vliet et al., 2013), or cooling when dams release water from deep below the surface of their reservoirs, i.e. the hypolimnion (Catenazzi & Kupferberg, 2013; Lugg & Copeland, 2014; Olden & Naiman, 2010). To predict how riverine species' distributions may shift in response to such temperature changes, the boundaries of their thermal niches may provide a structure for predicting extinction and colonisation locally (Angilletta & Sears, 2011; Moyle, Kiernan, Crain, & Quinones, 2013). This framework might be of limited use, however, when a species differs in habitat use from one river to another (Bondi, Yarnell, & Lind, 2013; Freeman, Bowen, & Crance, 1997; Wenger & Olden, 2012) or its thermal tolerances and preferences are plastic.

For poikilothermic aquatic animals, temperature is a key resource defining where they can live (Magnuson, Crowder, & Medvick, 1979; Magnuson & Destasio, 1997), yet across a broad array of taxa, even hard measures of physiological tolerance, such as critical thermal maximum and minimum (CTM), are not fixed. Thermal tolerance can vary geographically among populations and in relation to acclimation history and ontogenetic stage (Fangue, Hofmeister, & Schulte, 2006; Hossack et al., 2013; Sloat & Osterback, 2012; Stillman, 2003) with aquatic taxa displaying twice the phenotypic plasticity of terrestrial taxa (Gunderson & Stillman, 2015). Local adaptations to thermal conditions can span from cogradient to counter-gradient responses. Cogradient selection is manifest in shifts of traits that mirror changes in the environment, such as fish living in warmer water having higher CTMs than conspecifics living in cooler rivers (Myrick & Cech, 2000). On the other hand, counter-gradient response, as defined by Levins (1968), appears when the response to the environment is in the opposite direction of the change in prevailing conditions.

Rivers provide an excellent setting to study the connections between thermal adaptations and species distribution because water temperature is generated by micro-geographic factors (e.g. local landforms and vegetation) as much as it is by macro-geographic climatic factors like air temperature and precipitation (Johnson, 2004; Webb, Hannah, Moore, Brown, & Nobilis, 2008). River environments are primarily controlled by the hydrologic regime (i.e. the frequency, timing, magnitude, and duration of streamflow), and thermal conditions are in turn driven by heat exchange between water and the surrounding environment (Fullerton et al., 2015; Webb et al., 2008). Water generally warms as it flows downstream and receives heat from the sun, but factors such as tributary plumes, influx of groundwater, and canopy shading can create locally cooler habitats (Burkholder, Grant, Haggerty, Khangaonkar, & Wampler, 2008; Wawrzyniak et al., 2016; Webb et al., 2008). Thus the early life stages of river organisms, which require specific thermal conditions for development and survival yet have limited dispersal ability, can be exposed to a wide range of temperatures depending on location (Hossack et al., 2013). Characterising this thermal heterogeneity is necessary to understand population-level adaptation and the response of riverine biota to changing thermal regimes.

Here we focus on a target species in river conservation, the foothill yellow-legged frog (*Rana boylii*). Our three-part investigation illustrates intra-specific variation in thermal niche, demonstrates the genetic and phenotypic components of geographic variation in larval growth rate, and explores plasticity of thermoregulatory behaviour. First, we document river water temperature across a coastal-to-inland cline where human appropriation of water resources has created heterogeneous thermal environments in close proximity. We test the hypothesis that thermal conditions where frogs breed differ between coastal and inland rivers and between sites with and without dams. Using physical characteristics of sites in addition to thermal conditions, we classify environmental variation into discrete clusters and test the hypothesis that populations are smaller in the low-temperature clusters. Second, by assessing tadpole growth performance in relation to water temperature and geographic origin in rearing experiments, we test the hypothesis that there is local adaptation to the thermal conditions encountered by this species. Third, we examined temperature preference in relation to thermal rearing history to test the hypothesis that thermoregulatory behaviour is a plastic trait. Because this research may have implications for the operation of dams and the relicensing of hydropower projects, we focus on the thermoregulatory behaviour that could confer resilience to temperature-vulnerable species (Sunday et al., 2014). Our investigations are relevant for balancing multi-species management considerations in rivers where threatened warm and cold-adapted taxa simultaneously require conservation (Railsback et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study species

The foothill yellow-legged frog (*Rana boylii*), endemic to the rivers of California and Southern Oregon (U.S.A.), provides an ideal opportunity to explore ecological divergence in thermal habitat use and response to perturbation of the thermal environment. Because these frogs evolved in rivers flowing through a diverse set of bio-climatic regions, from relatively cool Pacific northwest coniferous forests to warm Mediterranean scrub and oak/grassland savannahs of interior foothills of the Sierra Nevada mountains (Stebbins & McGinnis, 2012), we expected a wide range of temperature tolerance as well as adaptation to local conditions. At present, *R. boylii* occupies less than half its historic range (Davidson, Shaffer, & Jennings, 2002; Hayes, Wheeler, Lind, Green, & Macfarlane, 2016). Absence is significantly correlated with the existence of large dams upstream (Kupferberg et al., 2012) and is pronounced in the southern half of the range. Dam-associated threats include loss of habitat when rivers are converted to lakes and mortality when extreme seasonal variation in stream flow causes stranding and scouring of early life stages. Predation by non-native species is a ubiquitous threat when prolonged low flow conditions (due to droughts affecting all rivers and dam operations in regulated rivers) allow them to proliferate (Fuller, Pope, Ashton, & Welsh, 2011; Kupferberg, 1997; Moyle et al., 2013). While these multiple stressors collectively contribute to the decline of *R. boylii* (Hayes et al., 2016), our goal here is to explore the influence of temperature conditions on the distribution and abundance of remaining populations.

2.2 | Niches occupied by frogs

We assessed water temperature from spring to autumn of 2009 and 2010 in 12 northern California river systems, pairing drainages affected by dams with drainages lacking dams (Figure 1; see Appendices S1 and S2 in Supporting Information). Each pair was in the same catchment, having similar geomorphology and habitats. We positioned data loggers (Thermocron iButtons DS1921G®, ±0.5°C accuracy, recording every 2 hr), in typical egg and tadpole habitats (Figure S2). We obtained additional water temperature data collected by dam operators in our six catchmentss (Placer County Water Agency, Pacific Gas & Electric, and San Francisco Public Utilities Commission) for 63 monitoring stations, of which 51 were used by frogs for reproduction and comprise the sample size of our analyses.

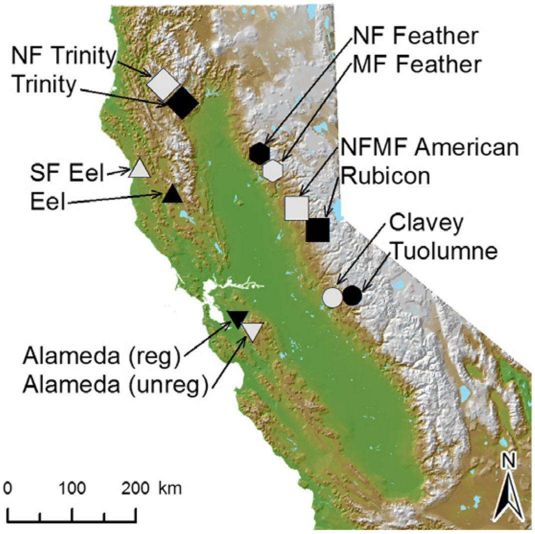

FIGURE 1 Locations of the 12 study river systems in California (MF = Middle Fork, NF = North Fork, SF = South Fork, black filled symbols = flow regulated by an upstream dam, white = unregulated and free flowing)

Using the recorded temperatures (example thermographs in Figure 2), we calculated a running mean of consecutive water temperature measurements from the previous 30 days for each day between May and October, averaging 2009, a cool year, and 2010, a warm year. We determined the temperature over the warmest 30 days of the summer, a period that coincides with rapid growth and development of tadpoles. Previous experiments have shown that although it is a relatively coarse time step, the maximum 30-day average temperature (M30DAT hereafter) is strongly and positively correlated with tadpole survival to metamorphosis for *R. boylii* (Catenazzi & Kupferberg, 2013).

We conducted surveys of frog reproduction by searching for clutches of eggs which females attach to rocks in shallow water. *Rana boylii* has a lek mating system in which frogs congregate and oviposit at areas of coarse sediment deposition in a river, such as lateral cobble bars (Kupferberg, 1996). By searching several riffle-pool sequences, approximately 500 m upstream and downstream of the water temperature monitoring stations, we covered multiple depositional environments where leks might occur. We repeated visits (≥2×) throughout the breeding season to ensure high detectability of clutches and followed an established protocol (Kupferberg et al., 2012) searching both banks and marking clutches to prevent double counting. We standardised clutch abundance by the linear distance searched. Survey periods varied among rivers because frogs breed earlier in the spring (March–May) in coastal rain-driven systems, and later (May–June) in the inland rivers at the foothills of the Sierra Nevada mountains (henceforth, inland rivers), which receive rain and snowmelt (Figure 2).

We hypothesised that thermal niches would diverge among the geographically distinct catchments. Because occupied sites ranged in elevation from 138 to 520 m on the coast and 238 to 1,100 m inland, we first conducted analysis of covariance relating M30DAT to elevation in the two regions. We then used the residuals as a response variable in a two-way ANOVA with river regulation (with or without dams) and catchment (six levels) as explanatory variables. Because we found no significant effect of catchment and no interaction with regulation (Table S3), we used a *t* test to assess the effect of dams on the temperatures of occupied sites.

We characterised physical habitat of occupied sites by performing Principal Component Analysis (PCA) of the following variables at each monitoring station: mean of M30DAT for 2009 and 2010, mean annual discharge over the full period of record for the nearest stream gauge (United States Geological Survey, http://relicensing.pcwa.net/html/science/hydrology.php), elevation, and catchment area upstream of the station. Variables were scaled prior to PCA on a correlation matrix. Following PCA, we extracted the first two

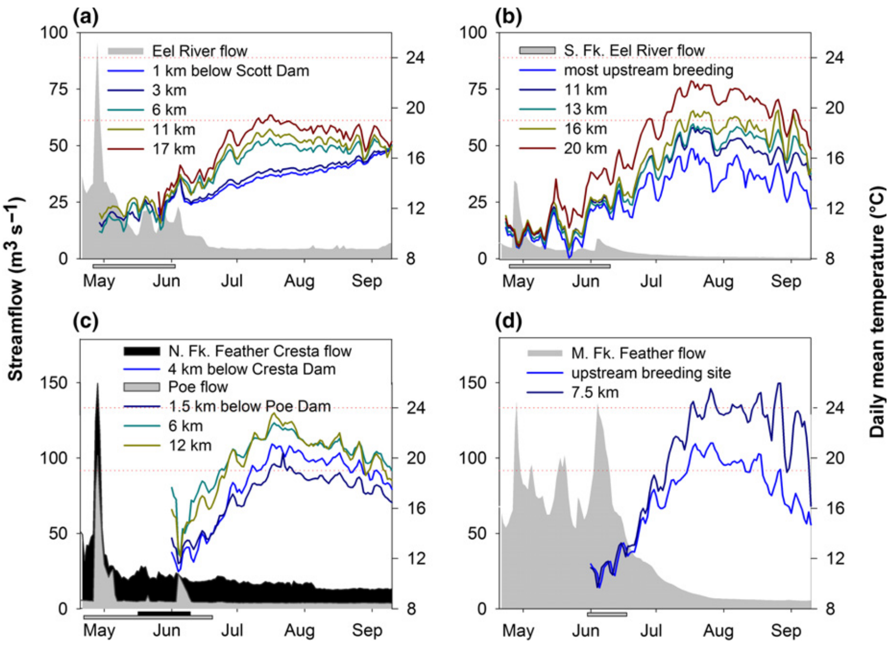

FIGURE 2 Hydrographs in 2010 (gray and black shaded areas), temperature range selected by tadpoles of *Rana boylii* (dashed lines), and thermographs (solid lines) at different distances from most upstream breeding sites or dams in two of the six focal catchments: the regulated coastal Eel River (a), the unregulated South Fork Eel River (b), the regulated inland North Fork Feather River (c), and the unregulated Middle Fork Feather River (d). Bars below the x-axes of each panel indicate the breeding period for frogs in each river when clutch censuses occurred

principal components, which accounted for 73% of the total variance. Discharge and drainage area loaded strongly on PC1, whereas M30DAT and elevation loaded strongly on PC2 (Table S2). We used k-means clustering of PC1 and PC2 to delineate the riverine environments occupied by breeding frogs. We examined scatter plots of PC1 versus PC2 using $k = 4$ and delineated distinct clusters of sites. We then compared the density of clutches (no./river km) among clusters to test the hypothesis that sites with colder water in summer would support relatively smaller populations.

2.3 | Growth performance

We measured tadpoles' growth in response to temperature conditions in a complementary set of manipulations conducted in three different experimental venues. First, within one catchment we translocated embryos from one source and reared them to metamorphosis in multiple streams with disparate thermal regimes. Second, we reared embryos from different catchments under controlled thermal conditions in the laboratory, and third, we used outdoor stream mesocosms to create a common-garden environment. All three experiments used high-quality algal food resources (*Cladophora glomerata* with epiphytic diatoms) that were available ad libitum, so performance in these trials quantifies the fundamental relationship between growth and temperature in the absence of dietary effects.

In 2008, and repeated in 2009, we raised full-sibling tadpoles from shortly after fertilisation until front limb emergence in flow-through stream enclosures placed in six locations in the catchment of the South Fork Eel River (hereafter SF Eel, Appendix S2). Details of animal husbandry methods are in Appendix S3. For each replicate we measured body length and mass of tadpoles weekly and calculated the mean growth rate of all tadpoles in the enclosure (mg/day and mm/day). We used least squares linear regression to relate growth and size at metamorphosis to M30DAT.

For the laboratory common-garden experiment, we collected embryos from three of the coastal study rivers (two with dams) and four of the inland rivers (two with dams) from April to June 2010 (Table S1). We transported embryos in chilled aerated river water to the laboratory and within 8 hr of collection placed them into temperature-controlled diurnal growth chambers (Shel Lab, Cornelius, OR, U.S.A.; cycle set to 14.5 hr light and warm, 9.5 hr dark and cool). After hatching, we randomly chose five tadpoles from each clutch and placed them in 3.8-L aquaria with an aerated mixture of river water and de-chlorinated tap water (changed 2×/week). To mimic warm summer conditions at locations with robust populations of frogs, one chamber was set at 18°C during the dark cycle, and 22°C during the light cycle. Daily mean temperature, calculated from 3 i-Button data loggers placed in randomly selected aquaria, was 19.5°C. To mimic conditions of the coolest occupied sites, the other incubator was set at 13°C dark cycle, 19°C light cycle, with a daily mean = 16.6°C. Each chamber held 35 aquaria (4–6 replicate clutches × 7 rivers). Due to the cost of growth chambers only two were available; the temperature treatments could not be replicated across multiple incubators. We measured body and total length of tadpoles with calipers to the nearest 0.1 mm at weekly intervals after hatching. Due to the differences in breeding phenology, the dates when we placed embryos in the chambers varied. We estimated the date of oviposition based on developmental stage when we collected the embryos and calculated growth up to 4 weeks after that date. The response variable was body growth, mm/day. We compared region (coastal versus inland as a fixed effect), source river (as a random effect), and temperature (two fixed levels), using a three-factor partially hierarchical design ANOVA in which source river was nested within regions.

Outdoor mesocosms at the University of California's Richmond Field Station (37.913536°N, −122.333303°W) had daily mean water temperature conditions similar to sites occupied in the field. We collected embryos in late May and early June 2010 from four rivers: a coastal unregulated (South Fork Eel), a coastal regulated (Eel below Scott Dam), an inland unregulated (Middle Fork Feather) and an inland regulated (North Fork Feather). At each river, we obtained embryos from three different egg masses; furthermore, at the North Fork Feather we collected from two reaches (below the Cresta and Poe dams). After transferring embryos to Richmond and rearing them to tadpole stage, we placed 10 tadpoles in separate mesocosms consisting of re-circulating troughs (Figure S3; total of 15 troughs, 3 for each river except for the North Fork Feather which had 6 troughs). We mounted PVC pipe cut in half (2.2 m × 15.3 cm diameter) on saw horses at a slight incline so water drained into a 946 L reservoir. Pumps and hoses continuously re-circulated water to the top of each trough lined with periphyton covered river rocks and loose algae. Tadpoles were reared indoors at 18°C until stage 25 (Gosner, 1960), and placed in the troughs on 21 July 2010. We measured and staged tadpoles weekly until front limb emergence (Gosner stage 42). We calculated a mean growth rate for each trough (mm of body length increase/day) and compared source populations with a nested ANOVA in which source river was nested within region. We monitored temperatures in the troughs with iButtons and determined that M30DAT = 17.8°C.

2.4 | Thermal preference

We assessed phenotypic plasticity in thermal preference by comparing behaviour of genetically similar tadpoles with different rearing histories and genetically dissimilar tadpoles with a common thermal rearing history. We tested tadpoles individually in controlled thermal gradients heated at one end and chilled at the other (3 m × 8 cm × 5 cm; 1 tadpole/12 L of aerated water; Appendix S4) and calculated an index of preference, the average of temperatures selected (T_{sel}). We conducted three trials: (1) a single population source (full-sibling set) of tadpoles reared under different thermal regimes in four streams of the coastal SF Eel catchment (described above); (2) wild collected tadpoles from populations at thermal monitoring stations that represent three distinct clades within the species (Lind, Spinks, Fellers, & Shaffer, 2010) and three of the four niche clusters (SF Eel, Alameda Ck and NF Feather); and (3) multiple population sources of tadpoles reared in a common thermal environment, the outdoor stream mesocosm experiment described above.

For all three trials, we kept tadpoles at room temperature for 2 hr, and then allowed them to adjust to the gradient for 1 hr. We conducted trials between 13:00 and 17:00 hours under uniform lighting. Small rocks provided cover along the length of the gradient in which we maintained the ends at 11.9 ± 0.1 and 34.7 ± 0.2°C. We checked gradient linearity periodically with a quick-reading thermometer and confirmed linearity from temperatures recorded every 3 min by 6 i-Buttons spaced at 50 cm intervals. We noted tadpole position every minute for 30 min and calculated temperature at those positions using the linear regression between distance along the gradient and temperature (Figure S4). We calculated T_{sel} by taking the arithmetic mean of temperatures corresponding to each tadpole's observed positions.

We compared T_{sel} among groups (i.e. rearing history or source population) with ANOVA (or Kruskal–Wallis ANOVA on ranks when data were not normal). Temperature preference can vary during ontogeny for some anuran species (Hutchinson & Dupré, 1992), but not others (Skelly, 2004). We generally did not observe relationships between T_{sel} and Gosner stage or body size (Trial 2: $n = 112$, $R_{Gosner}^2 = .21$, $p = .13$, $R_{size}^2 = .01$, $p = .26$; Trial 3: $n = 60$, $R_{Gosner}^2 = .013$, $p = .39$; $R_{size}^2 = .02$, $p = .26$), except Trial 1 for which we included stage as a covariate in the ANOVA. All statistical analyses were conducted using R (R Development Core Team, 2015).

3 | RESULTS

3.1 | Thermal niche and habitat occupied by frogs

Rana boylii reproduced at M30DAT from 15.7°C (coast, SF Eel at Branscomb; see KML Map in Appendix S2) to 24.2°C (inland, Clavey River). The range of summer water temperatures at locations supporting breeding populations of frogs was similar in coastal (6.3°C) and inland (6.6°C) rivers, but the range inland was shifted to higher temperatures (Figures 2 and 3a,b). Analysis of Covariance of M30DAT (Table S3) showed that this regional shift in the realised thermal niche is significant ($R^2 = .53$; $F_{1,48} = 51.2$, $p < .001$) in addition to the expected effect of elevation on temperature ($F_{1,48} = 8.59$, $p = .005$). Frogs in regulated rivers bred in colder waters than they did in unregulated rivers, as indicated by a significant dam effect ($t = -4.05$, $df = 47.2$, $p = .002$) using the residuals in the ANCOVA of M30DAT as the response variable.

The k-means cluster analysis (Figure 3c) identified habitat types: Group A, small and cold rivers; Group B, small and very warm; Group C small and moderately warm; Group D large and mostly cold. The frequency distribution of breeding density among the niche clusters (Figure 3d), highlights the relevance of these groups for reproductive success. Only Group C habitats supported high-density populations of breeding frogs.

3.2 | Growth performance

In stream enclosures of tadpoles reared from a single source population, growth rate to front limb emergence increased by 0.02 mm/day (Figure 4a; $R^2 = .94$, $F_{1,29} = 402.7$, $p < .0001$) and by 3 mg/day per degree Celsius increase in M30DAT (Figure 4b; $R^2 = .88$, $F_{1,29} = 219.0$, $p < .0001$). Size at front limb emergence also responded positively to increases in rearing temperature (Figure 4c; $R^2 = .91$, $F_{1,29} = 51.9$, $p = .002$). In the common-garden experiment conducted in growth chambers (Figure 4d, Table S4) embryos from multiple source populations developed and young tadpoles grew faster in the warm treatment than in the cold treatment ($F_{1,5} = 57.0$, $p < .001$). In both temperature treatments, individuals from inland sources grew (from age 0 to 1 month) faster than those from coastal populations ($F_{1,5} = 7.9$, $p = .038$), and there was no interaction

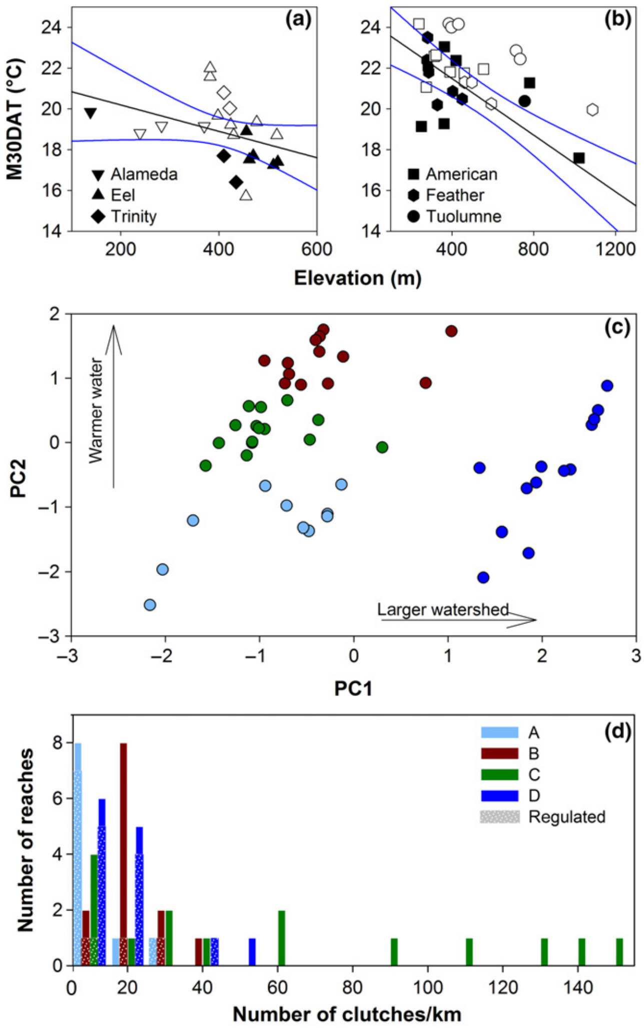

FIGURE 3 Relationship between elevation and water temperature during the warmest 30 days of summer (M30DAT of 2009, 2010) at sites (n = 51) used for breeding by *Rana boylii* in (a) coastal and (b) inland California rivers (white = free-flowing, black = dam-regulated; R^2 = .53; $F_{1,48\ \text{region}}$ = 51.2, p < .001; $F_{1,48\ \text{elevation}}$ = 8.59, p = .005). Cluster analysis (c) using data from Principal Components indicating catchment size, PC1, and temperature, PC2. Frequency distribution (d) of population size for the habitat groups as indexed by clutch density

between the region and temperature factors. We also observed no effect of source river, nested within regions ($F_{5,52}$ = 1.6, p = .313). In the outdoor stream mesocosm common-garden experiment spanning early rear limb bud development to front limb emergence (Figure 4e), tadpoles from inland sources (Habitat Group D) grew at a significantly higher rate (p = .026) than coastal tadpoles from groups A and C (Table S4).

3.3 | Thermal preference

Preferred body temperatures varied inversely to rearing temperature. Tadpoles reared at the lower boundary of temperatures suitable for growth selected warmer temperatures than tadpoles reared at temperatures facilitating rapid growth (Figure 5). This response occurred for full-sibling tadpoles transplanted to rivers with different temperatures (Trial 1), and wild tadpoles from geographically and genetically distinct populations developing in situ under different temperatures (Trial 2). In Trial 1, cool-reared siblings selected temperatures approximately 2.5°C warmer than warm-reared tadpoles. Analysis of covariance of ln(T_{sel}) indicated that the differences due to rearing temperature were significant ($F_{3,160}$ = 3.91, p = .01) and that less developed tadpoles chose warmer temperatures ($F_{1,160}$ = 3.95, p = .05). In Trial 2, wild tadpoles from Habitat Group D (the coldest site in Figure 2c) selected warmer temperatures than tadpoles from streams falling in Groups B and C (H = 17.0, df = 2, p < .001; Dunn's post hoc comparison Q = 4.1, p < .05). In Trial 3, which tested tadpoles from four source rivers (representing Groups A, C and D) and reared under common thermal conditions in mesocosms, differences in T_{sel} were not significant ($F_{3,56}$ = 0.53, p = .67).

4 | DISCUSSION

The thermal environment is crucial to a tadpole's rapid and successful development to metamorphosis (Smith-Gill & Berven, 1979) and for *Rana boylii* appears to structure the spatial distribution of populations within catchments, the evolution of regional differences in growth rate, as well as plastic behavioural responses to environmental variation. Our rearing experiments and monitoring results show that larval growth rate, size at metamorphosis, as well as frog population abundance, are all positively associated with average river temperature during the warmest month of summer (M30DAT) and generalise previous findings specific to individual catchments (Catenazzi & Kupferberg, 2013; Wheeler, Bettaso, Ashton, & Welsh, 2015). Under thermally challenging conditions such as downstream of a dam releasing cold hypolimnetic water (Figure 2a), impaired growth of early life stages likely limits this species' abundance and distribution.

The realised thermal niche for *R. boylii* varies regionally and appears to differ in accordance to flow regulation. Summer high temperatures (M30DAT) where we found viable populations (>5 breeding females per river km) were warmer inland (20.3–24.2°C) compared to coastal catchmentss (18.8–22.0°C). We also found sparse populations in regulated rivers with M30DAT as low as 17.5°C inland and 16.4°C coastal. We interpret this occupancy of cool sites in rivers where conditions have deteriorated under human management as a facet of an unfolding process of range contraction as populations decline (Kupferberg et al., 2012). Differences in abundance among the four Habitat Groups (Figure 3c) indicate that most of the river reaches falling in the colder clusters, Groups A and D, support small populations of frogs, which would be susceptible to local extinction. As ranges contract within each river, the likelihood of extirpation may increase for the metapopulations in which some or many of the sub-populations are living near the limits of the species' thermal niche and experiencing reduced larval fitness.

The negative effects of cold temperature on tadpoles may have greater consequences where the duration of suitable conditions for

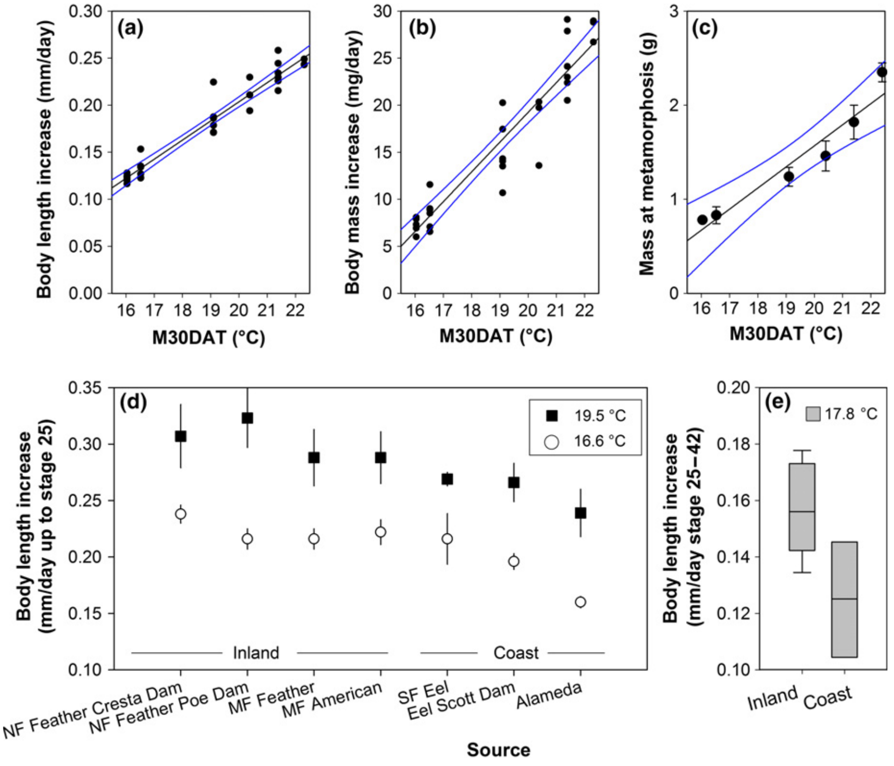

FIGURE 4 Rate of increase from hatching to metamorphosis in body length (a) and mass (b), and size at front limb emergence (c) for replicate groups of tadpoles transplanted to streams varying in the maximum 30 day running average of water temperatures (M30DAT). Rates of increase in body length of tadpoles in relation to rearing temperature and source population in common-garden laboratory incubators during the first 4 weeks of development (d) and outdoor stream mesocosms from Gosner stage 25–42, front limb emergence (e)

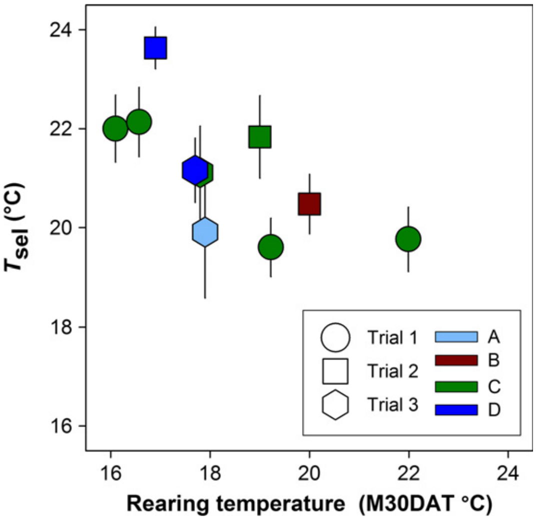

FIGURE 5 Mean ± *SE* selected temperatures (T_{sel}) by tadpoles in counter-gradient response to thermal rearing history (maximum 30 day running average of water temperature, M30DAT). Thermal gradient Trial 1 tested individuals ($n = 210$) from common sources of eggs translocated and reared in flow-through stream enclosures. Trial 2 tested wild caught tadpoles ($n = 112$). Trial 3 tested tadpoles ($n = 60$) reared from embryos collected at separate sources and living in a cool common-garden environment (see text for details). Fill indicates niche group from k-means cluster analysis (see Figure 3).

rearing is relatively short, such as the large rivers receiving snowmelt (11 out of 13 sites in Group D) or hypolimnetic releases of cold water (8 out of 10 sites in Group A). Recruitment limitation offers a plausible explanation for the small population sizes of Groups A and D for several reasons. As occurs in many rivers with altered thermal regimes, the recruitment of organisms with complex life-cycles can be significantly impaired (Haxton & Findlay, 2008). For benthic macroinvertebrates, low recruitment is associated with the effects of cold water on slowing rates of egg development and larval growth, creating asynchrony between the life cycle and seasonal patterns of resource availability, shifting the timing of emergence, and blocking life-cycle completion (Lehmkuhl, 1972; Olden & Naiman, 2010). For amphibians generally, small size and slow development increase risk and duration of exposure to predation in the aquatic life stages (Anderson, Kiesecker, Chivers, & Blaustein, 2001), and can have carry-over effects on growth performance and survival of juveniles (Altwegg & Reyer, 2003; Chelgren, Rosenberg, Heppell, & Gitelman, 2006). For *R. boylii* specifically, cool temperatures have negative effects on tadpole survival (Catenazzi & Kupferberg, 2013) and shift periphyton flora toward inedible taxa (Furey, Kupferberg, & Lind, 2014). These factors along with the increased fitness associated with large body size may explain why frog populations attained large numbers only among Habitat Group C that was characterised by warmer summer temperatures.

Our growth performance experiments are ecologically relevant because riverine tadpoles have a narrow time window for development. The duration of stable flow and warm conditions (henceforth, the stable hydroperiod) defines an important time constraint on recruitment of riverine organisms during the sequence of winter floods and summer droughts typical of the Mediterranean climate (Gasith & Resh, 1999). Hydrographs in smaller coastal rivers stabilise during spring when the rainy season ends, but thermographs increase slowly during early and mid-summer (Figure 2). Large inland rivers with high mean annual discharge fed by snowmelt may flood for a longer period, but they warm faster than coastal rivers during mid-summer. Over-wintering as tadpoles, which could be an effective life-history strategy to bypass these time constraints, has never been observed in *R. boylii* and the tadpoles lack morphological adaptations to survive high flow velocity conditions (Kupferberg, Lind, Thill, & Yarnell, 2011). Instead, we observed in the rearing experiments (Figure 4c,d) that growth rate increased for all tadpoles as temperature increased, and that those from inland rivers grew more rapidly.

Our common-garden results, that tadpoles from the more time-constrained populations had higher intrinsic growth rates, and site use results, that adults breed at significantly warmer sites inland compared to the coast, are consistent with a counter-gradient model of selection and may represent genetic adaptations to the local thermal conditions. The counter-gradient hypothesis is that a short growing season exerts strong selective pressure for rapid growth (Arendt, 1997) and compensatory responses after periods of slow growth (Metcalfe, Bull, & Mangel, 2001). Adaptive counter-gradient responses of growth rate to temperature have been documented along latitudinal and elevational gradients for a variety of aquatic species including snails, fish, amphibians, and turtles (Arendt, 1997; Berven, Gill, & Smith-Gill, 1979; Brown, Ehtisham, & Conover, 1998; Conover & Present, 1990; Snover, Adams, Ashton, Bettaso, & Welsh, 2015; Trussell, 2000). When placed in common settings, experiments have shown that montane and high-latitude genotypes have evolved higher growth rates of early life stages compared to low-elevation and low-latitude populations and can thus compensate for a short growing season (Berven et al., 1979; Nicieza, Reiriz, & Braña, 1994; Orizaola, Quintela, & Laurila, 2010). For example, growth rates of European ranid frogs (*Rana temporaria*, *Pelophylax lessonae*) from time-constrained northern or montane populations respond more strongly to temperature than southern or lowland populations (Merilä, Laurila, Laugen, Räsänen, & Pahkala, 2000; Orizaola et al., 2010; Ståhlberg, Olsson, & Uller, 2001). Less is known about phenotypic counter-gradient responses to microgeographic variation in thermal conditions, but examples include faster growth rates and greater food assimilation efficiency in tadpoles from cool waterbodies shaded by forest canopy compared to individuals from nearby warm sunny ones (Skelly, 2004; Skelly & Golon, 2003). Shifts in thermoregulatory behaviour (Freidenburg & Skelly, 2004; Snover et al., 2015), and shifts in the timing of hibernation (Bondi & Marks, 2013) provide other examples of phenotypic counter-gradient responses in neighbouring populations experiencing different thermal regimes. In our Mediterranean climate lotic study system, the time constraints are less severe in the coastal catchments. The longer stable hydroperiod may relax selection for rapid growth if tadpoles have time to reach metamorphosis before the onset of autumn precipitation.

Our observations of phenotypic plasticity in thermoregulatory behaviour illustrate that rearing history is also an important source of intraspecific trait variation in compensatory response. Tadpoles of *R. boylii* generally preferred temperatures associated with rapid growth and development in our rearing experiments, but if they lived in a cool environment they exhibited a counter-gradient response by selecting even warmer temperatures. The range of temperatures selected by *R. boylii* tadpoles is not unusual among larval anurans (Hutchinson & Dupré, 1992) and is consistent with other species at similar or more northerly latitudes (Herreid & Kinney, 1967; Wollmuth, Crawshaw, Forbes, & Grahn, 1987; Workman & Fisher, 1941). However, it is curious that tadpoles that had been growing quickly would choose temperatures that might slow their growth, suggesting that there may be costs and selective pressure against rapid larval development (Gomez-Mestre et al., 2010). When thermal rearing environment has been investigated in other anurans and fish, its effects on behaviour are species-specific ranging from negligible (Hutchinson & Hill, 1978; Wollmuth et al., 1987) to counter-gradient responses (Fangue, Podrabsky, Crawshaw, & Schulte, 2009; Freidenburg & Skelly, 2004). Our results show that for *R. boylii* the response does not appear to be genetic, since there were no differences in preference when we reared tadpoles from disparate regions in a common-garden setting (Trial 3).

4.1 | Implications for river management

When evaluating alternative flow regimes with the goal of balancing the thermal needs of multiple species, river managers can forecast the consequences to summer temperature downstream from a dam. Using the ranges we have documented for tadpole thermal niches of *R. boylii* in different regions, predictions can be made regarding the number of river kilometres of habitat to be lost or gained in a given flow scenario. Our finding that the thermal niche varies regionally indicates that thermal perturbations may cause greater habitat loss among inland rivers than coastal ones. Because inland regulated rivers have successive series of dams and reservoirs, distances sufficiently far from a dam where water is warm enough for frog reproduction are in close proximity to the next reservoir where non-native bullfrogs and predatory fish are well established (Fuller et al., 2011; Marchetti, Moyle, & Levine, 2004). The presence of predatory fish and bullfrogs (which are predators as adults and superior competitors as tadpoles) is correlated with the absence or small size of *R. boylii* populations (Fuller et al., 2011). Given these constraints on matching thermal niche requirements to general habitat suitability along regulated rivers, thermal refugia created by lateral warming at channel margins could provide an important resource to allow successful recruitment of native biota. Tadpoles could potentially compensate for cool conditions if warm water patches occurred at breeding sites, because their thermoregulatory behaviour is plastic and responds in a counter-gradient manner. Unfortunately, when upstream dam operations suppress flood disturbance and sediment supply, regulated river channels become narrower and woody riparian vegetation encroaches into the active channel (Poff & Zimmerman, 2010). Canopy shading of the channel margins thus limits opportunities for the compensatory thermoregulatory behaviour we observed. Creation of thermal habitat heterogeneity by restoring gently sloping gravel bars and enhancing edgewater habitats could relax seasonal time constraints for biota with flexible growth strategies.

Flow-related changes in river temperature are pushing many species to the limits of their thermal tolerances (Moyle et al., 2013; Olden & Naiman, 2010; Power, Bouma-Gregson, Higgins, & Carlson, 2015) and there is a need to fill knowledge gaps for organisms, such as amphibians, that are heavily under-represented in studies of ecological responses to flow alteration (Poff & Zimmerman, 2010). As concerns grow that many rivers are experiencing heat stress, hypolimnetic releases have been proposed as a potential method to mitigate climate change effects on the loss of habitat for cold-adapted taxa, such as salmonid fishes (Null, Ligare, & Viers, 2013). When warm-adapted amphibians, reptiles, and fish co-occur in the same river network as cold-adapted biota, actions to benefit one group can constrain the others (Ashton, Bettaso, & Welsh, 2015; Cocherell, Fangue, Klimley, & Cech, 2013; Railsback et al., 2015). In particular, lack of knowledge about spatial variation in the thermal niches of conservation target species (Angilletta & Sears, 2011) hinders the ability to predict whether a given thermal perturbation or management strategy would have similar impacts across the regions comprising a species' range. Our results specific to *R. boylii* indicate that different thermal management strategies would be required for inland rivers compared to the coast. Our empirical results show how intraspecific variation in plastic traits contributes to niche divergence and the fate of populations. Incorporating this variation in species distribution models predicting biotic responses to environmental change is important to improve their accuracy (Moran, Hartig, & Bell, 2016; Pearman, Guisan, Broennimann, & Randin, 2008).

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DATA ACCESSIBILITY

Environmental monitoring data, tadpole growth performance and preference are available from in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2g8p1.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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