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The importance of thermal conditions to recruitment success in stream-breeding frog populations distributed across a productivity gradient

Alessandro Catenazzi [a,b,*], Sarah J. Kupferberg [b,c]

[a] Department of Zoology, Southern Illinois University, Carbondale, IL 62901, USA
[b] Department of Integrative Biology, University of California, Berkeley, CA 94720, USA
[c] Questa Engineering, P.O. Box 70356, 1220 Brickyard Cove Road, Suite 206, Pt. Richmond, CA 94807, USA

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ABSTRACT

Predicting the vulnerability of species to environmental change requires integrating observations of individual ecophysiological and behavioral responses with community level constraints. To assess the response of stream-breeding frogs (*Rana boylii*) to thermal stressors, such as cold water released from the depths of upstream reservoirs or warm water that results from climate change, we combined field manipulations with population censuses and environmental correlations. These frogs migrate between shaded tributaries and open canopy mainstem channels to oviposit where algal food is abundant for tadpoles. Within this context of spatial variation in aquatic primary productivity, we evaluated whether tadpole thermoregulatory behavior is a useful indicator of survival to metamorphosis and adult distribution. In a thermal gradient, tadpoles selected temperatures between 16.5–22.2 °C (mean, 19.60 ± 0.6 °C). We reared tadpoles in streams colder, warmer, or close to thermal preference. Temperature effects were mediated through algal quantity and quality. Mortality increased with increasing deviation from preferred temperatures, but the effects were ameliorated when tadpole diet was supplemented with algae (*Cladophora glomerata* with epiphytic nitrogen-rich diatoms, *Epithemia* spp.) harvested from sun-lit channels. Distribution of frogs in free-flowing and dammed reaches within a northern California watershed was in equilibrium with tadpole thermal preference. Populations were dense ($\geqslant$125 breeding females/km) where July water temperatures averaged 17.5–19 °C in 2010, a relatively cool summer. Below 16 °C, frogs were sparse with open canopy and absent under closed canopy. Integration of thermoregulatory behavior with ecological context can thus be useful to forecast recruitment when the thermal regimes of rivers are altered by anthropogenic factors.

1. Introduction

Global climate change has been implicated as one of the major drivers behind the current biodiversity crisis (Lovejoy and Hannah, 2005). The threat to freshwater organisms is considerable because interactions with hydrological modification, habitat fragmentation, and the introduction of exotic species may combine to limit the ability of populations to persist or shift distribution (Benke, 1990; Dynesius and Nilsson, 1994; Finlay and Vredenburg, 2007). Freshwater species currently have higher extinction rates than terrestrial taxa (Ricciardi and Rasmussen, 1999), and amphibians in particular are experiencing losses at alarming rates (Wake and Vredenburg, 2008). For riverine systems, a global analysis of the anticipated consequences of climate change suggests that biota in rivers with dams are particularly vulnerable in regions where water stress, defined as withdrawal-to-availability ratios, is high (Palmer et al., 2008). For example, on the west coast of North America, runoff is highest during wet winters, yet electrical and agricultural demand for hydropower and water peaks during dry summers (Grantham et al., 2010). Climate change predictions for this region forecast decreased precipitation and river warming (Kiparsky and Gleick, 2003; Snyder et al., 2004; Webb et al., 2008). In regulated rivers, however, where water is released from the depths of upstream reservoirs, organisms can experience summer thermal regimes several degrees C cooler than historic pre-dam temperatures (Angilletta et al., 2008). In addition to water temperature, flow regime influences periphyton assemblage (Wootton et al., 1996; Wu et al., 2009). Therefore, flow regulation could either exacerbate or offset the effects of climate change on water temperature (Olden and Naiman, 2010), while simultaneously

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* Corresponding author. Address: Department of Zoology, Southern Illinois University, 1125 Lincoln Dr., Carbondale, IL 62901, USA. Tel.: +1 (618) 453 4109.
E-mail address: acatenazzi@gmail.com (A. Catenazzi).

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altering the resources available to grazing consumers such as tadpoles.

There is much debate about how to predict the effects of thermal change on specific organisms (Walther et al., 2002; Krebs and Berteaux, 2006; Araújo and Peterson, 2012). Niche-based bioclimatic envelope models, built upon correlations between current geographic patterns of presence–absence and an organism's physiological tolerances, can simulate the future distribution of suitable climate space for a species (Peterson, 2001; Hijmans and Graham, 2006), but have limitations (Davis et al., 1998; Loiselle et al., 2003). These models often treat species as units and are not derived from hypotheses about individual behavioral or community-level responses to climate stressors that can be tested with manipulative experiments. Responses such as phenological shifts in the breeding season (Both et al., 2009; Bauer et al., 2010) and interactions with food resources (Pelini et al., 2009) can have substantial influence on vital rates, and unexpected responses have been shown to reverse scenarios based on climate envelope models alone (Davis et al., 1998; Suttle et al., 2007). To design appropriate management and conservation programs, ecologists thus need to know how birth and death rates are influenced by abiotic conditions, such as temperature, within the context of biotic factors such as spatial heterogeneity in primary productivity.

We focused on the nexus of climate change, flow regulation, and amphibian decline by measuring the effects of thermal regime on the foothill yellow-legged frog (*Rana boylii*). The species is endemic to rivers of California and Oregon, USA, and has disappeared from more than half of its range (Davidson et al., 2002). Absence from historically occupied sites is more common downstream of large dams and in the southern part of its range compared to free-flowing systems and northern locations where precipitation is more abundant (Lind et al., 1996; Lind, 2005; Kupferberg et al., 2012). Within a dendritic watershed network, *R. boylii* occur in diverse channel types from low stream order and high gradient cascade and step-pool reaches to lower gradient alluvial reaches, but the best predictor of breeding (i.e., tadpole abundance) is water temperature (Welsh and Hodgson, 2011). Additionally, previous experiments have shown that diatom-rich algal patches are preferred food sources and enhance development and growth of *R. boylii* tadpoles (Kupferberg 1997a,b). These patterns suggest that hydrologic factors, including water temperature, may play a causative role in the decline of this species and that effects of temperature may be mediated by tadpole feeding ecology.

To understand the response of *R. boylii* to thermal regime change, we integrated investigations across several spatio-temporal levels and life stages. We conducted censuses of adult frog breeding density throughout a drainage network, and combined studies of short-term individual thermoregulatory behavior with field manipulations of water temperature and food resources. To test the hypothesis that temperature effects are mediated by food quality, we reared tadpoles across a gradient of cool to warm stream temperatures and low to high primary productivity, with or without food supplementation. We assessed whether thermoregulatory behavior by tadpoles in a thermal gradient could be used to predict the observed effects of temperature on survival to metamorphosis. To determine the relevance of these experiments to conservation of frog populations in rivers with dams, we examined broad-scale spatial patterns of density of breeding by adult frogs in relation to temperature and indicators of primary productivity. Our goal was to define the combination of habitat conditions and thermal regime needed to maintain breeding populations of frogs and to provide information that would be useful to dam operators and regulatory agencies.

2. Methods

2.1. Study sites

We worked in Mendocino Co., California, USA, in the watersheds of the mainstem Eel River downstream of Scott Dam (Mendocino National Forest) and the South Fork of the Eel River (Fig. 1, KML file in Supplementary Data) (University of California Angelo Coast Range Reserve and Admiral Standley State Recreation Area). The South Fork Eel River (SF Eel hereafter) on the Angelo Reserve has one of the most dense breeding populations of *R. boylii* in northern California (Kupferberg et al., 2012). The Eel River flows through steep terrain vegetated by mixed coniferous forest. Adults of *R. boylii* spend much of their time in tributaries (both permanent and ephemeral) but travel to mainstem channels to mate at lek sites and deposit eggs in shallow slow moving water (Kupferberg, 1996; Wheeler and Welsh, 2008). To avoid flood disturbance and optimize feeding by tadpoles, the timing of reproduction occurs in synchrony with the seasonality of runoff and algal blooms (Power et al., 2008) during the predictable cycle of wet winters and dry summers typical across the range of *R. boylii*. Specifically, the period of fastest tadpole growth coincides with the bloom of epiphytic nitrogen-fixing diatoms. The distribution of algal blooms along the stream network is regulated by abiotic and biotic factors that scale with watershed size (Finlay, 2004; Power et al., 2008). For example, small tributaries have dense canopies which limit the light available for primary producers whereas broad channels further down the drainage network are broad and sun-lit (Table 1).

2.2. Tadpole thermal preference

Given that tadpoles of *R. boylii* are active thermoregulators (Brattstrom, 1962), we assayed preferred temperatures for the SF Eel population by observing behavior in a controlled thermal gradient. We tested tadpoles individually ($n = 56$ (Gosner, 1960), developmental stage range 27–42, median stage 39) in 3 m long, 8 cm wide, 5 cm deep (1 tadpole/12 l of water), thermal gradients made from metal gutters heated at one end and chilled at the other. We used aquarium pumps and airstones to oxygenate the water during acclimation and between trials. Tadpoles were reared in flow-through enclosures in the SF Eel (Table 1) and fed algae *ad libitum*. We transported tadpoles to the laboratory (15 min), kept them at room temperature for 2 h and then allowed them to adjust to the thermal gradient for 1 h. In order to account for potential diurnal variation in thermoregulatory behavior (Brattstrom, 1962), we conducted all trials between 1300 h and 1700 h under uniform lighting conditions. We placed small rocks as cover along the length of the gutters and maintained a linear thermal gradient from the cold (11.9 ± 0.1 °C, $n = 108$) to the warm (34.7 ± 0.2 °C, $n = 108$) ends throughout the adjustment and experimental periods. The temperature at the cold end of the gradient was 2–3 °C warmer than temperatures experienced by tadpoles in the wild as embryos and early hatchlings. Therefore, we are confident that our measurements produced reliable estimates of preferred temperatures (Dillon et al., 2012). We checked gradient linearity periodically during the experiment with a quick-reading IR thermometer. We noted tadpole position every minute for 30 min ($n = 31$/trial) and calculated the temperature at those positions using the linear regression between distance (0 = cold end) and temperature. Although temperature preference might vary during ontogeny for some taxa (Hutchison and Dupré, 1992), we did not observe a relationship between Gosner stage and temperatures selected, consistent with results obtained by Skelly (2004).

Thermal gradient observations yielded two response variables, the mean selected temperature and the set-point range (T_{set}). The

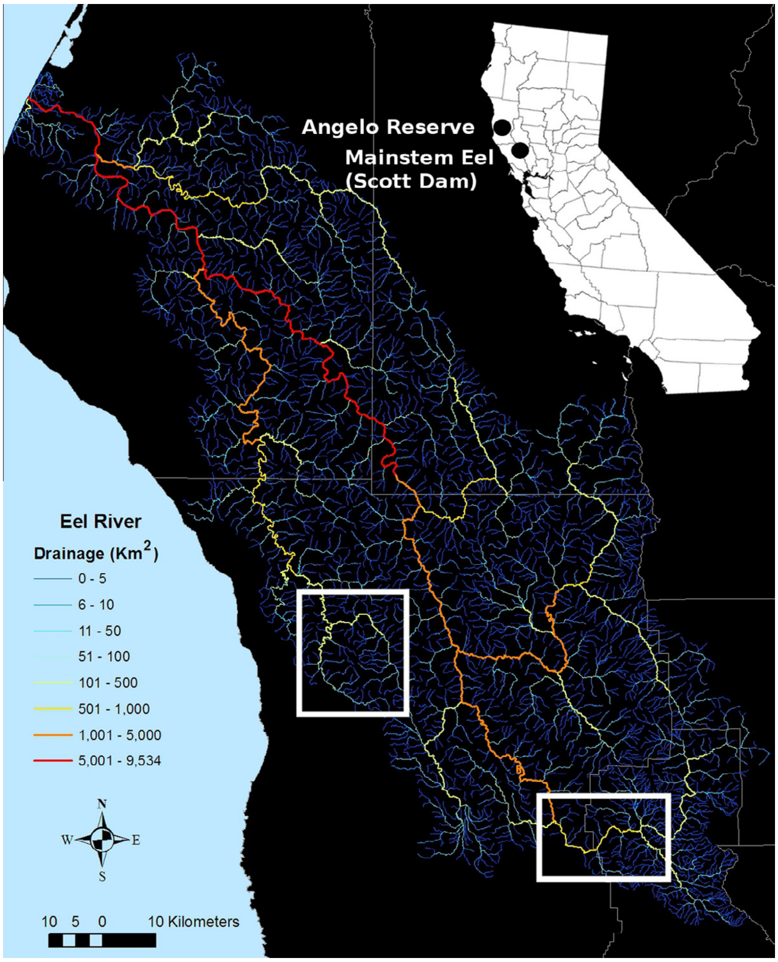

Fig. 1. Location of the South Fork Eel and mainstem Eel study reaches (white boxes) in Mendocino County, CA, USA in the context of the entire Eel River watershed.

Table 1
Thermal environments in the 4 unregulated streams of the South Fork Eel River watershed used to rear tadpoles of *Rana boylii* in enclosures.

Stream	Watershed (km^2)	Canopy cover (%)	Chlorophyll[a] (μg·cm^{-2})	Mean light intensity[b] (lux)	July daily mean water temperature[c] (°C)		
					2008	2009	2010
Fox	2.6	96.4 ± 0.5	0.9	3785 ± 1157	15.8	16.2	15.9
Elder	17.0	93.0 ± 2.9	1.9	4304 ± 1085	16.5	16.6	15.6
SF Eel	126.0	48.9 ± 4.0	1.6	11,823 ± 753	19.5	19.5	17.6
Tenmile	169.4	16.7 ± 1.6	2.1	38,070 ± 3995	21.5	21.5	21.7

[a] Data on chlorophyll *a* from Finlay (2004).

[b] Light intensity data from 30 August to 1 September 2008, using Hobo® Loggers.

[c] Temperatures for 2008 represent means from sensors placed in experimental enclosures ($n = 7$ per site). Temperatures for 2009–10 from sensors placed in the open stream ($n = 3$ per site).

metric T_{set} was defined as the central 50% of the temperatures selected by animals in a thermal gradient (Hertz et al., 1993). We calculated mean selected temperature with two approaches. First, for each tadpole we calculated the arithmetic mean of its 31 observed positions in the gradient, and then calculated the mean across all 56 tadpoles. Second, by bootstrapping (1000 times) values drawn one at a time from the 31 measurements for each tadpole, we calculated the mean across the 56 tadpoles. We report means ± SE and performed analyses in R (R Core Team, 2012).

2.3. Rearing experiment

We reared tadpoles from unhatched embryos to metamorphosis in four unregulated streams (Appendix, Fig. A1) which naturally differ in thermal regime (Fig. 2) and algal food availability (Table 1). The streams differ in watershed size and canopy cover which affect primary productivity. We measured light intensity from 30 August to 1 September 2008 using Hobo® Loggers at each tadpole rearing site. Although adult and juvenile *R. boylii* occur in all four streams, only the two largest streams (Tenmile and SF Eel) are used for breeding. We collected embryos at the gastrula stage (Gosner 10) from two egg masses laid on the night of May 11, 2008. We separated clusters of 30 embryos from each clutch, placed them in vials with stream water and the vials were carried in backpacks to the rearing locations. We placed embryos in flow-through enclosures constructed from plastic laundry baskets (55 × 38 cm) with 1 mm fiberglass mesh covering the openings. Water depth inside the enclosures was 15–20 cm. Cobbles with epilithic periphyton

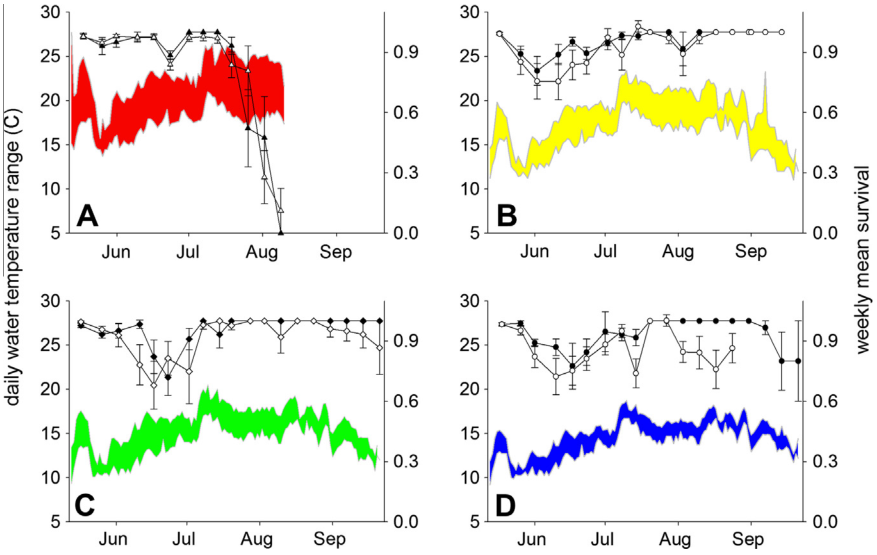

Fig. 2. Weekly mean proportion of surviving tadpoles fed epilithic algae only (low-quality food, white circles) or epilithic algae + epiphytized *Cladophora* macroalgae (high-quality food, black circles), and thermal regimes (shading between daily minimum and maximum temperatures) of the four streams (*A* = Tenmile Ck., *B* = SF Eel River, *C* = Elder Ck., *D* = Fox Ck.) where tadpoles were reared at the Angelo Coast Range Reserve, California between 12 May and 21 September 2008.

from each rearing location (low quality food) covered the bottom of each basket. We deployed 14 baskets in each stream, and randomly assigned clusters from one clutch to seven baskets and clusters from the second clutch to the remaining seven baskets. Clutch had no effect on mortality and was henceforth excluded as a factor in analyses. We randomly chose half of the baskets in each stream to receive the same weekly supplementation (high quality food) consisting of 40 g (damp mass) of the filamentous macroalga *Cladophora glomerata* covered with a heavy growth of epiphytic diatoms (including species of *Epithemia*, *Cocconeis*, and *Gomphonema*, C:N ratio = 10.13 ± 0.41). We selectively harvested macroalgae supporting large numbers of epiphytic diatoms, which can be recognized by their rusty-red coloration (Furey et al., 2012).

To mimic the natural decline in density that occurs in the open river as tadpoles disperse and are killed by predators, we periodically removed groups of tadpoles, creating stepped decreases in density over the course of the experiment (Appendix, Table A1 for schedule of reductions). We determined that this strategy was effective at avoiding crowding effects by comparing the body length of tadpoles in baskets (measured weekly to the nearest 0.1 mm with dial calipers) to equivalent stage free-living tadpoles in the SF Eel (Appendix, Fig. A2). We removed tadpoles from enclosures when front limbs emerged (Gosner stage 42).

We monitored thermal regime inside the enclosures with temperature data loggers (Thermocron iButtons DS1921G®, ±0.5 °C accuracy, programmed to record every 2 h) placed inside a subset of seven enclosures at each of the four sites. We consider temperatures recorded inside the enclosures to be equivalent to operative temperatures (T_e; Hertz et al., 1993) for tadpoles, because the high thermal conductivity of water, small size of tadpoles, and limited habitat heterogeneity inside the experimental enclosures effectively reduced the probability that tadpoles could experience a wider range of temperatures.

For mortality as the response variable, we calculated the difference between number of tadpoles present at the previous weekly visit (after excluding tadpoles removed during scheduled reductions and accidental losses) and the number of tadpoles still present. We assumed mortality for all tadpoles still alive at the end of the experiment in the coldest stream (21 September 2008), because they could not have completed metamorphosis before the onset of the fall floods given their developmental stages and slow growth.

We used ANOVA and multiple logistic regression models to explore the relationships among tadpole mortality from hatching to stage 42, thermal conditions, and food resources in the enclosures. Mortality data were transformed (arc sin square root) to meet the assumption of normality prior to ANOVA (Shapiro–Wilk Normality Test, $p = 0.722$). We performed separate logistic regression analyses for tadpoles reared with low vs. high quality food because post hoc power analysis of the 2-way ANOVA indicated there was low power to detect the interaction between rearing location and food level. The predictor variables in the logistic regression were watershed size and an index of thermal suitability, d_e (Hertz et al., 1993) which is calculated as the difference (absolute value) between T_e and T_{set}. Each d_e value represents the individual deviation of T_e from the closer (upper or lower) bound of T_{set}. When T_e falls within the set-point range, the resulting d_e value is zero. The mean d_e represents the thermal quality of a habitat from a tadpole's perspective. We restricted T_e to July ($n = 2232$ measurements/stream) because this month: (1) is when Gosner stages of tadpoles reared in the field enclosures were similar to those of tadpoles used to measure T_{set}; and (2) coincides with the period of fastest tadpole growth. We included watershed size because it accounts for algal productivity (i.e., the amount and quality of epilithic diatoms available to tadpoles in the un-supplemented treatment). Additionally, there was large overdispersion when the logistic regression model did not include watershed size.

2.4. Annual breeding activity as a function of habitat thermal quality

We combined monitoring of stream temperatures and measurements of canopy cover with breeding censuses to assess the relationship between light, thermal regime, and abundance of frogs at the watershed scale. At eight sites in the SF Eel watershed (drainage area range 2.6–169.4 km^2) and at eight sites in the Eel drainage downstream of Scott Dam (13.6–897.5 km^2), we installed Thermochron iButtons DS1922L® (±0.5 °C accuracy) in habitats with clutches of eggs or in locations where water velocity and depth were suitable for oviposition. Sensors were in place from May 3 2010 through September 30 2010. Similar to the 2008 survival analyses, we considered July temperatures to calculate the mean d_e. To place 2010, a high winter/spring precipitation year, in the context of inter-annual variation in temperature, we report 2008–2010 summer temperatures at the four rearing sites

(Table 1). We also calculated a 16 years July mean water temperature from the Angelo Reserve gaging station on the SF Eel (1990–2011, 16 years had complete records for July, i.e., no equipment failures or missing days). We evaluated, and found reasonable, our assumption that the thermal conditions experienced by mobile tadpoles can be accurately described with fixed sensors by comparing temperature readings at exact tadpole locations to readings from data loggers (Appendix, Figs. A3 and A4).

For each temperature monitoring site, we conducted censuses of adult breeding populations by tallying the number of egg masses laid during spring over a stream distance of 0.5–1 km. The number of clutches represents the number of successfully reproducing females in the reach for a given year, because females breed once per year and every oviposition results in a single clutch of eggs. Capture–recapture estimates of adult female population size for *R. boylii* in a Sierran creek were in close correspondence to number of clutches found (Van Wagner, 1996). We made multiple visits to the 16 study reaches within the breeding season to search for clutches and marked each with a bamboo skewer placed nearby in the river bed. Any previously overlooked clutches plus new clutches were found and tallied upon subsequent visits. Visits continued until we found no new clutches. We visited all 16 reaches in at least 2 years, and a subset of five SF Eel reaches have been surveyed annually since 1992. We used all available data to calculate mean density (clutches km^{-1} $year^{-1}$).

We performed Principal Component Analysis to explore relationships among the physical characteristics of the surveyed reaches. For each thermal monitoring reach we used the following variables: upstream watershed area (km^2), calculated using ArcGIS (Environmental Systems Research Institute, Redlands, CA); mean canopy cover (%), measured with a spherical densiometer at three breeding sites per reach; mean daily water temperature during the warmest 30 days period (M30DAT) in 2010; July d_e; number of days between egg laying date and the week when M30DAT was highest; calendar date when average daily temperature reached the range of T_{set}; and the mean July temperature. We analyzed data (non-transformed, after checking for normality) with the princomp function using eigen on the correlation matrix in the statistics package in R 2.10.1 (R Core Team, 2012). Principal components 1 and 2 (representing 86.9% of variation) were used to produce a scatter plot to visualize the effect of temperature and productivity variables on frog breeding population density. We performed nonlinear regression using SigmaPlot 11 (Systat Software, San Jose, CA) to relate breeding population density (clutches km^{-1} $year^{-1}$) to July mean water temperature and PC 1 as a composite predictor variable. We used an information theoretic approach for choosing the best fit thermal performance curves (Angilletta, 2006).

3. Results

3.1. Tadpole thermal preference

In the thermal gradient trials, set-point temperature (T_{set}) ranged from 16.5 to 22.2 °C ($n = 56$ tadpoles). Mean selected temperature was 19.60 ± 0.58 °C (19.60 ± 0.03 °C with the bootstrapping approach). There was no relationship between Gosner stage and mean selected temperature ($R^2 = 0.002$, $p = 0.72$; with bootstrapped regression, $p > 0.20$). Similarly, there was no relationship between mean selected temperature and body length ($R^2 = 0.008$, $p = 0.52$) or weight ($R^2 = 0.007$, $p = 0.54$).

3.2. Rearing experiment

Weekly survival patterns differed among the experimental enclosures in four different streams in relation to both temperature and food treatment (Fig. 2; Table 2). There was no significant interaction of rearing site and food quality ($p = 0.31$; Table 2). Weekly survival was generally lower at early stages of development, with the exception of the warmest site (Tenmile Ck.), where maximum daily temperatures in excess of 25 °C in July corresponded to a sharp drop in weekly survival when tadpoles had reached advanced developmental stages (Gosner 35–42). The index of habitat thermal quality, d_e, in the experimental enclosures in July 2008 ranged from 0.04 ± 0.16 °C (SF Eel) to 0.92 ± 0.92 °C (Fox Ck.). On the basis of the observed mean July d_e values, our logistic regression model assessed the probability that an embryo would not successfully reach metamorphosis. Deterioration of the thermal quality of the habitat by 1 °C (i.e., a 1 °C change in the mean July d_e) increased the odds of mortality by a factor of 8.40 (95% confidence interval = 1.13–79.60).

Table 2
Results of ANOVA testing the effects of food quality and site (streams with different thermal and light regimes) on tadpole mortality within enclosures. Low-quality food was epilithic diatoms only, whereas and high-quality food included epilithic diatoms and richly nutritious epiphytized macroalgae.

Effect	*df*	SS	MS	*F*	*p*
Site	3	1.208	0.403	5.956	0.002
Food	1	1.141	1.141	16.874	<0.001
Site × food	3	0.251	0.084	1.238	0.307
Residual	46	3.111	0.068		
Total	53	5.788	0.109		

The multiple logistic regression model provides mortality estimates after controlling for watershed size, our proxy for productivity (Table 3; Fig. 3). Among the replicates not receiving food supplementation, we compared tadpole mortality associated with deviation from preferred temperature in a larger watershed (150 km^2), where channels are broad and sunlit, to mortality in a small watershed (60 km^2) with narrow shaded channels and low productivity. The predicted probability of not reaching metamorphosis comparing these two watershed areas was 70.1% vs. 87.9% for a mean July d_e of 0 °C, and 87.6% vs. 95.5% for a mean July d_e of 0.5 °C. The mean July d_e did not influence mortality when tadpoles received supplements of high-quality food containing N-fixing diatoms (Table 3). A stronger influence of habitat thermal quality with low-quality food than with high-quality food was also found after bootstrapping regressions of tadpole mortality as a function of mean July d_e for each basket (49.7% vs. 29.3% of regressions were significant).

3.3. Annual breeding activity as a function of habitat thermal quality

Two principal components explained 86.9% of the variation in the thermal (PC1) and productivity related (PC2) environmental variables (Table 4). The regulated and free-flowing study reaches

Table 3
Results of multiple logistic regression models of the probability of tadpole mortality in enclosures with low-quality food (epilithic diatoms only) and high-quality food (epilithic diatoms + epiphytized macroalgae) as a function of mean 2008 July d_e and watershed area (km^2).

Effect	*z*	*df*	*p*	Estimate ± SE
Low-quality food				
Intercept	2.491	3	0.013	2.718 ± 1.091
Mean July 2008 d_e	2.014	3	0.044	2.128 ± 1.057
Watershed area	−1.567	3	0.117	−0.012 ± 0.008
High-quality food				
Intercept	0.640	3	0.522	0.369 ± 0.577
Mean July 2008 d_e	1.420	3	0.156	0.962 ± 0.678
Watershed area	0.463	3	0.644	0.001 ± 0.003

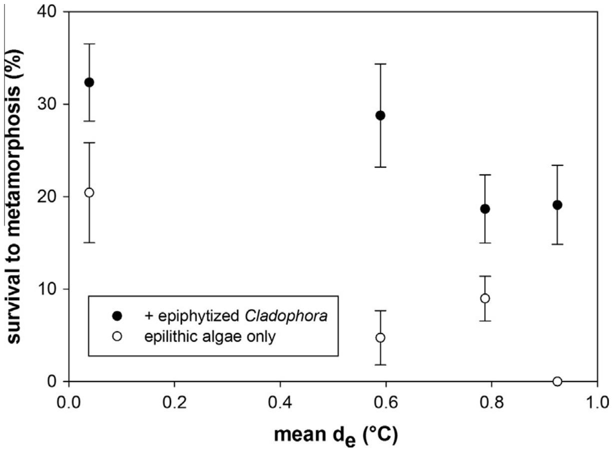

Fig. 3. Survival to metamorphosis for *Rana boylii* tadpoles as a function of the deviation between thermal preference and water temperature during July 2008, d_e; (Hertz et al., 1993).

Table 4
Summary of principle component loadings for temperature and productivity-related variables (see Section 2 for details) within 16 stream reaches of the Eel River, California, USA where foothill yellow legged frogs (*Rana boylii*) occur.

Variable	"Temperature" PC1	"Productivity" PC2
July mean water temperature	−0.50	−0.16
Calendar date when T_{set} reached	0.49	−0.01
July d_e	0.43	0.19
Canopy closure	−0.02	−0.61
Watershed area	0.31	−0.46
Days from oviposition to warmest month	0.35	−0.43
Maximum 30 days moving average temperature	−0.30	−0.41
Eigenvalue	3.54	2.54
Percent of variance	50.5	36.4

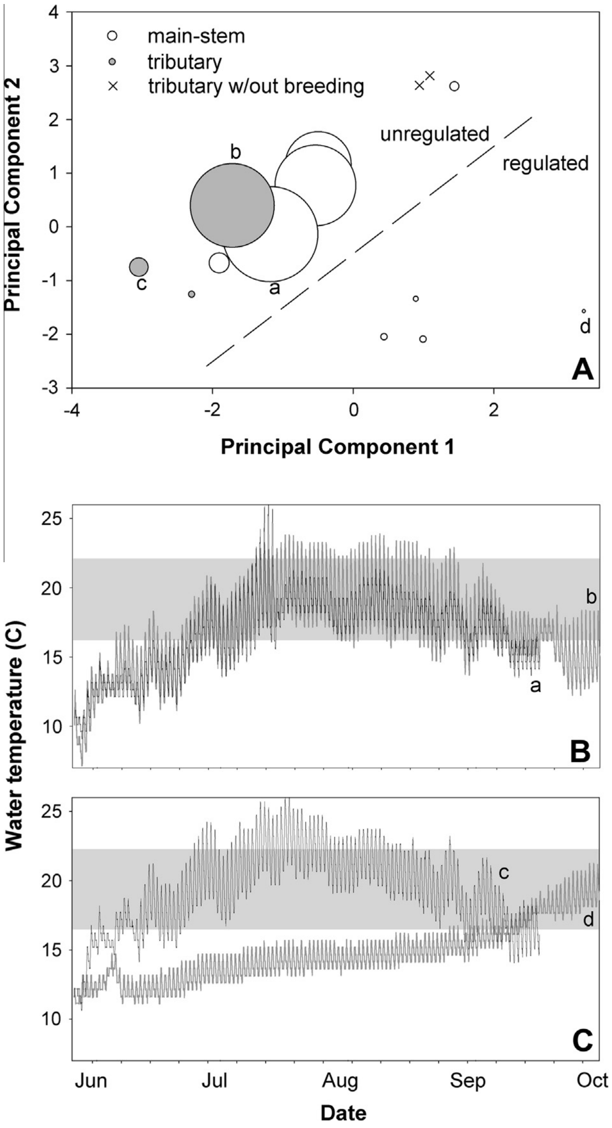

Fig. 4. (A) Scatter plot of Principal Components 1 and 2 for 16 stream reaches in Eel River watershed. The size of dots is proportional to mean clutch density. (B) Comparison of water temperatures at two unregulated stream reaches with large populations of *Rana boylii*: SF Eel at 150 km^2 watershed area (a) and Bucknell Creek (b). (C) Comparison of water temperatures at two reaches with similar values of PC2 and small populations of *R. boylii*: Tenmile Ck. (c, unregulated) and the Eel River 1.9 km downstream of Scott Dam (d, regulated). Grey boxes represent temperatures preferred by tadpoles (T_{set}).

clustered in opposite quadrants of a scatter plot of PC1 vs. PC2 (Fig. 4A). The first principal component, PC1, is negatively correlated with July temperature and positively correlated with time between egg laying and warming to T_{set}. Low values thus characterize sites that warm quickly (Fig. 4B), and high values indicate cold sites that do not reach appropriate temperatures until late in the season (Fig. 4C). Using PC1 as a composite measure of thermal suitability, a 3-parameter Gaussian function relating population abundance to PC1 (abundance = $ae^{[-0.5*((PC1-b)/c)2]}$) was the best fit thermal performance curve ($AIC_c = 46.8$, $\Delta AIC = 0$, $R^2 = 0.9$) (Fig. 5A). For ease of interpretation we also plot July 2010 water temperatures (the variable with the highest correlation with PC1) to show that populations were dense ($\geqslant 125$ breeding females km^{-1}) where water temperature averaged 17.5–19 °C, were sparse below 16 °C with open canopy, and absent below 16 °C with closed canopy (Fig. 5B). Specifically, the thermal quality at the most upstream breeding site along the SF Eel River and in the mainstem Eel below Scott Dam was lower than at shadier, less productive sites not used for reproduction in smaller watersheds (e.g., Fox and Elder Creeks). Data from the SF Eel gaging station indicates that July 2010 mean daily temperature, 16.9 °C, was at the 25th percentile of a 16 years range 15.7–20.2 °C, (mean = 18.3 ± 0.3 °C).

4. Discussion

Our results show that measurements of individual thermoregulatory preferences in a freshwater ectotherm can be used to predict recruitment success for populations throughout a watershed. Populations of frogs were most dense where mid-summer water temperatures matched thermal preferenda of tadpoles and were most favorable for survival to metamorphosis in our feeding and rearing manipulation. While the benefits of operating at temperatures near an organism's thermal preference include many physiological and biochemical processes (Huey and Stevenson, 1979), the benefits may be greater in rapidly developing stages, such as tadpoles, compared to adults. Temperature directly influences differentiation and growth rates (Berven, 1982; Berven and Gill, 1983), which are key processes during ontogeny (Smith-Gill and Berven, 1979). Selecting temperatures that are optimal for consumption rate, food conversion efficiency, metabolism, and growth is important for algal grazing tadpoles specifically (Skelly and Golon, 2003) as well as other aquatic ectothermic vertebrate herbivores such as marine iguanas and fish (Wikelski et al., 1993; Clements et al., 2009). For

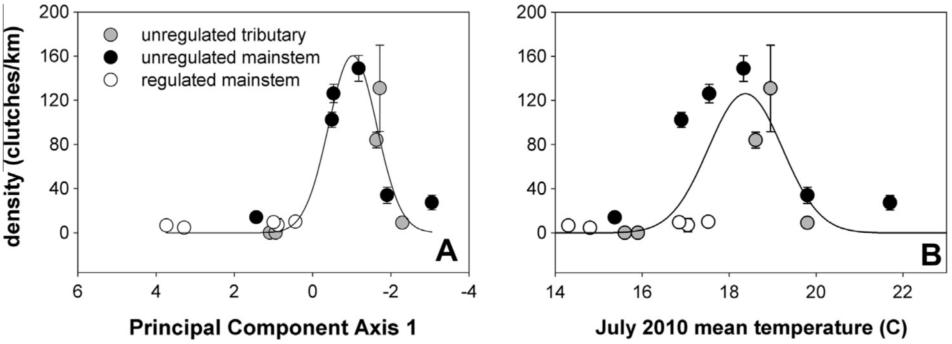

Fig. 5. Mean ± 1 SE population density of *Rana boylii* in the 16 study reaches in the Eel River watershed in relation to (A) Principal Component 1, and (B) July 2010 mean water temperature.

tadpoles of *R. boylii*, T_{set}, which denotes a range of values, provides a conservative estimate for our models relating summer water temperature to survival to metamorphosis and population size. A wide range for T_{set} restricts high d_e values to habitats which differ considerably from the temperature selected by tadpoles. The temperature range selected by tadpoles in our thermal gradient experiment is not unusual among larval anurans (Hutchison and Dupré, 1992) and the mean value is consistent with other ranid species at similar or more northerly latitudes (Workman and Fisher, 1941; Herreid and Kinney, 1967; Wollmuth et al., 1987). Notably, T_{set} of *R. boylii* is warmer than the temperature selected by tadpoles of the tailed frog (*Ascaphus truei*), which breeds in the colder streams (De Vlaming and Bury, 1970) where only adults of *R. boylii* are found. Although tadpoles of *Ascaphus* are similarly limited by low light effects on algal productivity (Mallory and Richardson, 2005), they can utilize multiple growing seasons to reach metamorphosis because they are morphologically adapted to withstand winter floods. Tadpoles of *R. boylii* do not overwinter and thus cold summer temperatures can limit successful recruitment.

The quality of algal food available to tadpoles can ameliorate the negative effects of cold temperature on recruitment success. When receiving supplements of algae harvested from the productive mainstem SF Eel, even tadpoles from the coldest rearing site, Fox Ck., were able to reach metamorphosis, albeit slowly, after 122.2 ± 0.6 days compared to 79.3 ± 1.7 days at the warmest site (Tenmile Ck.). Lower temperatures may reduce metabolic costs and might allow tadpoles to allocate a greater proportion of absorbed nutrients to growth, as found in other ectothermic organisms (Miller et al., 2009; Coggan et al., 2011). Despite the possible compensation, tadpoles reared at the coldest site grew to only half the size of those reared in the warmest stream; body mass at full tail resorption (stage 46) was 0.5 ± 0.02 g vs. 1.08 ± 0.08 g. Similar to the survival, development, and growth responses we observed at the individual tadpole level, variation in adult frog density appears to be a function of both habitat thermal quality and the ecological context of position in the watershed. The number of clutches laid, a recognized proxy for total population size in ranid frogs (Crouch and Paton, 2000; Loman and Andersson, 2007; Petranka et al., 2007), was highest where the combined temperature and productivity conditions were most favorable to tadpoles (Figs. 4A and 5). As watershed area, channel width, and levels of incident light increase, so does algal production, measured either as epilithic chlorophyll *a* or percent cover of the dominant filamentous green macroalga, *C. glomerata* (Finlay et al., 1999; Finlay, 2004). *Cladophora* with a heavy growth of epiphytic diatoms is rich in proteins and lipids (Kupferberg et al., 1994). Preliminary stable isotope research indicates that epiphytic diatoms containing N-fixing endosymbionts, such as *Epithemia*, contribute a substantial portion of N in the diet of *R. boylii* tadpoles at the Angelo Reserve (unpubl. data). The results of our rearing experiment indicate that this nutritional value can compensate, at least partially, for the negative effects of cool temperatures such as limited consumption rate and low assimilation efficiency in tadpoles (Altig and McDearman, 1975) which likely contributed to low survival at the cold sites.

Phenotypic variation in thermal preference may exist across populations, but our response variables of interest, T_{set} and d_e, showed predictive value for determining response to thermal regime change. Selected temperatures may be affected by temperatures experienced prior to testing, and this potential source of variation was minimized because we estimated T_{set} from tadpoles collected from a single location and reared under similar conditions in flow-through enclosures. Furthermore, we compared preferences to wild caught tadpoles from scattered locations in the watershed and verified that the response was similar. Acclimation temperature could also influence thermal preference, so we minimized transport and holding times prior to testing tadpoles in the thermal gradient. When acclimation has been investigated directly in other anurans, its effects are species-specific ranging from negligible (De Vlaming and Bury, 1970; Hutchison and Hill, 1978; Wollmuth et al., 1987) to counter-gradient responses (Freidenburg and Skelly, 2004; Skelly, 2004). Counter-gradient response means that tadpoles reared in colder locations have higher thermal preferenda than tadpoles reared in warmer locations. When we tested tadpoles of *R. boylii* reared in the colder streams (Catenazzi and Kupferberg, unpubl. data), we observed a counter-gradient response which thus makes our model conservative for assessing the thermal quality of habitats and for predicting thermal effects on frog recruitment.

A limitation of d_e as a metric is that it does not discriminate between conditions being too warm or too cold. This distinction is important because thermal performance curves for most physiological processes are asymmetric and generally point to a gradual decline in process rate or fitness with decreasing temperatures but a sharp drop with increasing temperatures approaching the critical maximum (Huey and Stevenson, 1979). We did observe sudden mortality of tadpoles at the warmest site (Fig. 2A). Husbandry is an unlikely cause for the observed deaths, because mortality in the enclosures coincided with mortality in wild tadpoles. We observed a large number of dead wild tadpoles and metamorphs on 25 July 2008. The date of the die-off corresponds to the midpoint in the sharp declines in the weekly survival curve (Fig. 2A). Death could have been caused directly by heat stress (De Vlaming and Bury, 1970), or indirectly by high temperatures promoting infection by pathogens or parasites (Kupferberg et al., 2009a). We hypothesize that the critical thermal maximum for *R. boylii* is higher than the temperatures at Tenmile Ck. because we observed successful metamorphosis from isolated side pools elsewhere in the

Eel watershed where daily maxima can reach 30 °C. Our model indirectly takes into account the asymmetrical aspect of thermal response because it incorporates watershed size and summer water temperatures, which are positively correlated with increasing drainage area throughout the geographically diverse microclimates of the Eel watershed (Lewis et al., 2000).

4.1. Conservation Implications

Physiological, behavioral and ecological factors act in concert, and knowledge of these interactions will improve the ability to forecast a species' response to environmental change (Kearney et al., 2009). As illustrated by the dependency of larval *R. boylii* survival on both the thermal and food quality of the habitat, appreciation of these factors is especially relevant for populations of this declining amphibian in regulated rivers. The retention of water behind a dam can result in artificially low summer base flow discharges and warm downstream temperatures (Lessard and Hayes, 2003). Alternatively, when summer base flows are drawn from the hypolimnion of the reservoir, temperatures downstream are often colder than un-impaired conditions (Angilletta et al., 2008; Olden and Naiman, 2010). For example at our study site in the mainstem Eel River downstream of the artificial reservoir of Lake Pillsbury, July mean daily temperatures were 1.1–5.5 °C degrees lower than those observed in the coolest of the unregulated tributaries where frog breeding occurred (Fig. 4B). Temperatures did not reach the preferred range of tadpoles until very late in the summer (Fig. 4C) and the distribution of breeding frogs in the regulated watershed shifted to the relatively warmer, but shadier and hence less productive, tributaries. Thus, when river managers and dam operators consider alternate flow proposals, the impacts of anticipated thermal changes should be evaluated within the context of the thermal suitability of tributaries to provide substitute habitat for species requiring warm water.

The composition of the local algal and diatom flora is also sensitive to flow regulation. For example, spread of the invasive benthic diatom, *Didymosphenia geminata*, appears to be positively correlated with cool summer water temperatures and artificially stable base flows (Kilroy et al., 2008; Kumar et al., 2009). *Didymosphenia* covers rock surfaces with a mucilaginous sheath to the exclusion of edible algal species, and does not provide adequate nutrition for large bodied grazers such as tadpoles (Furey et al., 2013). Reduced flow fluctuation and flood frequency also promotes extensive encroachment of riparian vegetation into formerly active channels (Poff and Zimmerman, 2010). Encroachment of the banks by woody species ultimately leads to higher canopy cover, shading, and thus poor conditions for periphyton growth in the shallow channel margins which are vital nursery habitats for early life stages of fish as well as amphibians.

Considering the combined effects of water temperature and food quality will improve management strategies aimed at preserving populations of these and other threatened ectotherms. A population viability analysis conducted for *R. boylii* indicates that its populations are very sensitive to early life stage mortality (Kupferberg et al., 2009b), as occurs when clutches are scoured or stranded by un-timely releases from dams. Populations of many river fish taxa similarly depend on survival of early life stages (Strange et al., 1993; Humphries and Lake, 2000; Pusey et al., 2001). Interactions between productivity and changes in water temperature also affect adult aquatic consumers, such as Pacific loggerhead sea turtles, for whom nesting abundance declines as ocean productivity and foraging opportunities decline with warming temperatures (Chaloupka et al., 2008). By integrating the impact of local productivity on survival with an index of environmental thermal quality derived from thermoregulatory behavior, our hybrid approach of field experimentation and correlational analysis illustrates a method to understand the mechanisms linking thermal regime change to population dynamics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.09.010. The data include an Appendix, Table A1 and Figures A1, A2, A3 and A4, as well as Google maps of the most important areas described in this article.

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