



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



Alessandro Catenazzi<sup>a,b,\*</sup>, Sarah J. Kupferberg<sup>b,c</sup>

<sup>a</sup> Department of Zoology, Southern Illinois University, Carbondale, IL 62901, USA

<sup>b</sup> Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

<sup>c</sup> 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 boylei*) 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 (≥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.

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## 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 antic-

\* 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](mailto:acatenazzi@gmail.com) (A. Catenazzi).

ipated 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

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 boylei*). 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. boylei* 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. boylei* 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. boylei* 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. boylei* in northern California (Kupferberg et al., 2012). The Eel River flows through steep terrain vegetated by mixed coniferous forest. Adults of *R. boylei* 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. boylei*. 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. boylei* 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 ( $11.9 \pm 0.1$  °C,  $n = 108$ ) to the warm ( $34.7 \pm 0.2$  °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

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