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ORIGINAL ARTICLE

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Consequences of dam-altered thermal regimes for a riverine herbivore's digestive efficiency, growth and vulnerability to predation

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Abstract

1. Rivers around the world are undergoing shifts in thermal regime due to climate change and human appropriation of water resources. The local impacts of thermal regime change are challenging to predict because water temperature can influence aquatic organisms and communities at multiple levels simultaneously. For example, thermal change can influence the phenology of periphyton blooms, primary consumer physiology and behaviour, and interspecific interactions with predators.
2. Using tadpoles of the threatened river-breeding foothill yellow-legged frog (*Rana boylii*, Ranidae), their algal foods and their invertebrate predators, we mimicked dam-induced changes in temperature and observed the outcome of consumer–resource interactions. In stream enclosures, we reared tadpoles across a gradient of cold to warm conditions, quantified the ash content of diet, digestive efficiency and growth rate, and assessed their vulnerability to hemipteran and odonate predators.
3. Tadpoles reared in a cool stream (15.5°C daily mean) digested epilithic periphyton poorly (6.6 ± 0.4% assimilation efficiency). In contrast, average assimilation efficiency of tadpoles reared at 19°C was 11.6 ± 0.1%. Access to nutritious diatoms (i.e. dinitrogen-fixing *Epithemia* spp., Rhopalodiaceae) increased assimilation efficiency to 10.1 ± 0.1% and 13.8 ± 0.1% in the cool and warm treatments, respectively. Assimilation efficiency correlated positively with tadpole growth rate ($R = 0.66$, $p < .001$).
4. The effect of temperature on mortality due to predation was mediated by low tadpole growth rates at cool temperatures and not by the temperature of predator exposure. Non-lethal effects of predators on tadpole growth and tail injury, however, depended on both rearing temperature and exposure temperature. Contrary to the expectation that the cost of predator avoidance behaviours may be greater at warmer exposure temperatures because basal metabolic rates are higher, our results indicated that the energetic cost of foraging less was amplified at cool temperatures.
5. Our results show that when thermal conditions impair digestion in a species' early life stages, recruitment bottlenecks are likely to arise due to the combined

negative effects of cool temperatures on assimilation efficiency and growth, and increased predation by invertebrates.

KEYWORDS
amphibian conservation, hydropower, river, tadpole ecology, water temperature

1 | INTRODUCTION

The thermal environments of rivers around the world have undergone substantial alteration because of climate change and human appropriation of water resources (Van Vliet, Ludwig, Zwolsman, Weedon, & Kabat, 2011; Van Vliet et al., 2013). The local impacts of thermal shifts in rivers are difficult to manage because the population-level responses of aquatic organisms to temperature appear to be highly variable (Bowler et al., 2017). Predicting the outcome of altered thermal conditions is further complicated by the many ways in which water temperature can affect riverine organisms and communities. The acute effects include increased disease and parasite prevalence (Adams et al., 2017; Kupferberg, Catenazzi, Lunde, Lind, & Palen, 2009) and mass mortality events (Fey et al., 2015) when individuals experience episodes of low or high temperatures beyond their critical limits (Beitinger, Bennett, & McCauley, 2000; Gunn & Snucins, 2010; Richter & Kolmes, 2005). In contrast, mortality and fitness can change incrementally when thermal conditions alter an organism's basic physiological processes such as the conversion of food into body tissue (Robinson & Childs, 2001; Windell, 1978), or indirectly by altering the outcome of species interactions (Cao, Li, & Jeppesen, 2014; Grigaltchik, Ward, & Seebacher, 2012; Power, Bouma-Gregson, Higgins, & Carlson, 2015). Along with the differential responses of interacting species to temperature, thermal shifts can decrease the strength of trophic cascades controlling the flow of energy and nutrients in river food webs (Kishi, Murakami, Nakano, & Maekawa, 2005; Power et al., 2015). Collectively, these mechanisms pose a threat to freshwater biodiversity (Kaushal et al., 2010; Olden & Naiman, 2010; Van Vliet et al., 2013).

Disentangling the complexities of resource–consumer interactions when a river's thermal regime changes in response to regulation of streamflow and climate change is important for conservation of freshwater biodiversity in general and amphibians in particular. Tadpoles, along with their algal foods and invertebrate predators, provide an excellent model system to parse the overall effects of thermal change on vulnerable taxa into component parts. These organisms can be readily maintained in flow-through enclosures and manipulated in field experiments (Kupferberg, Lind, Thill, & Yarnell, 2011; Kupferberg, Marks, & Power, 1994). They are highly responsive to thermal conditions (Bush, Theischinger, Nipperess, Turak, & Hughes, 2013; Catenazzi & Kupferberg, 2013; Wheeler, Bettaso, Ashton, & Welsh, 2015) and temperature can directly affect fitness, because the larval stages of biphasic organisms like amphibians and insects require fast growth and development for metamorphosis (Rowe & Ludwig, 1991; Wassersug, 1975). Larvae of biphasic organisms represent a substantial portion of imperilled freshwater biodiversity (Balian, Segers, Lévêque, & Martens, 2008; Collen et al., 2014) and can play important ecosystem roles as grazers and recyclers of nutrients (Flecker, Feifarek, & Taylor, 1999; Whiles et al., 2006), or as predators (Corbet, 2004). Tadpoles and their invertebrate predators are thus broadly relevant for understanding the consequences of shifts in thermal regime that can uncouple factors that usually operate in synchrony, such as breeding phenology, the timing of peak resource abundance and thermal suitability for early stages of organisms with complex life cycles. Such ecological mismatches are an underappreciated aspect of human alteration of river water flows (Olden & Naiman, 2010; Schiemer, Keckeis, & Kamler, 2002).

We worked with invertebrate predators and tadpoles of a river-breeding frog endemic to California, USA, the foothill yellow-legged frog, *Rana boylii* (Ranidae). In California, most major river systems are harnessed for agricultural and municipal use (Mooney & Zavaleta, 2016) and hydroelectric power generation meets up to 21% of demand for electricity (California Energy Commission, 2016). Water abstraction and storage have contributed to the decline of these frogs as well as many other freshwater organisms in the state (Howard et al., 2015; Kupferberg et al., 2012; Moyle, Katz, & Quiñones, 2011). An important driver of decline is the direct negative effect of dam-altered thermal conditions on development and survival of early life stages (Catenazzi & Kupferberg, 2017; Clarkson, Childs, & Schaefer, 2000; Wheeler et al., 2015). Thermal changes downstream of dams also shift the composition of periphyton flora towards taxa offering poor nutritional value to fast-growing larval consumers (Furey, Kupferberg, & Lind, 2014; Rost & Fritsen, 2014). For example, breeding populations of foothill yellow-legged frog are sparse or absent where water is naturally cold or dams release cold water from upstream reservoirs (Catenazzi & Kupferberg, 2017; Welsh & Hodgson, 2011). We explore possible mechanisms underlying this distribution pattern by exposing tadpoles and their predators to thermal regimes representative of natural and managed rivers in watersheds occupied by foothill yellow-legged frogs. Altered regimes in managed rivers include continuously cooler (up to 8°C lower) daily mean water temperature compared to neighbouring un-managed reference sites, as well as fluctuations between warm and cool conditions when dam discharge alternates between surface spills and hypolimnetic releases (Catenazzi & Kupferberg, 2017). We ask three focal questions: (1) What are the relationships among water temperature, digestive efficiency, food quality and growth of tadpoles? (2) How does temperature influence the vulnerability of tadpoles to predators? (3) For survivors, how does the cost of predator avoidance behaviour vary with temperature?

2 | METHODS

2.1 | Study system

At University of California's Angelo Coast Range Reserve (Mendocino Co. CA, USA), we utilised the spatial heterogeneity in stream environments to manipulate the thermal conditions and quality of algal food resources available to tadpoles. During the spring and summer of 2009 and 2010, we enclosed tadpoles at three locations in the South Fork Eel River (SF Eel hereafter) and in two of its tributary streams. A warm tributary, Tenmile Creek (169 km^2 watershed area), flows through open grazing land in an east–west direction. A cold tributary, Fox Creek (2.6 km^2), flows through dense mixed-coniferous forest. The SF Eel which flows in a north–south oriented confined canyon provided a range of intermediate thermal conditions: at the confluence with Fox Creek, 150 m downstream of this confluence (126 km^2) and 2.7 km further downstream (154 km^2). The algae-based food webs in these streams are governed by Mediterranean seasonality of rainfall and temperature. The food webs reassemble during the transition between the scouring floods of winter and the drought of summer (Finlay et al., 2011; Power, Parker, & Dietrich, 2008). After hatching in early spring, tadpoles graze on epilithic periphyton and then later on filamentous green algae and their diatom epiphytes, which proliferate as the water warms (Furey, Lowe, Power, & Campbell-Craven, 2012). In the shallow near-shore habitats, where tadpoles are most common, the dominant invertebrate predators identified as strong interactors in trophic cascades include dragonfly nymphs and hemipterans (Sabo, Finlay, & Post, 2009).

2.2 | Assimilation

To understand the role that thermal sensitivity of assimilation efficiency plays in producing growth differences, we conducted a short-term (7 days), two-factor, fully crossed experiment (3 levels of thermal regime × 2 food levels × 5 replicates per treatment = 30 total replicates). In late spring 2010, we collected embryos from five different clutches of foothill yellow-legged frogs in the SF Eel and reared the tadpoles for approximately 8 weeks in situ. On 31 July 2010, we placed flow-through enclosures (each housing one tadpole) in Fox Ck. (cold), at the confluence with the SF Eel (intermediate), and in the South Fork Eel 150 m downstream of the confluence with Fox Ck. (warm). We assigned one tadpole from each clutch to each treatment. At the start and end of the experiment, we weighed, measured and staged each tadpole. Median stage (Gosner, 1960) at the start of the experiment was 34 (range = 31–37). We monitored temperature at the three sites every two h using one iButton deployed in each type of algal food treatment.

Water temperature in the warm treatment was 3–4°C greater than the other two locations in terms of daily mean (±1 *SE*): Fox = 15.5 ± 0.05°C, Confluence = 15.7 ± 0.06°C, SF Eel = 19.1 ± 0.07°C. Although daily mean temperature at the confluence was only slightly warmer than the tributary, there was an influence of greater insolation on the baskets and the floating mats of the filamentous green alga *Cladophora glomerata* (Cladophoraceae) resulting in higher daily maximum temperatures (Fox = 16.6 ± 0.1°C, Confluence = 17.5 ± 0.2°C, SF Eel = 20.9 ± 0.3°C).

The food treatments were (1) periphyton attached to cobbles or (2) periphyton supplemented with floating mats of 25 g damp mass *C. glomerata* with epiphytic diatoms. We provided a mix of cobbles from the SF Eel and Fox Ck. sufficient to cover the bottom of each enclosure. Mixing compensated for differences in the composition of the epilithic flora between the two locations as determined by microscopic examination and identification of the diatoms and algae present (Table S1). We replenished enclosures with fresh rocks and filamentous algae about halfway through the experiment to prevent possible resource depletion. To determine organic content of algal foods, we placed rock scrapings and filamentous algal samples onto pre-weighed and pre-ashed 2.5 cm diameter glass microfiber filters (GF/C), and then dried at 60°C for 48 hr. We cooled samples to room temperature in a desiccator and weighed to 0.0001 g on a Mettler balance. We incinerated samples in a muffle furnace held at 500°C for 1 hr. After cooling and re-weighing (ashed mass), we calculated the ash-free dry mass (AFDM = dry mass − ashed mass) and organic content (% organic = AFDM/dry mass).

The response variables were tadpole growth (i.e. change in mass), AFDM of ingested food in the anterior small intestine and Conover's (1966) index of assimilation efficiency. We obtained AFDM of ingested food as described above for algae. Efficiency is defined as $[(F' - E') \times (1 - E') - 1 \times F'] \times 100$, where F' = AFDM/dry mass of food, E' = AFDM/dry mass ratio for tadpole faeces. We removed all faecal material from enclosures once daily with plastic bulb pipettes, and began processing samples 48 hr after we placed tadpoles into enclosures to allow sufficient time for passage of any food ingested prior to the start of the experiment. We calculated efficiency using the mean of the five daily samples of faeces collected from 2 to 6 August. At the experiment's conclusion, we euthanised the tadpoles with MS-222, weighed, measured and froze at −18°C for later dissection. To examine whether food type or temperature had any effect on gut length, we also measured the length of anterior and posterior small intestine. We removed the intestine from each tadpole and measured length of anterior small intestine (from the manicotto glandulare to the inflection point of the coiled gut), and posterior small intestine (from inflection to the beginning of the colon). We added those two lengths to calculate total gut length.

We assessed the interactive effects of temperature and food type on Conover's index of assimilation efficiency, growth and per cent biomass of the food in the anterior small intestine with two-way ANOVAs. We used linear regression to relate gut length to body size and correlated tadpole growth to ash content of ingested material, a proxy for predominance of diatoms in the diet (Malkin, Sorichetti, Wiklund, & Hecky, 2009).

2.3 | Predation

We designed two experiments to separate the effects of exposure temperature and rearing temperature (i.e. size-related susceptibility) on the outcome of interactions between tadpole prey and invertebrate predators. We define exposure temperature as the thermal regime during the period of time when tadpoles were enclosed with predators and rearing temperature as the thermal regime in the weeks preceding the predation trials. We reared tadpoles from eggs for 8 weeks under four different thermal regimes followed by 2 weeks in June with or without exposure to predators (Figure 1a,b). For the next experiment in July, we used the 10-week-old tadpoles that had not been exposed to predators for a reciprocal transplant to the coldest and warmest thermal regimes, and similarly exposed (or protected) the tadpoles to a predator (Figure 1c,d). Density was 10 tadpoles per enclosure from May through the June exposure to predators, equalised at five per enclosure after the first round of predation and then set at three tadpoles per enclosure in July. The stepped decrease in tadpole number per enclosure mimics the natural decline in density in the open river due to dispersal and attrition to predators (Catenazzi & Kupferberg, 2013).

We separated embryos from a clutch of eggs on 15 May 2009 and reared them in 72 flow-through enclosures, 18 replicates at each of four thermally distinct sites. Enclosures were 40 × 60 cm plastic baskets with 1-mm fibreglass mesh glued over the openings. Tadpoles had ad libitum access to epilithic periphyton on cobbles lining the bottom of the enclosures plus floating mats of *C. glomerata* with diatom epiphytes (re-stocked at 40 g every 7 days). We achieved consistent damp mass by processing the algae in a salad spinner for 50 rotations. Among the most common diatom epiphytes, *Epithemia spp*. (Rhopalodiaceae), along with its dinitrogen-fixing cyanobacterial endosymbionts, promotes rapid growth and development of tadpoles and is a preferred food source (Kupferberg, 1997). We calculated daily mean water temperatures from data recorded every 2 hr on Thermochron iButtons DS1921G® (±0.5°C accuracy) placed in three randomly selected enclosures within each site. From 18 June to 3 July 2009, we enclosed one water scorpion, *Ranatra brevicollis* (Nepidae), in each of six replicates and excluded predators from 12 control enclosures at each site.

When tadpoles were 10 weeks old on 17 July 2009, and size had diverged as a result of rearing temperature (Figure 1d), we used dragonfly nymphs, *Aeshna walkerii* (Aeshnidae, body length = 36.2 ± 2.8 mm, *n* = 12), as the predator, because *Ranatra* appeared to no longer prey on the largest warm-reared tadpoles. We transferred tadpoles from the control replicates to enclosures in the warmest and coldest streams. The differences in mean daily rearing temperature over the 10 weeks prior to the start of the trial and the mean exposure temperature during the predation trial ranged from −4.3 to +8.0°C. After 24 hr of acclimation, half of the replicates received one nymph of *Aeshna*. We checked enclosures at 3-day intervals and replaced predators if they died.

Our response variables were the proportion of surviving tadpoles in each enclosure, and the enclosure mean rates of growth. At the start and end of the predation trials, we measured tadpoles with dial callipers and weighed them to the nearest 0.001 g using an OHaus® portable electronic balance. We examined tadpoles with a 10× hand

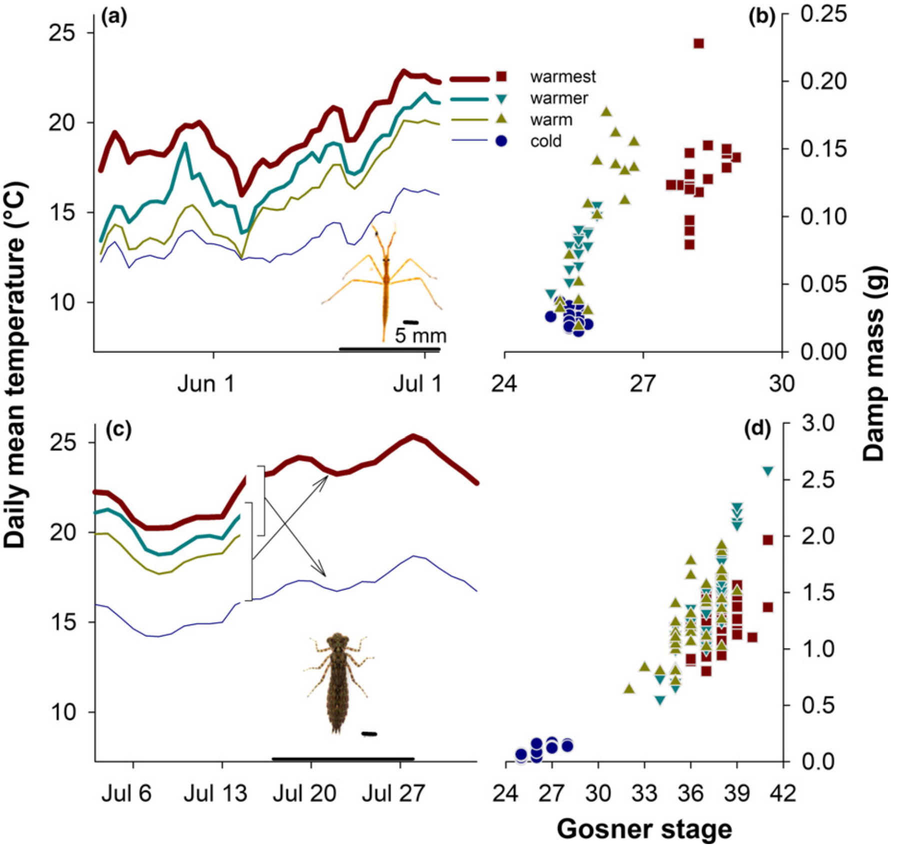

FIGURE 1 Water temperature at four stream sites where tadpoles of *Rana boylii* were reared and exposed to water scorpions (*Ranatra brevicollis*) in June (a) and design of reciprocal transplant predation experiment in July (c) when tadpoles reared at the four sites were exposed to dragonfly nymphs (*Aeshna walkerii*) in the warmest and coldest sites. Brackets and arrows indicate transplant design; symbols (b, d) indicate developmental stage and mass of tadpoles at the beginning of the predation trial periods (bold lines on x-axes a, c). Each thermograph line represents the mean of three sensors placed inside enclosures at each site. Insect photo credit: S. Pneh

lens to assess developmental stage (Gosner, 1960) and noted any tail damage. We calculated growth as a proportional increase in mass and length, the mg or mm gained per day per mg or mm at the start of the predation exposure period. For the *Ranatra* trial, two-way analysis of variance (ANOVA) tested the effects of temperature and predation. For the *Aeshna* trial, three-way ANOVA tested the added effect of rearing temperature. We also tested the effects of predation and temperature using linear mixed-effects models, with starting tadpole size (consequence of rearing temperature), exposure temperature and predator presence/absence as fixed effects, and experimental basket as a random effect, using the "lme4" package in R (R Development Core Team, 2015). We selected the best model predicting variation of survival on the basis of the lowest Akaike Information Criterion values corrected for sample size (AICc; Burnham & Anderson, 2002), change in AICc (ΔAICc) between the best candidate model and all other models, and the models' AIC weights (wAIC, higher weight indicates better model).

3 | RESULTS

3.1 | Assimilation

Temperature and food type influenced the digestive efficiency and growth of tadpoles (Figure 2; Table 1). Assimilation of organic content and growth rates were greatest at the warmest site, and were greater when tadpoles consumed the epiphytes from *Cladophora* filaments compared to periphyton attached to cobbles (Table 1). The per cent of organic content of material in the anterior small intestine was lowest at the warm site, especially for tadpoles receiving supplements of mats of *Cladophora* and its epiphyte flora (Figure 2c,d). Both food type and temperature influenced growth (Figure 2e,f). There was a significant interaction, however, in which the effect of temperature depended on the type of food; tadpoles eating epiphytised *Cladophora* at the intermediate temperature grew as much as the tadpoles eating the same diet at the warm site (Table 1). Growth was positively associated with the proportion of ash to total dry mass of ingested material in the small intestine (R = 0.49, $P = 0.006$, n = 30; Figure S1). We observed no internal anatomical differences among the six treatments in response to diet and temperature manipulations, as illustrated by the consistent relationship between tadpole size and gut length, which scaled at a rate of 10.97 ± 0.26 times body length ($F_{1,28} = 71.7$, $p \ll .001$, $R^2 = .72$; Figure S2).

TABLE 1 F_{df} statistics from two-factor ANOVAs for organic content of food (ash-free dry mass/total dry mass) in the anterior small intestine ($R^2 = .46$); assimilation efficiency ($R^2 = .91$); and mass increase in *Rana boylii* tadpoles ($R^2 = .68$) when reared on low- versus high-quality algal foods (epilithic periphyton on cobbles versus epiphytised *Cladophora glomerata*) at three different temperatures

Factor	Organic material anterior small intestine	Conover's index of assimilation efficiency	Mass Δ
Food	$1.78_{1,24}$	$115.2_{1,24}^{***}$	$2.23_{1,24}$
Temperature	$6.02_{2,24}^{**}$	$76.6_{2,24}^{*}$	$20.5_{2,24}^{***}$
Food × temperature	$0.85_{2,24}$	$1.19_{2,24}$	$3.65_{2,24}^{*}$

$^{*}p \le .05$; $^{**}p < .01$; $^{***}p < .001$.

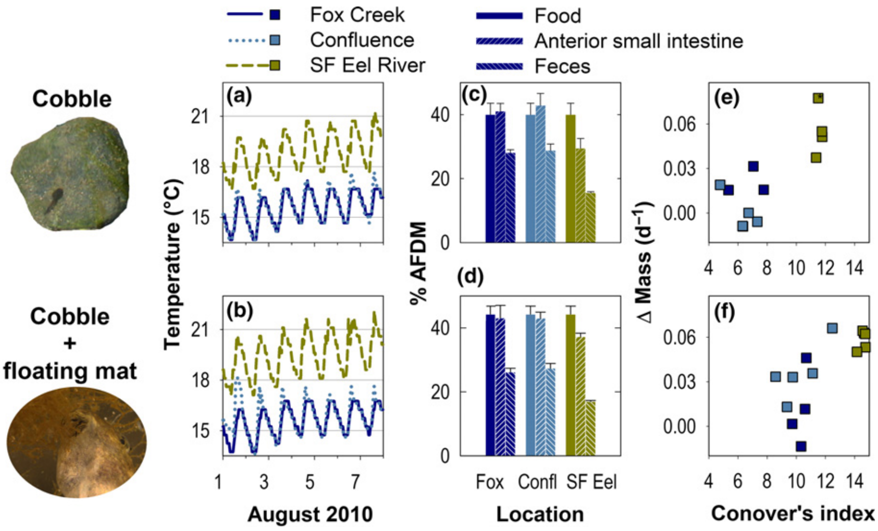

FIGURE 2 Water temperature (a, b) in stream enclosures of *Rana boylii* tadpoles grazing epilithic periphyton on river cobbles (top row), or a relatively higher quality diet consisting of periphyton plus floating mats of the green alga *Cladophora glomerata* epiphytised by diatoms (bottom row). Organic content (c, d) per cent ash-free dry mass of food (solid bars), anterior small intestine (right leaning diagonals) and faeces (left leaning diagonals). Conover's index of assimilation efficiency and growth of tadpoles (e, f). Treatment means covered by a horizontal line not significantly different in post hoc comparisons ($n = 30$, five replicates per treatment, mean ± 1 *SE*, asterisk indicates outlier). Tadpole photo credit: A. Catenazzi

3.2 | Predation

In June, *Ranatra* significantly decreased survival of tadpoles (Figure 3a; Tables 2 and 3), and larger tadpoles had greater survival than small tadpoles in the presence of this predator (Figure 3b). The ANOVAs indicate significant effects of temperature, in which tadpoles at the warmer sites had higher growth and survival, and a significant predator by exposure temperature interaction for growth. In the presence of *Ranatra*, tadpole growth was diminished at the two intermediate temperatures relative to no predator controls, but not at the coldest and warmest sites (Figures 3c and S3). For survival, the interaction was not significant. In our comparison of linear mixed-effects models, survival was best predicted by the interaction of predator presence and starting tadpole mass; exposure temperature was not predictive (Table 3).

In July, *Aeshna* affected survival of the smallest and least developed tadpoles that had been reared in the coolest study stream (Figure 4a; Tables 2 and 4). There was a significant interaction between rearing temperature and exposure temperature in the ANOVA (Table 2). The tadpoles which had been reared in Fox Creek (30-day running average prior to reciprocal transplant = 16.0°C) were small and relatively undeveloped compared to tadpoles from the other three sites (Figure 1d) and were vulnerable with 66.7% and 89.9% of tadpoles eaten when the mean temperatures of predator exposure were 17.2°C and 23.8°C, respectively. Post hoc comparisons indicate that predators only had a significant impact on cold-reared tadpoles with respect to mortality ($t = 2.1$, $p = .04$). However, in our comparison of linear mixed-effects models, survival was best predicted by the interaction of predator presence and starting tadpole length; exposure temperature was not predictive (Table 4).

We observed tail damage after exposure to *Aeshna*, but only in the cold treatment, where 23.1% of the tadpoles had injured or partially missing tails.

With respect to growth, the effect of *Aeshna* depended on whether size was measured in terms of tadpoles' body mass (Figures 4b and S4) or length (Figures 4c and S5), and on the difference between rearing and predator exposure temperatures. For change

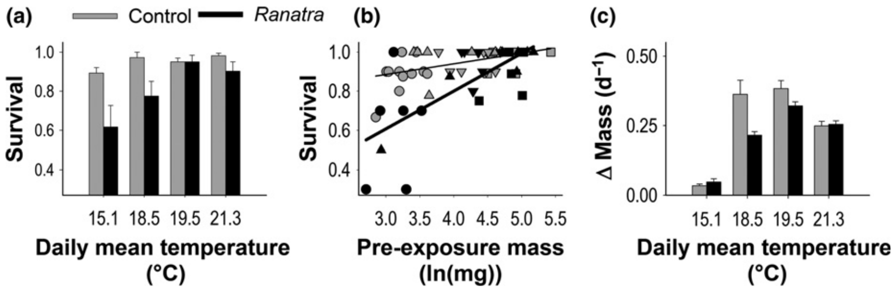

FIGURE 3 Survival (a, b) and size-specific growth rates or Δ Mass (c) of 8-week-old *Rana boylii* tadpoles in the presence or absence of water scorpions (*Ranatra brevicollis*) in relation to mean daily water temperature over the 2 weeks of predator exposure, and as a function of tadpole size ($n = 71$ enclosures of 10 tadpoles each; error bars = 1 *SE*). Δ Mass is the incremental mass (mg) gained per day per mg of starting mass

TABLE 2 Statistics for the effects of predators and water temperature on survival and growth of larval *Rana boylii*. Two-factor ANOVAs for survival and relative growth rate of tadpoles in June when exposed to water scorpions (*Ranatra brevicollis*) at four thermally distinct stream sites. Three-way ANOVAs for survival and relative growth rates in July after tadpoles exposed to dragonfly nymphs (*Aeshna walkerii*). *Ranatra*: $n_{\text{survival}} = 71$ enclosures, density = 10 tadpoles/enclosure, multiple $R^2 = .37$; and $n_{\text{growth}} = 68$ enclosures with surviving tadpoles, multiple $R^2 = .84$. *Aeshna*: $n_{\text{survival}} = 48$ enclosures, density = 3 tadpoles/enclosure, multiple $R^2 = .40$; and $n_{\text{growth}} = 45$ enclosures with surviving tadpoles, multiple $R^2 = .875$

	Ranatra		***Aeshna***		
Factor	**Survival**	**Mass Δ (mg day^{-1} mg^{-1})**	**Survival**	**Mass Δ (mg day^{-1} mg^{-1})**	**Body length Δ (mm day^{-1} mm^{-1})**
Predator	$13.2_{1,63}^{***}$	$5.1_{1,60}^{*}$	$11.4_{1,32}^{**}$	1.33	$35.3_{1,29}^{***}$
Temperature	$6.53_{3,63}^{***}$	$84.3_{3,60}^{***}$	$0.01_{1,32}$	$26.7_{1,29}^{***}$	$14.9_{1,29}^{***}$
Predator × temperature	$2.17_{3,63}^{***}$	$3.52_{3,60}^{*}$	$1.35_{1,32}$	$0.21_{1,29}$	$16.0_{1,29}^{***}$
Rearing temperature			$14.7_{3,32}^{***}$	$55.3_{3,29}^{***}$	$17.0_{3,29}^{***}$
Rearing temperature × predator			$15.5_{3,32}^{***}$	$1.62_{3,29}$	$1.81_{3,29}$
Rearing temperature × exposure temperature			$0.23_{3,32}$	$9.02_{3,29}^{***}$	$26.5_{3,29}^{***}$
Rearing temperature × predator × exposure temperature			$0.60_{3,32}$	$1.59_{3,29}$	$1.12_{3,29}$

$^{*}p \le .05$; $^{**}p < .01$; $^{***}p < .001$.

TABLE 3 AICc scores of linear mixed-effects models predicting survival as a function of starting tadpole mass (size), *Ranatra* predator presence/absence (predator) and water temperature (temperature), where *k* is the number of parameters, Δ(AICc) is the change in AICc with respect to the best candidate model (in bold), and w(AICc) is the AICc weight

Model variables	*k*	AICc	Δ(AICc)	w(AICc)
Predator × size	**4**	**337.97**	**0.00**	**0.39**
Predator × temperature	4	350.92	12.95	0.00
Size	4	351.66	13.68	0.00
Size + predator × size	5	337.97	0.00	0.39
Size + predator × temperature	5	344.13	6.16	0.02
Predator + temperature	5	347.21	9.23	0.00
Size + predator + temperature	6	340.40	2.43	0.11
Size + predator + temperature + predator × size	7	341.54	3.56	0.06
Size + predator + temperature + predator × temperature	7	344.13	6.16	0.02
Size + predator + temperature + predator × size + predator × temperature	8	345.62	7.65	0.01

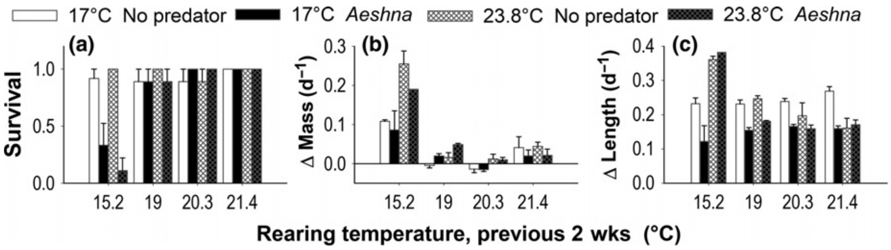

FIGURE 4 Dragonfly nymph (*Aeshna walkerii*) effect on survival (a) and growth in terms of mass, Δ Mass (b), and length, Δ Length (c) of 10-week-old *Rana boylii* tadpoles in relation to shift in thermal regime (daily mean temperature of predator exposure and rearing temperature). Δ Mass and Δ Length are the incremental mass (mg) and length (mm) gained per day per mg and mm of starting mass and length, respectively

TABLE 4 AICc scores of linear mixed-effects models predicting survival as a function of starting tadpole length (size), *Aeshna* predator presence/absence (predator) and water temperature (temperature), where *k* is the number of parameters, Δ(AICc) is the change in AICc with respect to the best candidate model (in bold), and w(AICc) is the AICc weight

Model variables	*k*	AICc	Δ(AICc)	w(AICc)
Predator × size	**4**	**77.30**	**0.00**	**0.33**
Size	4	85.72	8.42	0.00
Predator × temperature	4	102.83	25.53	0.00
Size + predator × size	5	77.30	0.00	0.33
Size + predator × temperature	5	86.97	9.68	0.00
Predator + temperature	5	101.42	24.13	0.00
Size + predator + temperature	6	85.13	7.83	0.01
Size + predator + temperature + predator × size	7	79.48	2.18	0.11
Size + predator + temperature + predator × size + predator × temperature	8	80.38	3.09	0.07
Size + predator + temperature + predator × temperature	7	86.97	9.68	0.00

in mass, there was a significant interaction between rearing temperature and exposure temperature, such that cold-reared tadpoles transferred to warmer water (+8°C) gained 2.4× more mass than tadpoles that stayed at the coolest site with no predators (+1.9°C). Predators dampened the compensatory growth response of cold-reared tadpoles transferred to warm water. Cold-reared tadpoles transferred to warm water gained only 1.7× more mass than tadpoles that stayed at the coolest site when predators were present. Tadpoles reared at the three warmer sites and then transferred to cool conditions (shifts of −1.8, −3.1 and −4.3°C) increased their body length without increasing their mass (Figure 4). There was a significant rearing temperature × exposure temperature interaction such that cold-reared tadpoles had significantly greater mass and length growth compared to tadpoles reared at the intermediate sites when exposed to warmer temperatures. There was also a significant predator × exposure temperature interaction: *Aeshna* presence consistently decreased body length growth rate at 17°C across all four groups of tadpoles, but not at 23.8°C.

4 | DISCUSSION

Our results show that water temperature affects tadpole digestive efficiency and growth, and thus influences vulnerability to predators. The finding that consumption by predators was a function of rearing temperature's influence on body size provides a plausible mechanism explaining the absence or low abundance of reproductive populations of foothill yellow-legged frogs downstream of dams that release cold water within otherwise occupied watersheds (Catenazzi & Kupferberg, 2017; Wheeler et al., 2015). In all our manipulations, cool temperatures impaired conversion of periphyton food to body tissue and tadpoles grew slowly to small sizes. The cold water and poor timing of pulsed flows associated with hypolimnetic releases from hydroelectric reservoirs have been shown to reduce survival and population growth of the foothill yellow-legged frog, and are likely drivers of the species' drastic decline across its distribution range (Catenazzi & Kupferberg, 2013; Kupferberg et al., 2012; Lind, Welsh, & Wilson, 1996).

In the assimilation experiment, tadpole growth was positively correlated with digestive efficiency and the positive effects of temperature on increased absorption of organic material occurred primarily in the anterior small intestine. The per cent organic content of material in the anterior small intestine at *c.* 19°C was significantly lower at the warm site compared to the cooler sites (Figure 4a). The nutritional quality of the ingested food also appears to have mediated the effect of temperature on digestive efficiency of the tadpoles. The improvement in efficiency from the cool to the warm treatment was more pronounced for tadpoles eating epilithic diatoms and green algae (6.6 ± 0.4% to 11.6 ± 0.1%) than those with access to highly nutritious floating mats of green algae epiphytised by *Epithemia* (10.1 ± 0.1% and 13.8 ± 0.1%). Diatoms of the genus *Epithemia*, which dominate the epiphyte flora in late summer at the Eel River (Furey et al., 2012), are rich in protein and lipids relative to other periphyton (Furey et al., 2014; Kupferberg et al., 1994). *Epithemia*-rich diets promote rapid growth and development of a wide variety of aquatic grazers including insects (Gresens, 1997; Power et al., 2009), snails (Blinn, Truitt, & Pickart, 1989) and tadpoles (Kupferberg, 1997). Our results suggest that when high-quality food is efficiently assimilated, it partially offsets the negative effect of cool temperature. Other freshwater herbivores fed low-quality diets have similarly shown increased assimilation efficiency with increasing temperature, but no change in efficiency when eating high-quality food (Benavides, Veloso, Jiménez, & Méndez, 2005; Calow, 1975). There may be little marginal benefit from the increased hydrolysis and absorption of nutrients at higher temperatures if the food is more easily broken down or higher in nutrients to begin with.

With respect to the lethal effects of predation, the small cold-reared tadpoles exposed to water scorpions and dragonfly nymphs had lower survival than larger tadpoles regardless of temperature at the time of predator exposure. This result is contrary to expectations based on short-term behavioural and modelling studies (Anderson, Kiesecker, Chivers, & Blaustein, 2001; Hayden et al., 2015) that survival might be low at higher temperatures because predator attack rates and capture success increase as tadpoles become more active in warm water. Possible explanations for greater survival of warm-reared individuals are that larger tadpoles have faster burst swimming speeds (Wilson & Franklin, 2000) and that warmer temperatures also promote faster swimming (Goldstein, Hoff, & Hillyard, 2017).

The sublethal effects of insect predators we observed, which are significantly diminished tadpole growth and injured tails, occurred predominantly at lower temperatures, a result which could further explain the gap between the lower limit of the fundamental and realised thermal niche of foothill yellow-legged frogs (Catenazzi & Kupferberg, 2017). Non-consumptive fear effects of predators on the foraging behaviour and physiology of prey can shape prey population dynamics (Preisser, Bolnick, & Benard, 2005; Zanette, Clinchy, & Suraci, 2014) and could contribute to small population sizes where temperatures are low, but still within the range of tolerance. While defensive responses such as decreasing overall activity and spending less time foraging help prey evade detection and reduce encounters with predators, these behaviours have physiological costs (Relyea & Werner, 1999; Skelly, 1994). Contrary to the expectation that the cost to prey of hiding and consuming less food might be greater in a warm environment relative to a cool one because basal metabolic requirements are higher (Niehaus, Wilson, Seebacher, & Franklin, 2011), we found that the cost of not foraging was amplified under cool conditions. Digestive efficiency generally declines as temperature decreases (Altig & McDearman, 1975; McConnachie & Alexander, 2004; Nicieza, Reiriz, & Braña, 1994), so that in our experiment what little food the tadpoles may have ingested was not readily assimilated.

Based on a thermal monitoring study of regulated and free-flowing rivers across northern California conducted concurrently with these experiments (Catenazzi & Kupferberg, 2017), the temperature treatments we employed are ecologically relevant for understanding the effects of cooling from hypolimnetic dam releases or warming from climate change. Transferring tadpoles among warm and cool sites is relevant because flow regulation by dams increases variability in temperature at short time scales within the biologically active summer season (Steel & Lange, 2007). In particular, the treatments in which tadpoles went from the colder streams to the warmest site mimic the thermal regime of some dammed rivers in California with hypolimnetic releases where water does not warm until very late in the summer when flow volumes are low. To the extent that tadpoles need to grow rapidly early in the summer to evade predators, the warming comes so long after the egg-laying period that a substantial portion of the cohort may have already been consumed. When thermal regimes are not in synchrony with the physiological requirements of a species' early life stages, recruitment bottlenecks can thus occur (Coleman & Fausch, 2007; Humphries, Richardson, Wilson, & Ellison, 2013; Schiemer et al., 2002). Although our experiments demonstrate that tadpoles can compensate for early slow growth if temperature conditions improve, the late summer shift from cold to warm temperatures observed downstream of some dams could still be insufficient for tadpoles to reach metamorphosis. Even if they did avoid predation, a lack of time before the onset of the next rainy season's high flows could prevent their timely migration from flood-prone mainstems to tributaries and other off-channel waterbodies.

Thermal variation in the opposite direction from warm to cold water may also be detrimental. Theory and experiments with aquatic invertebrate larvae predict that fast-growing individuals may not cope as well as slower growers when facing suboptimal temperatures (Gotthard, 2001). For example, fast-growing damsel fly nymphs have lower levels of stress proteins that improve survival and confer cold resistance (Stoks & De Block, 2011). Furthermore, fluctuating flows and cool water releases from dams cause shifts in attached algal assemblages towards mucilaginous species that are difficult to digest (Furey et al., 2014). Our experiment showed that nutritious algal food promotes digestive efficiency and tadpole growth, thus decreasing vulnerability to predation, but this compensatory effect might not occur in thermally impaired rivers, where inedible or toxic algae are more common under warm conditions (Power et al., 2015).

Although the United States is currently experiencing an era of dam removal (O'Connor, Duda, & Grant, 2015), the need to replace fossil fuels for producing electricity is accelerating dam construction in biodiverse basins such as the Amazon, Congo and Mekong (Kano et al., 2016; Van Vliet et al., 2016; Winemiller et al., 2016). Collectively, these planned projects will decrease by 21% the number of rivers on earth that remain free-flowing (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2014). When we consider the influence of dams in the context of extreme climatic events, like heat waves and droughts, we expect that an ever-growing portion of biodiversity in running waters will be exposed to altered thermal environments (Ledger & Milner, 2015). Dams and diversions will substantially alter water temperature through prolonged hypolimnetic releases that markedly decrease summer water temperatures (Lugg, 1999; Todd, Ryan, Nicol, & Bearlin, 2005), pulsed releases that accentuate diurnal variability (Schülting, Feld, & Graf, 2016; Zolezzi, Siviglia, Toffolon, & Maiolini, 2011) and low baseflows that allow rapid heat exchange with air and raise temperatures (Arora, Tockner, & Venohr, 2016; Van Vliet et al., 2011).

To balance the needs of aquatic organisms and humans when managing rivers, there is a growing understanding that the thermal regime has an influence comparable to that of the flow regime on the ecological integrity of riverine ecosystems (Arthington, Naiman, McClain, & Nilsson, 2010; Olden & Naiman, 2010). Here we have extended to amphibians findings well documented for fish that ecological mismatches occur when shifts from cold to warm temperatures increase predation on small individuals that experienced poor growth due to low food assimilation (Marine & Cech, 2004; Sylvester, 1972). When shifts from warm to cool conditions prevent life cycle completion, recruitment bottlenecks are likely (Coleman & Fausch, 2007; Humphries et al., 2013; Schiemer et al., 2002). Our findings specific to the foothill yellow-legged frog will be valuable to the adaptive management of California's regulated rivers now that this species is a candidate for protection under the state's Endangered Species Act. Our approach of using small-scale experiments to elucidate the mechanisms underlying the effects of thermal change is applicable to any region where amphibians breed in rivers and where dams might disrupt the natural progression of temporal changes in temperature or the community composition of small and cryptic algae that are so vital to freshwater food webs (Vadeboncoeur & Power, 2017).

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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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