Water Velocity Tolerance in Tadpoles of the Foothill Yellow-legged Frog (*Rana boylii*): Swimming Performance, Growth, and Survival

Sarah J. Kupferberg[1], Amy J. Lind[2], Vanessa Thill[3], and Sarah M. Yarnell[4]

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We explored the effects of large magnitude flow fluctuations in rivers with dams, commonly referred to as pulsed flows, on tadpoles of the lotic-breeding Foothill Yellow-legged Frog, *Rana boylii*. We quantified the velocity conditions in habitats occupied by tadpoles and then conducted experiments to assess the tolerance to values at the upper limit of, and outside, the natural range. In laboratory flumes and field enclosures we mimicked the velocities observed during pulsed flows. In all experimental venues, the behavioral response of tadpoles was to seek refuge in the channel substrate when velocity increased. In a large laboratory flume, tadpoles moved freely at low water velocities (0–2 cm·s^{-1}) and then sheltered among rocks when velocity increased. In a smaller scale laboratory flume, the median critical velocity was 20.1 cm·s^{-1}. Critical velocity varied inversely with tadpole size, developmental stage, and proportion of time spent swimming. Velocities as low as 10 cm·s^{-1} caused tadpoles approaching metamorphosis to be displaced. In field mesocosm experiments, tadpoles exposed to repeated sub-critical velocity stress (5–10 cm·s^{-1}) grew significantly less and experienced greater predation than tadpoles reared at ambient velocities. Responses to velocity manipulations were consistent among tadpoles from geographically distinct populations representing the three identified clades within *R. boylii*. The velocities associated with negative effects in these trials are less than typical velocity increases in near shore habitats when recreational flows for white water boating or peaking releases for hydroelectric power generation occur.

BREEDING at the right time of year, in synchrony with benign physical conditions and abundant food resources, is a critical component of reproductive success across diverse taxa and environments, whether terrestrial, freshwater, or marine (Lack, 1968; Milton and Arthington, 1983; Cushing, 1990; Van Noordwijk and Müller, 1994). Synchrony is especially crucial for organisms living in highly variable environments such as rivers, where recruitment depends on the ability to avoid flood induced mortality of early life stages (Humphries and Lake, 2000; Fausch et al., 2001; Pusey et al., 2001). When rivers are regulated by dams, populations are threatened if there is a mismatch between the timing, magnitude, duration, and frequency of large floods and the life cycles of native biota (Marchetti and Moyle, 2001; Propst et al., 2008; Yarnell et al., 2010). Mismatched timing as a risk factor is understudied compared to flow magnitude (Poff and Zimmerman, 2010), despite its relevance for riverine organisms whose flow regime adaptations evolved in climates where there is a high degree of seasonal predictability in the timing of flooding (Gasith and Resh, 1999; Lytle and Poff, 2004).

Hydrologic alteration generally threatens a wide array of taxa (Richter et al., 1997; Rosenberg et al., 2000; Bunn and Arthington, 2002), but the taxonomic focus of investigation for studying flow regime effects has not often included amphibians (Poff and Zimmerman, 2010). With growing awareness of global amphibian declines (Wake and Vredenburg, 2008) and local legal protections (Jennings and Hayes, 1994; California Department of Fish and Game, 2004), amphibians are now receiving attention during the relicensing of hydroelectric projects in California by FERC, the Federal Energy Regulatory Commission (Kupferberg et al., 2009), creating a need to understand how amphibians respond to altered conditions. In unregulated rivers in

California, amphibians normally experience slowly declining discharge over the course of the larval period (Fig. 1, Alameda Creek, 37.498°N, 121.773°W, and South Fork Eel River 39.719°N, 123.652°W). Example hydrographs from 2005 (a year with relatively high winter and spring precipitation and flow levels; Fig. 1) illustrate that depending on dam operations, discharge can be static (North Fork Feather River below Poe Dam, 39.794°N, 121.451°W), fluctuate daily for generating power to meet peak demands (Middle Fork American River, 39.006°N, 120.760°W), fluctuate at monthly intervals for recreational boating (North Fork Feather River below Cresta Dam 39.853°N, 121.391°W), or fluctuate sporadically due to reservoir spills (San Joaquin River below Redinger Lake Dam, 37.144°N, 119.454°W). When decision makers at utilities and regulatory agencies evaluate flow regimes like these, they confront a gap in understanding whether amphibians, especially early life stages, can thrive under such conditions.

The purpose of this investigation was to quantify the response of a representative larval amphibian to water velocity fluctuations and thus predict potential consequences of unnaturally timed, i.e., aseasonal, pulsed flows. Many amphibian species breed along the margins of California's regulated waterways including newts (e.g., *Taricha torosa*, *T. granulosa*, *T. sierrae*) and anurans (e.g., Western Toads, *Bufo boreas*; California Red-legged Frogs, *Rana draytonii*; Pacific Chorus Frogs, *Pseudacris regilla*), but we focused on the Foothill Yellow-legged Frog, *Rana boylii*, because it breeds exclusively in flowing waters while other taxa primarily use lentic habitats. There are over 800 dams within the historic geographic range of *R. boylii*, and it has disappeared from over 50% of known historic sites (Davidson et al., 2002; Lind, 2005). To evade flood mortality, the life cycle of *R. boylii* matches the seasonality of runoff during the predict-

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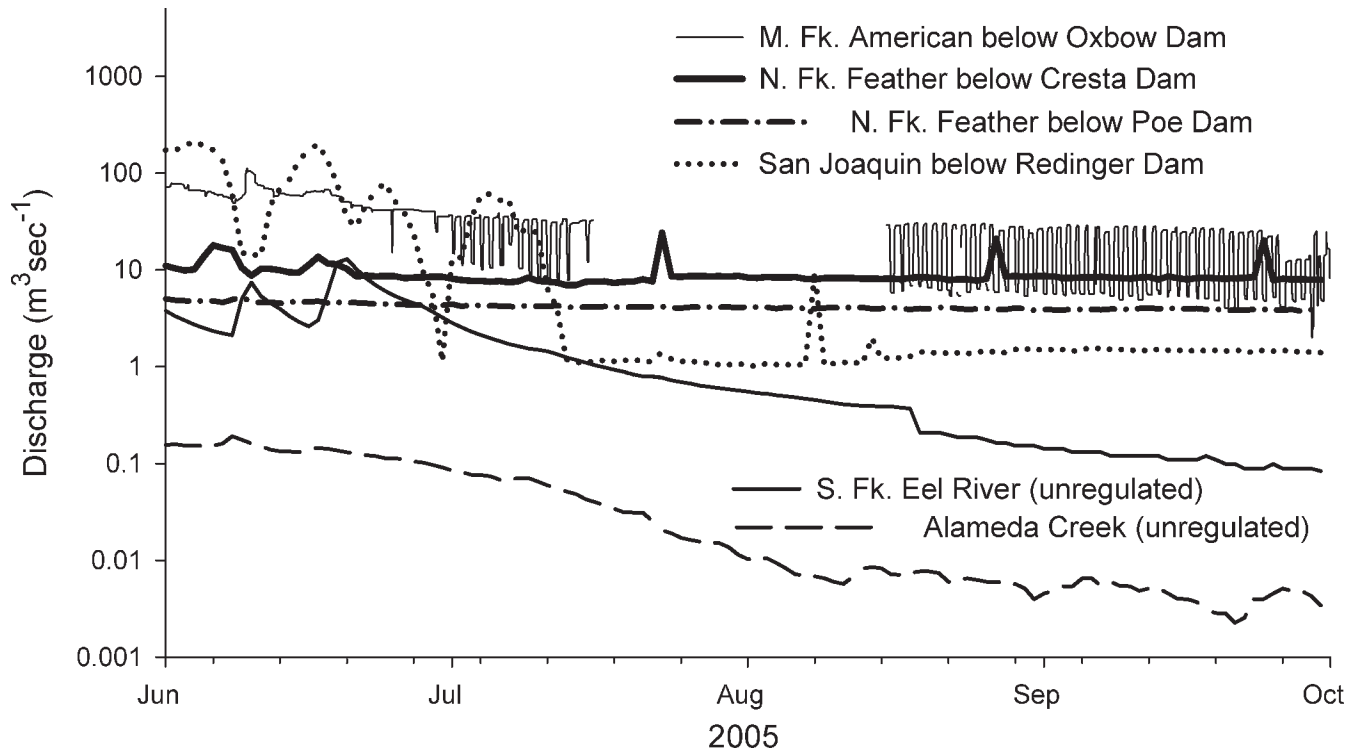[2] USDA Forest Service, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, California 95618; E-mail: alind@fs.fed.us.
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Fig. 1. Discharge during the summer of 2005 depicts the range of flow conditions experienced by eggs and tadpoles of *Rana boylii*, the Foothill Yellow-legged Frog in six California locations. For the Middle Fork American River, the data gap indicates equipment failure.

able cycle of wet winters and dry summers across its range in California and Oregon, USA (Kupferberg, 1996; Lind, 2005). Juvenile and adult frogs move throughout drainage networks (Bourque, 2008) and spend the rainy season in flood refugia such as tributaries, springs, and seeps (Nussbaum et al., 1983; Jones et al., 2005; Rombough, 2006). In spring, adults migrate to breeding sites (Wheeler and Welsh, 2008). Clutches of eggs are attached to rocks after peak spring runoff in shallow slow channel margins and are vulnerable to ill-timed dam releases (Lind et al., 1996). Tadpoles hatch as discharge declines and reach metamorphosis prior to the onset of the next rainy season. To determine the consequences of perturbations to the timing of discharge fluctuation to tadpoles, we quantified the typical velocity conditions they experience and conducted eight related laboratory and field experiments. We explored three focal questions: How do tadpoles of *R. boylii* behave when faced with velocity fluctuation? What factors determine their ability to maintain position in the stream channel? What are the effects of repeated exposure to increased water velocity on growth and survival?

MATERIALS AND METHODS

Study sites and flow conditions for tadpoles.—We assessed the velocity conditions experienced by tadpoles at locations representing three geographic regions and genetically distinct clades identified within the species (Lind et al., 2011). We compiled measurements made by the authors during spring spawning and summer quadrat surveys conducted at two free-flowing sites: South Fork Eel River representing the North Coast (SF Eel, University of California, Angelo Coast Range Reserve, Mendocino Co.) and Alameda Creek of the Central Coast (East Bay Regional Park, Alameda Co.). Data from a

population in the Sierra Nevada on the North Fork Feather River (NF Feather, downstream of Poe Dam, Plumas Co.) were collected by Pacific Gas and Electric Company and garnered from a report filed with FERC (Garcia and Associates, 2004). Current velocity conditions at frog breeding sites during manufactured pulse flows were also collected by Pacific Gas and Electric Company downstream of Cresta Dam (Garcia and Associates, 2005; J. Drennan, pers. comm.). See Table 1 for site and sampling details.

Open river relocation (Expt. I).—To assess the feasibility of observing responses of tadpoles to velocity in natural settings, relocation trials were conducted at the SF Eel in June 2005. We moved individual tadpoles ($n = 14$) 1–2 m away from shore to velocities of 5–10 cm·s^{-1}. Tadpoles had five minutes to acclimate by having a flow-through plastic container (8.5 cm diameter with 1 mm mesh windows) inverted over them. After removing the shelter, we observed tadpoles with mask and snorkel for as long as possible. As a control, tadpoles ($n = 5$) were released at point of origin, then observed. Tadpoles were between Gosner (1960) stages 27–31, 12–15 mm SUL. Response categories were: returns to shore, is swept away, or finds interstitial refuge. The snorkeler measured time with a stopwatch and placed a white marble on the stream bed to mark the location where tadpoles found refuge or were swept into currents too swift to maintain visual contact. Distance from origin to each marker was measured with a meter tape.

Artificial stream (Expt. II).—We assessed response under more controlled conditions by manipulating velocity and substrate in a large raised rectangular doughnut-shaped tank at the USDA Forest Service, Redwood Sciences Lab, Arcata, CA (Fig. 2A). By engaging different arrays of re-circulating

Table 1. Characteristics and Data Sources for the Example River Systems where Foothill Yellow-legged Frogs (*Rana boylii*) Occur in California. Sample sizes and years indicate egg mass and quadrat surveys documenting velocity conditions of occupied habitat.

River	USGS gage station[a]	Latitude and longitude	Regulation	Drainage area (km²)	Mean ± 1 SD annual discharge[b] (m³·sec⁻¹)	Velocity conditions year (# egg masses, # tadpole quadrats)
San Joaquin	11242000	37.144°N, 119.454°W	Redinger Lake Dam	3354	16.34 ± 20.7	
MF American	11433300	39.006°N, 120.760°W	Oxbow Dam	1357	33.2 ± 20.1	
NF Feather	11404330	39.853°N, 121.391°W	Cresta Dam	4976	22.5 ± 25.6	
	11404500	39.794°N, 121.451°W	Poe Dam	5078	25.9 ± 27.4	2003 (56, 57)
SF Eel	11475500[c]	39.719°N, 123.652°W	none	114	4.88 ± 1.70	1991–1994, 2005 (172, 277)
Alameda	11172945	37.498°N, 121.773°W	none	88	0.77 ± 0.42	2006, 2009 (22, 102)

[a] Data accessible from http://cdec.water.ca.gov/riv_flows.html and http://waterdata.usgs.gov.
[b] Based on the following years of record: San Joaquin, 1980–2006; MF American, 1980–2006; NF Feather Poe, 1980–2006, Cresta, 1986–2006; SF Eel, 1946–1970 and 1991–2006; Alameda, above diversion 1995–2006.
[c] Branscomb gage USGS 1946–1970, re-established by Dietrich and Power 4/1990, US Forest Service 2004.

pumps, we created three distinct levels of velocity (cm·s⁻¹): $V_1 = 0.95 ± 0.15$, $V_2 = 6.20 ± 0.50$, $V_3 = 17.00 ± 0.70$. Variation around these means and all others reported henceforth are ± 1 SE, unless otherwise noted. Means were calculated from uniform grids of measurements taken with electronic flow meters (Marsh-McBirney, Flo-mate, Hach Company, Frederick, MD) during calibration flows and at a fixed probe during five replicate trials (Table 2). Observers stood inside the rectangle watching tadpoles in the tank at eye level.

To evaluate the importance of interstitial flow refugia, we constructed two shallow (0.2 m) cobble beds (habitat patches) by placing 55 rocks (median size = 0.11 m) on top of, or within, a foam pad (2.65 by 0.75 m). Each pad was placed on a frame to create a false bottom and a transition to a deeper pool (0.8 m). Foam was used because sediment would damage the pumps. For one bed, we mimicked the armoring of the river bed that is sometimes observed downstream of dams by recessing each rock into the foam. These "embedded" rocks lost 53.3 ± 1.4% of their height as compared to their height on a solid surface, while the "un-embedded" rocks on the other pad lost 12.3 ± 1%. The difficulty of moving the rocks and the wet foam pads precluded alternating patch position. Tadpoles between Gosner stages 28 and 38 (57% at stage 35) were captured at the SF Eel and acclimated in large holding tanks at the site of the artificial stream for 48 hours prior to experimental trials. Tadpoles were fed *ad libitum* floating mats of the filamentous green alga *Cladophora glomerata* with a heavy growth of epiphytic diatoms collected from the SF Eel. Swimming trials consisted of three 20-min velocity intervals with groups of 20 tadpoles randomly assigned to embeddedness treatment. Trials were conducted under constant bright artificial lights to compensate for variation in start
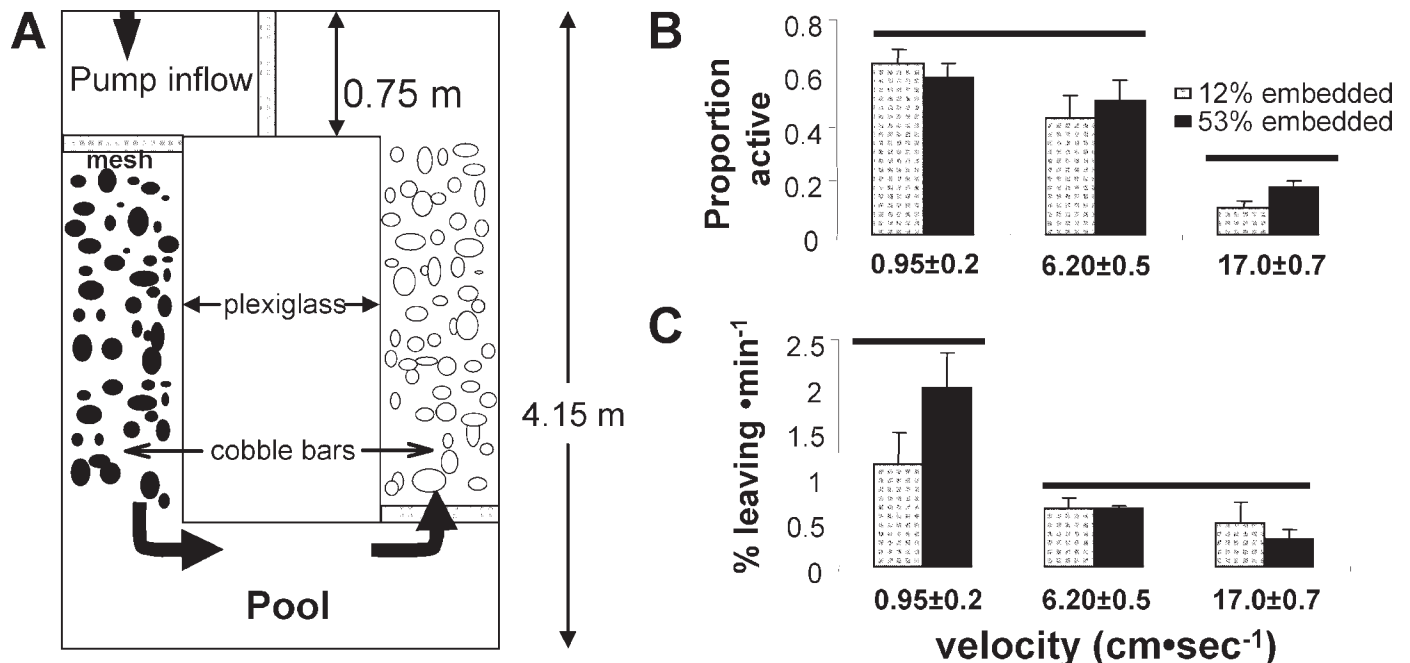
Fig. 2. Schematic diagram (A) of a rectangular re-circulating flume where the ability to withstand elevated flow velocities by tadpoles of *Rana boylii* was tested (Expt. II). Rocks, not drawn to scale, were embedded (black ellipses) or un-embedded (white ellipses) in a foam bed. Arrows indicate direction of current. Behavioral responses are activity (B) and emigration (C) from the simulated cobble bars to the downstream pools.

Table 2. Variation in Mid-Column Velocity (cm·s^{-1}) through Space and Time Created by Different Pump Arrays in an Artificial Stream Channel. Spatial variation was measured during calibration flows and temporal variation measured during trials from a mounted probe.

Substrate	Spatial variation ($n = 12$)		Temporal variation ($n = 20$)	
Pump configuration	Mean ± SE	Range	Mean ± SE	Range
Un-Embedded (away from pumps)	approx. 1	0–2	0.95 ± 0.15	0–2
V_1 = filter only				
V_2 = filter + chiller, valve 2/3 open	4.8 ± 0.27	4–6	6.20 ± 0.50	3–10
V_3 = filter + chiller + small pump	19.0 ± 0.92	13–23	17.00 ± 0.70	16–22
Embedded (near pumps)	approx. 1	0–2		
V_1 = filter only				
V_2 = filter + chiller, valve 2/3 open	4.4 ± 0.6	0–8		
V_3 = filter + chiller + small pump	17.0 ± 1.7	0–26		

times (1530 and 2030 h on 12 August 2005; 1000, 1330, and 1600 h on 13 August 2005) which could be problematic as some tadpoles change swimming behavior in response to time of day (Warkentin, 1992) and illumination (Beiswinger, 1977; Jamieson and Roberts, 2000).

Response variables were emigration from test patches, monitored continuously; and activity level, assessed every five min. Emigration rate was calculated as the slope of number of individuals leaving vs. time using least squares regression. Activity level was calculated as the proportion of remaining tadpoles that were swimming or moving. Treatment effects were assessed with repeated measures analysis of variance using Systat 11 (Systat Software, Inc., Chicago, IL; http://www.systat.com), and activity data were subjected to the angular transformation (Sokal and Rohlf, 1981).

Brett chamber (Expts. III–V).—To more narrowly quantify the velocity tolerances of tadpoles, we used a small scale Brett-type (Brett, 1964), re-circulating swimming flume (9.1 cm diameter × 24 cm) at the Center for Aquatic Biology and Aquaculture, University of California, Davis. Two sets of trials included small cobbles and pebbles (Expts. III, IV) while Expt. V focused on stamina without flow refugia. Experiments consisted of replicate trials with individual tadpoles (III: $n = 57$, IV: $n = 13$, V: $n = 8$) conducted between 0930 and 2100 h during August 2006. We collected tadpoles across a range of developmental stages from the three populations noted above. Tadpoles were held in 155-liter tanks under a natural photoperiod, grazed periphyton from rocks gathered at their natal streams, and were provided with *ad libitum* supplements of dried *Spirulina*. Post-trial, we measured body length and height, tail length and height (mm), weight (mg), and stage. In Expt. III, all tadpoles swam 2–4 days after collection. In Expt. IV, Alameda Ck. (Central Coast) tadpoles held in the laboratory for four weeks swam a second time. These tadpoles had grown, but did not increase in Gosner stage, probably because the temperature at which they were held ($\leq 18°C$) hindered development as occurs in other larval anurans (Smith-Gill and Berven, 1979; Hayes et al., 1993). To separate developmental constraints from the effects of body size alone, we compared the performance of these tadpoles to similarly staged, but significantly smaller, Feather River (Sierran) tadpoles (held one week and also swimming for a second time). In Expt. V, we tested the response to velocity increases without substrate refugia, and a random set of tadpoles swam for a second time, 7–9 days after their first trial.

In the trial protocol, tadpoles acclimated for five minutes at zero cm·s^{-1}, then velocity was increased every five minutes. When the tadpole collided against the mesh at the downstream end of the tube and could not free itself, velocity was returned to zero. After a two-minute rest, the trial continued, with a return to that velocity. The trial stopped when the tadpole impinged on the mesh a second time. Critical velocity, U_{crit}, was calculated using the equation: $U_{crit} = U_i + [U_{ij}(T_j \cdot T_i^{-1})]$. The highest velocity maintained is U_i, and U_{ij} is the incremental increase from U_i to the fatigue velocity, U_j. The mean increase in velocity for each time step was 3.3 ± 0.2 cm·s^{-1}. T_j is the time elapsed at the fatigue velocity, and T_i is the five-minute interval between one velocity and the next higher increment. In Expt. V, after acclimation, velocity was set at 5 cm·s^{-1}, and the duration of time in which tadpoles could maintain position was monitored. To reduce disturbance to tadpoles, we observed them remotely on a video monitor via a camera mounted behind a screen surrounding the Brett chamber. To make accurate time budgets and quantify the percent of time tadpoles spent swimming in Expt. III, we reviewed video recordings of a subset of 12 size and stage matched individuals (four each at 12 mm SUL, stage 30; 18 mm, stage 35; and 23 mm, stage 41).

Analysis of covariance was used to assess the effects of source population on U_{crit}. The size covariate was ln(body mass) because it was highly correlated with other measures of size and development (body length r = 0.94, tail length r = 0.92, and Gosner stage r = 0.87). To assess diel patterns in performance, as some species of tadpoles have diel shifts in habitat use (Warkentin, 1992; Hampton and Duggan, 2003), we also calculated correlations between trial start time and U_{crit}. For Expt. IV, we compared U_{crit} of the two different size groups with a t-test. We also evaluated the correlation between U_{crit} and tail area in proportion to body mass, using tail height and length in the formula for area of an ellipse. Because tadpoles create thrust with their tails (Wassersug and Hoff, 1985), we hypothesized that having a small tail relative to the total mass that must be propelled forward against the current would be a disadvantage.

Mesocosms in rivers (Expts. VI–VIII).—To evaluate the cumulative impact of interstitial refuge use, we raised tadpoles in plastic laundry baskets (40 × 60 cm) with 1 mm fiberglass mesh glued over the openings, placed in different velocity environments. Pulses of velocity stress were imposed at weekly intervals by capitalizing on the natural tendency of mesh to be covered with debris and flows to decline. After
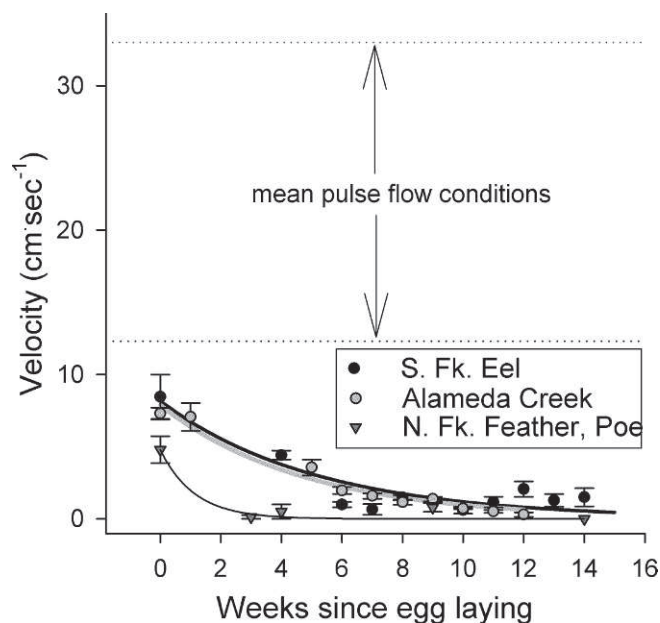
Fig. 3. Flow conditions measured at Foothill Yellow-legged Frog, *Rana boylii*, egg masses and tadpoles in three California rivers. Exponential declines in velocity curves r^2 values: the unregulated South Fork Eel River = 0.64, a free-flowing reach of Alameda Creek = 0.96, North Fork Feather River downstream of Poe Dam = 0.95. Horizontal reference lines indicate the range of mean velocities measured at breeding sites in the Feather River downstream of Cresta Dam during pulsed flows (17–35.4 $m^3 \cdot sec^{-1}$) above base discharge = 7 $m^3 \cdot sec^{-1}$.

the first 24 hours, velocity in the elevated treatments decreased an average of 54.5 ± 5%. Cleaning mesh and relocating baskets closer to the thalweg at weekly intervals re-imposed the disturbance. This manipulation was not intended to mimic any particular regulated river, but is justified in that some flow alterations occur over extended periods or repeatedly in watersheds where *R. boylii* occurs (Fig. 1), and weekly interval recreational flows are under consideration in some rivers, such as the San Joaquin downstream of Redinger Lake Dam.

Expt. VI focused on growth. At three weeks of age full-sibling tadpoles at the SF Eel (hatched on 15 June 2005) were divided among 12 replicates, 15 per enclosure. Baskets were randomly assigned to two treatments: low (1.7 ± 0.3 $cm \cdot s^{-1}$) or once weekly velocity stress (8.8 ± 0.6 $cm \cdot s^{-1}$). Tadpoles grazed rocks (changed weekly) with turfs of the filamentous green alga *Cladophora glomerata* epiphytized by diatoms including *Epithemia*, *Cocconeis*, and *Gomphonema* spp., and received supplements of copious loose mats of epiphytized *Cladophora*. In each basket, temperature was measured hourly, with 0.5°C precision (iButton, Maxim Integrated Products, Sunnyvale, CA). Response variables were tadpole length (mm), weight (g), and developmental stage after six weeks, with data pooled to calculate means for each replicate. Treatment effects and temperatures were com-

pared using t-tests with Bonferroni adjustments (significance at $P < 0.0125$ for an experimentwise $\alpha = 0.05$).

Experiments VII and VIII focused primarily on survival. For experiment VII, in Alameda Ck. on 12 May 2006, 25 full-sibling recently hatched tadpoles were placed in each of 15 replicates deployed across a flow range of 1–13 $cm \cdot s^{-1}$. The effect of velocity on survival after two weeks was assessed using linear regression. Experiment VIII, also conducted in Alameda Ck., assessed whether velocity stress altered the risk of predation. Enclosures containing 15 three-week-old full-sibling tadpoles were deployed at ambient (1.2 ± 0.1 $cm \cdot s^{-1}$, $n = 10$) or elevated velocity (9.1 ± 0.3 $cm \cdot s^{-1}$, $n = 12$). Predators were added to half of the enclosures. The predation treatment reflected the phenological shifts in size-specific vulnerability to benthic macroinvertebrates common at the site. Megalopteran alder fly larvae (*Sialis* sp.), one per enclosure, were added initially. When tadpoles outgrew susceptibility, the predators were switched to dragonfly nymphs (*Aeshna* sp.). When there was tail injury, but little new mortality, we concluded the experiment. Predator and velocity effects on survival were tested with repeated measures ANOVA, treating the presence vs. absence of a predator and velocity as fixed factors. For growth as the response to velocity, ANCOVA was used with tadpole density (which varied due to presence and effectiveness of predators) as the covariate.

RESULTS

Ambient flow conditions for tadpoles.—Among the three focal rivers, mean mid-column water velocities ranged from 4.8–8.5 $cm \cdot sec^{-1}$ at oviposition down to 0–2.1 $cm \cdot sec^{-1}$ by late summer near the time of metamorphosis (Fig. 3). Once tadpoles hatch, approximately two weeks after oviposition, they experience an exponential decay in ambient velocity as discharge declines over the course of the summer months.

Open river relocation (Expt. I).—No relocated tadpoles successfully returned to the low velocity environment near shore (Table 3), whereas all control tadpoles stayed close to shore. Most swimming occurred within a few cm of the rocky bottom, within a boundary layer of low water velocity, and tadpoles were swept downstream if they entered the water column. Twenty-one percent found shelter in the interstices among rocks in faster water, but the rest were swept away. Prolonged observations of tadpoles once caught in the current were not feasible (average distance of feasible observation = 0.95 ± 0.2 m) due to their small size and cryptic coloration. These observations indicated the need for the controlled experiments which follow, but provided a useful reference for assessing the realism of behavior in artificial settings.

Artificial stream (Expt. II).—The main behavioral response we observed was that tadpoles sheltered in low velocity refugia, decreasing activity levels as velocity increased (Table 4, Fig. 2B). At low velocity (V_1, 0–2 $cm \cdot s^{-1}$), tadpoles swam

Table 3. Results of Field Relocation Trials when *Rana boylii* Tadpoles Were Moved 1–2 m from Shore to Patches where Velocity Was 10 $cm \cdot s^{-1}$.

Final location of larvae	% ($n = 14$)	displacement (m) (mean ± 1SE)	time (min) (mean ± 1SE)
Swept away/disappears	78.6	0.94 ± 1.0	8.8 ± 2.4
Finds interstitial refuge	21.4	1 ± 0.4	7.7 ± 2.4

Table 4. Repeated Measures Analyses of (A) Rates of Emigration by *Rana boylii* Tadpoles from Simulated Cobble Bar Habitat Patches to Pools and (B) the Proportion of Tadpoles Active when Mean Flow Velocity (± 1 SE) Was Increased in a Step-wise Fashion over Three Time Periods in an Artificial Stream Channel from $V_1 = 0.95 \pm 0.15$, to $V_2 = 6.20 \pm 0.50$, and $V_3 = 17.00 \pm 0.70$ cm·sec^{-1} (Expt. II).

Response variable	Wilks' λ	F	df	P
(A) Rate of emigration from test patch (% of tadpoles leaving per minute in velocity time periods 1, 2, and 3)				
Velocity	0.30	8.13	2,7	0.015
Velocity × Substrate Embeddedness	1.39	1.76	2,7	0.24
Substrate Embeddedness	*	1.286	1	0.29
B) Proportion of tadpoles active (arcsin $\sqrt{\%}$)				
Velocity	0.09	36.8	2,7	<0.001
Velocity × Substrate Embeddedness	0.74	1.2	2,7	0.36
Substrate Embeddedness	*	0.94	1,8	0.36

* The tests of substrate as a source of variation are univariate ANOVAs and use emigration rate and proportion active values totaled across velocity time periods 1, 2, and 3.

throughout the artificial stream and some swam into the pools. At the moment pumps were switched on (V_2, 3–10 cm·s^{-1}) tadpoles briefly swam against the current, then sank or swam to the bottom. As velocity increased from V_2 to V_3 (13–23 cm·s^{-1}) tadpoles sought refuge behind rocks and in crevices, with a significant decrease in activity ($P < 0.001$). With respect to emigration from the habitat patches to the downstream pools (Fig. 2C), fewer tadpoles left at V_2 and V_3 compared to V_1 (Bonferroni adjusted P-values for emigration rate at V_1 vs. V_2 = 0.017, V_1 vs. V_3 = 0.008, V_2 vs. V_3 = 0.66). Tadpole behavior followed a common sequence at V_2 and V_3. Initially, tadpoles swam against the current with a short burst of activity (up to a few seconds), then stopped tail movements, drifted horizontally downstream for several seconds, and then swam vertically toward the bottom. Finally, the tadpoles attempted to anchor themselves onto rocks with their mouthparts and move along the surface of the rock toward a crevice. If that was unsuccessful, they were swept out of the habitat patch. During a pilot trial including a higher velocity, 40–50 cm·s^{-1}, all tadpoles were immediately flushed out of the cobble habitat patches. There were no significant differences in tadpole activity level or emigration rate between the two sides of the flume although the embedded side had local turbulence due to the position of the pumps (Table 2). There was no interaction between the embeddedness and velocity factors (Table 4).

Brett chamber (Expts. III–V).—These small scale flume trials determined the velocities at which an ontogenetic sequence of tadpoles were unable to maintain position. In Expt. III, critical velocity varied negatively with body size and developmental stage (Fig. 4A, B), such that tadpoles close to metamorphosis were most vulnerable ($F_{1,53} = 16.9$, $P < 0.001$). Geographic source of tadpoles, and source × size interaction did not significantly influence U_{crit} ($F_{2,53} = 2.3$, $P = 0.1$; $F_{2,51} = 1.5$, $P = 0.24$). Time budgets of a subset of Expt. III tadpoles (Fig. 4C) reveal an inverse functional relationship ($r = -0.58$, $P < 0.05$) in which the tadpoles with the highest critical velocities were those that spent the least time swimming. For many individuals, U_{crit} fell within 20–40 cm·s^{-1}, the range that could not be produced in the artificial stream channel (Expt. II) given the pump arrays available. However, the key behaviors for maintaining position, i.e., finding micro-eddies and using mouthparts

to maintain position on rocks or the chamber wall, were consistent among all these experiments.

The results of Expt. IV indicate that the primary determinant of susceptibility to displacement may be size. For similar developmental stages (Gosner 34–35), large Central Coast tadpoles (1.7 ± 0.4 g) had significantly lower critical velocities (t = −2.8, df = 7, $P = 0.027$) than small Sierran tadpoles (0.95 ± 0.1 g). Tadpoles with large tails relative to their body mass were able to withstand higher velocities (Fig. 4D), with r = 0.89, $P = 4 \times 10^{-5}$. There was a positive, but not statistically significant, relationship between the time of day of a trial and tadpole performance (r = 0.24, $P = 0.09$), with tadpoles in later trials having higher critical velocities.

Tadpole stamina was short relative to the duration of typical recreational pulsed flows or peaking flows for hydroelectric power generation (e.g., several hours, full-day, or successive weekend days). In the absence of flow refugia (Expt. V), time to impingement at 5.0 cm·s^{-1} was 7.4 ± 2.6 minutes, with a maximum of 25 minutes. In the presence of refugia, maximum duration was 85 minutes.

Cumulative effects of velocity in mesocosms (Expts. VI–VIII).—Tadpoles from the SF Eel exposed to repeated velocity stress at weekly intervals were significantly less developed and smaller, on average weighing half as much as tadpoles reared at continuous low velocity. Mean Gosner stage of six-week old tadpoles was 34.5 ± 0.3 for low velocity replicates and 32.37 ± 0.24 for velocity stressed replicates (t = −4.4, df = 10, $P = 0.003$). Low velocity tadpoles weighed 0.62 ± 0.05 g vs. 0.33 ± 0.04 g for velocity stressed tadpoles (t = −4.8, df = 10, $P = 0.003$). Temperature conditions which could influence growth and development were nearly identical (elevated velocity = 18.46 ± 0.26°C vs. low velocity = 18.46 ± 0.21°C, t = −0.40, $P = 0.97$).

Velocity effects on tadpoles from Alameda Ck. were similarly negative. Survival of recently hatched tadpoles in Expt. VII (Fig. 5A) was impaired by elevated velocity ($F_{1,13} = 20$, $P = 0.001$, $r^2 = 0.61$). Older tadpoles (three- to seven-weeks-old in Expt. VIII) experienced significant negative consequences when velocity and predator stressors acted in concert (Fig. 5B), but in the absence of predators, there was little difference (0.6 fewer tadpoles) in mean survival between the elevated velocity (8.3 cm·s^{-1}) and low velocity
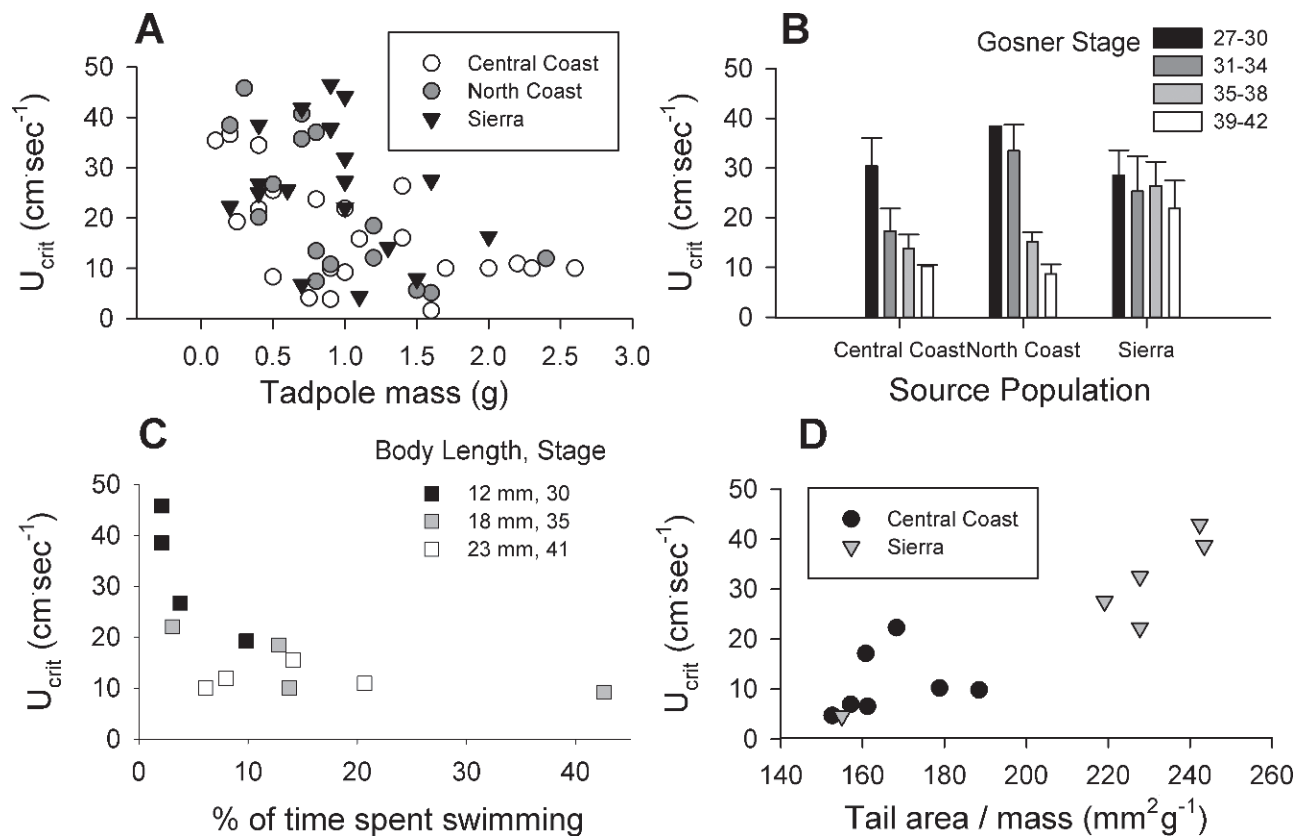
Fig. 4. The critical velocities (U_{crit}) at which tadpoles of *Rana boylii* could no longer maintain position in a small flume (Brett Chamber Expt. III) as a function of size (A), developmental stage (B), and proportion of time spent swimming (C). Tadpoles with large tail area (stages 34–36, Expt. IV) relative to body mass withstood higher velocities (D).
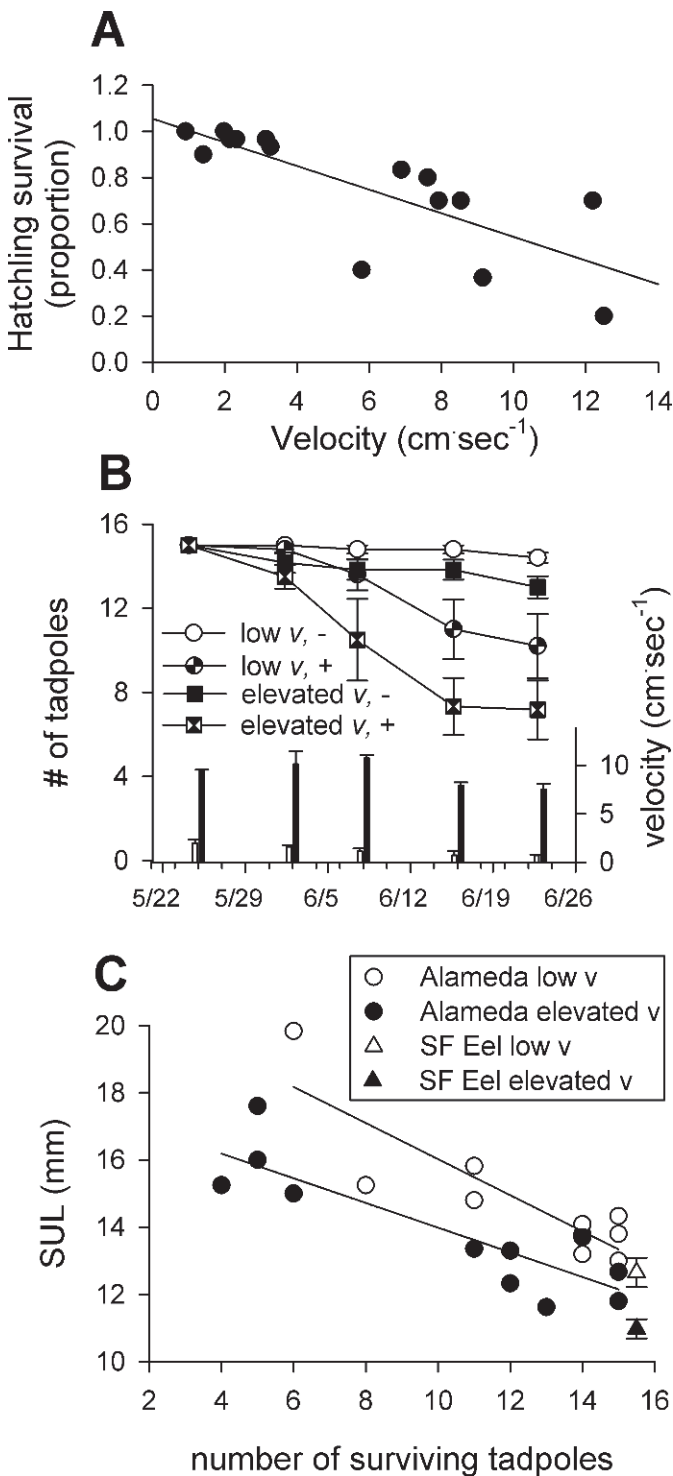
(1.3 cm·s^{-1}) enclosures. In contrast, when a predator was present, the velocity effect size was on average a difference of 3.24 tadpoles. This difference suggests that predator and velocity effects may be multiplicative. However, the interaction term in the repeated measures ANOVA (Table 5) is not statistically significant ($P = 0.1$). Additionally, density effects occurred on growth. When tadpoles died, either due to predators or the repeated velocity stress, the survivors grew larger, indicating a release from intraspecific competition (Fig. 5C). Tadpole snout–urostyle length (SUL) varied inversely with density ($F_{1,18} = 54.8$, $P < 0.001$) and velocity ($F_{1,18} = 4.6$, $P = 0.046$), with no interaction between velocity and density ($F_{1,18} = 0.9$, $P = 0.35$).

DISCUSSION

Under a natural flow regime in California's rivers, discharge gradually declines in early summer, such that tadpoles of *R. boylii*, as well as larvae of other amphibians whose life cycles are similarly timed, do not often encounter large magnitude floods or high water velocities. The general problem for amphibians breeding in regulated rivers is analogous to the limits some birds face with respect to adaptive plasticity in timing their reproduction earlier in response to climate warming (Van Noordwijk and Müller, 1994). The adult animal reacts to the environment when eggs form and are laid, but these conditions may have little predictive value in terms of food resources or conditions for offspring weeks or months later (Visser et al., 2005). Downstream of dams with

summer pulsed flows, spring cues for oviposition such as water temperature, depth, and velocity conditions have little predictive value for the environment of selection on tadpoles. In other words, there is no mechanism that would lead frogs in spring to avoid unfavorable dam operations in summer, perhaps by altering their migratory patterns and ovipositing in the un-dammed tributaries where they overwinter. Our experiments illustrate that detrimental consequences occur when velocities are elevated above the levels tadpoles usually experience in unregulated rivers. These results highlight an opportunity to protect a declining amphibian by operating dams to mimic the natural timing of flow variation.

Summer pulsed flows that elevate velocities in nearshore environments can not only displace individual tadpoles, but may exert artificial selection toward small body size and have negative effects on population growth rates. The mean critical velocity for tadpoles being swept out of refugia and swimming to exhaustion was approximately 20 cm·s^{-1}, but even values of 10 cm·s^{-1} caused more developed and heavily bodied tadpoles to be displaced. This is opposite to the direction of natural selection in anurans which favors large larval body size. Large tadpoles have lower risk of predation, higher post-metamorphic growth rates, and shorter times to reproductive maturity (Altwegg and Reyer, 2003). In our elevated velocity rearing treatments, tadpoles spent more time sheltering in the substrate, rather than feeding on the surface. The energetic costs were exhibited in slower growth and development. Larval growth and development rate

Table 5. The Effects of Velocity Manipulation and Predators on *R. boylii* Tadpoles Reared in Flow-Through Enclosures (Alameda Creek, Expt. VIII).

Response variable	Wilks' λ	F	df	P
ln(number surviving)				
Analysis of differences (MANOVA)				
Time	0.42	7.4	3,16	0.002
Time × Velocity	0.56	4.2	3,16	0.022
Time × Predator	0.49	5.6	3,16	0.008
Time × Velocity × Predator	0.74	1.9	3,16	0.172
Between (ANOVA)				
Velocity		5.5	1,18	0.03
Predator		14.5	1,18	0.001
Velocity × Predator		2.8	1,18	0.11

The pattern we observed of decreasing critical velocity with larger tadpole body size is counter to expectations about performance based on the positive relationship between burst swimming speed and tadpole size (Wassersug and Hoff, 1985; Van Buskirk and McCollum, 2000), but is consistent with work illustrating the importance of the relative proportions of body and tail size to swimming performance (Kaplan and Phillips, 2006). Specifically, the larger tadpoles we tested had less tail area for producing thrust relative to their body mass compared to smaller individuals at the same developmental stage. With respect to interpreting the results presented here, it is important to distinguish critical velocity, U_{crit}, from maximum swimming velocity, U_{max}. Generally, there is a positive allometry between the total length of a tadpole and acceleration to U_{max}, meaning that the rate of increase in speed is proportionally greater than the increase in length that occurs as tadpoles grow (Wilson and Franklin, 2000). Large size and high burst speed may confer a selective advantage in terms of avoiding predation in a low velocity environment (Chovanec, 1992) where it is possible to rest after exertion, but in a higher velocity environment we observed large body size to be a disadvantage. Near metamorphosis, internal changes, such as lung development, affect buoyancy and neurological changes affect surfacing behavior (Gdovin et al., 2006). Hind limbs increase frontal drag on a stationary tadpole and also decrease swimming performance (Wassersug and Sperry, 1977; Dudley et al., 1991). For later stage tadpoles, these morphological changes may have contributed to the observed vulnerability in addition to the effects of size.

Instead of relying on swimming in the water column as a strategy, tadpoles inhabiting fast-flowing streams generally have one of two body plans enabling them to maintain position on, or in, the stream bed. Some taxa are dorso-ventrally flattened and anchor themselves to rocks using an enlarged mouth or abdominal adhesion pad (Altig and Johnston, 1989; Haas and Richards, 1998; Richards, 2002; Jones et al., 2005), while others are long and thin and find refuge from the current in the interstitial spaces of the substrate (Haas et al., 2006; Handrigan et al., 2007). *Rana boylii* has neither body plan, but in comparison to tadpoles of other western North American ranids, its body is more flattened and the tail fin is less broad, with thick musculature (Zweifel, 1955:fig. 2). Despite not having an elongate

Fig. 5. Survival of *Rana boylii* tadpoles in stream mesocosm enclosures exposed to elevated flow velocity levels as hatchlings (A, Expt. VII), and over seven weeks in a factorial manipulation of velocity and predation (B, Expt. VIII). Presence of an insect predator is indicated by black and white hourglass filled symbols. Velocity conditions inside enclosures are indicated by bars, units on right axis. Tadpole snout–urostyle length (C) as a function of velocity (filled symbols = elevated conditions) and density in Expt. VIII (Alameda Creek, circles) and in Expt. VI (South Fork Eel River, triangles).

correlate with components of adult fitness (Smith, 1987; Semlitsch et al., 1988; Berven, 1990) and are important demographic factors influencing population growth rate (Govindarajulu et al., 2005).

body with a small cross-sectional area suited for negotiating interstitial spaces (Gans, 1975; Nodzenski et al., 1989; Inger and Wassersug, 1990), we did observe tadpoles of *R. boylii* hiding in cracks and crevices, and tadpoles with relatively high critical velocities spent most of their time in shelter and very little time swimming. However, this strategy was not effective for the larger tadpoles we tested in the Brett chamber. In the mesocosm rearing experiments, time spent sheltering under rocks came at the cost of decreased growth and increased risk of predation. The availability of interstitial flow refugia can be limited downstream of dams or in watersheds with high inputs of fine sediments (<2 mm diameter) from natural or human activities (e.g., road construction, timber harvesting) which fill the spaces among larger rocks (Waters, 1995; Salant et al., 2006). Fine sediment loading and bed armoring have negative effects on benthic macroinvertebrate diversity and abundance (Angradi, 1999), growth and survival of the juvenile fish that consume them (Suttle et al., 2004), as well as larval amphibians (Welsh and Ollivier, 1998; Welsh and Hodgson, 2008). Although our artificial stream channel 'embeddedness' manipulation was insufficient to eliminate the cracks and crevices used by *R. boylii* tadpoles, the difference in time to exhaustion for tadpoles swimming in the Brett Chamber with and without rocks highlights the importance of interstitial spaces as refugia from high flow events. With respect to mouthparts, *R. boylii* is notable for its 6–7 rows of keratinized teeth (Zweifel, 1955), which are efficient for scraping diatoms and attached algae (Kupferberg, 1997). High speed videography and surgical removal of tooth rows confirms that denticles do play an anchoring role in other anuran tadpoles (Wassersug and Yamashita, 2001; Venesky et al., 2010), but the importance of denticles as a high-flow adaptation for *R. boylii* requires further investigation.

Conservation implications.—Our results add a link to a chain of evidence connecting aseasonal pulsed flows and other alterations of hydrologic regimes to the decline of *R. boylii* in regulated rivers, where absence from historic localities is more common in close proximity to large dams compared to un-dammed sites (Lind, 2005). At each scale of observation and manipulation, we made compromises between verisimilitude and experimental control, but the aggregated results of the eight trials indicate that the aseasonal pulsed flows which occur in many of California's regulated rivers have negative effects on recruitment of *R. boylii*. The Brett chamber data in particular illustrate that conditions sufficient to sweep tadpoles out of refugia under experimental conditions (20–40 cm·sec^{-1}) are within the range of velocities observed during real pulsed flows (Fig. 3). The mean time to exhaustion, 36.34 ± 2.75 min in the Brett chamber, was also much shorter than the duration of typical pulsed flows manufactured for hydroelectric power generation or recreational boating, 6–18 hours. When pulsed flows detrimental to eggs and tadpoles occur, population consequences can be detected in annual egg mass censuses (Kupferberg et al., 2009). At the unregulated SF Eel River where censuses have been conducted annually since 1992, population fluctuations track the velocity conditions for eggs and tadpoles three years prior, a lag representing the time it takes a female to reach reproductive maturity. Decreases in breeding population size follow naturally occurring, but infrequent and uncommonly late, spring rains that cause flooding, while increases follow years with benign flows. At the NF Feather River where manufactured pulsed flow releases

have occurred when eggs and tadpoles were present, similar declines ensued (Kupferberg et al., 2009).

Our results are relevant to developing frog-friendly flow recommendations in California where every major river system has been affected by the construction of dams and reservoirs to secure water for human use (Moyle, 2002). California has more hydropower dams than any other state (Hall, 2006), with 50 hydropower projects scheduled to be re-licensed over the next 15 years by FERC (Rehn, 2009). Conservation in these rivers will increasingly depend on the details of dam operations. In some European countries, there has been a market-driven move to develop certification standards for 'green-labeling' of hydropower electricity (Renöfält et al., 2010). A central hydrological requirement of such certifications would be that instream flows mirror the natural seasonal variability in discharge (Bratrich et al., 2004). Transforming vague certification criteria into detailed guidelines will depend on continued efforts to document cause and effect relationships between specific attributes of dam operations and the status of focal organisms (Souchon et al., 2008). In the case of *R. boylii*, our results show that elimination of manufactured pulsed flows once breeding begins in the spring and suspension of these flows through the early fall when metamorphosis occurs will enhance recruitment. Similar to native fish recruitment which benefits from a naturally timed flow regime (Marchetti and Moyle, 2001), we expect that recruitment of the other amphibians (toads, chorus frogs, newts, etc.) which breed in the shallow, slow moving margins of California's regulated rivers would be protected. Their larvae similarly lack the morphological specializations seen in high-flow adapted taxa (Stebbins, 2003). Because licenses typically have 30–50 year terms, the conditions stipulated now will determine whether populations will persist or be able to re-colonize sections of rivers where they have been extirpated.

ACKNOWLEDGMENTS

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