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HYDROLOGIC AND GEOMORPHIC FACTORS AFFECTING CONSERVATION OF A RIVER-BREEDING FROG (*RANA BOYLII*)[1]

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Abstract. Organisms that live in highly variable environments, such as rivers, rely on adaptations to withstand and recover from disturbance. These adaptations include behavioral traits, such as habitat preference and plasticity of reproductive timing, that minimize the effects of discharge fluctuation. Studies linking hydrologic regime, habitat preference, and population processes, however, are predominantly limited to fish. Information on other sensitive taxa is necessary to facilitate conservation of multispecies assemblages and restoration of biodiversity in degraded river channels.

I studied the functional relationship between physical habitat and reproduction of the foothills yellow-legged frog (*Rana boylii*), a California State Species of Special Concern. From 1992 to 1994, I mapped breeding sites along 5.3 km of the South Fork Eel River in northern California and monitored egg survival to hatching. Frogs selected sites over a range of spatial scales and timed their egg-laying to avoid fluctuations in river stage and current velocity associated with changes in discharge. The main sources of mortality were desiccation and subsequent predation of eggs in a dry year and scour from substrate in wet years, both caused by changes in stage and velocity. At the finest spatial scale, frogs attached eggs to cobbles and boulders at lower than ambient flow velocities. At larger scales, breeding sites were near confluences of tributary drainages and were located in wide, shallow reaches. Clutches laid in relatively narrower and deeper channels had poor survival in rainy as well as dry springs. Most breeding sites were used repeatedly, despite between- and within-year variation in spring stage of the river. This pattern of site selection suggests that conservation of *Rana boylii* may be enhanced by maintaining or restoring channels with shapes that provide stable habitat over a range of river stages.

Key words: amphibians; Anura; frogs; geomorphology; hydrology; oviposition; physical habitat; Rana boylii; *reproductive success; river; spatial scale.*

INTRODUCTION

The loss of aquatic biodiversity in rivers and streams is a global conservation problem (Master 1990, Allan and Flecker 1993, Sparks 1995). In these habitats, species declines are often associated with water diversion, impoundment, flow regulation, channelization, and other habitat modifications (Williams et al. 1989, Bianco 1990, Moyle and Williams 1990, Elvira 1995). Such perturbations alter sediment and water flow regime, which, in turn, cause geomorphic change. Impacts include incising of channels downstream from dams, broadening and deepening of channels after in-stream gravel mining, and filling of interstices with fine sediments (Kondolf and Matthews 1993, Ligon et al. 1995). Thus, channel restoration to mitigate for biodiversity loss has become a priority (NRC 1992), underscoring the need for design recommendations based on balancing the requirements of many species. Studies of biotic response to physical channel properties, however, have focused primarily on fish habitat use and classification (Wesche 1985, Sullivan 1986, Orth 1987, Nestler et al. 1989, Kershner and Snider 1992). We need data linking birth and death rates of many species to geomorphic and hydraulic parameters if rivers are to be managed as whole ecosystems. This has been done theoretically in models of river food chains (Power et al. 1995).

In the Pacific Northwest, most studies linking hydrology and geomorphology to population processes emphasize salmonid spawning and rearing habitat (Lister and Genoe 1970, Bisson et al. 1982, Laufle et al. 1986, McMahon and Hartmann 1989), rather than habitats of a variety of aquatic organisms (but see Power 1992*a*) that may include other sensitive taxa. One such species is the foothills yellow-legged frog, *Rana boylii*, which lives in rivers and streams of California and Oregon (Zweifel 1955, Stebbins 1985). This frog is a California State Species of Special Concern (Jennings and Hayes 1994). It has experienced significant population declines, especially in the southern and inland parts of its range relative to northern coastal areas (G. Fellers, National Biological Service, *personal communication*). Decline has occurred with the modification of river habitats, introduction of bullfrogs (*Rana catesbeiana*) that are predators and competitors of *R.*

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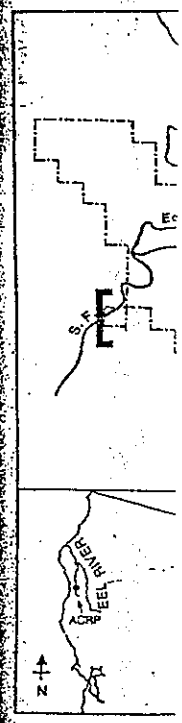

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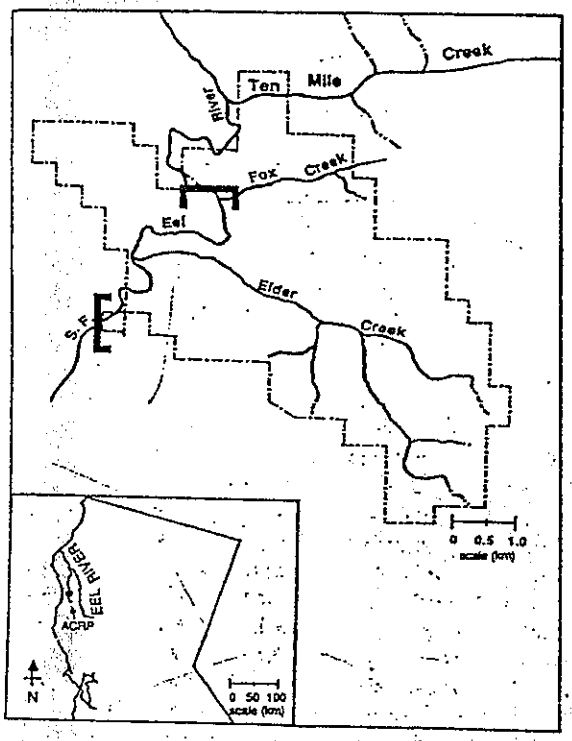

FIG. 1. Location of the Angelo Coast Range Preserve (ACRP, dotted outline) in northern California. Study reach is enclosed by large brackets.

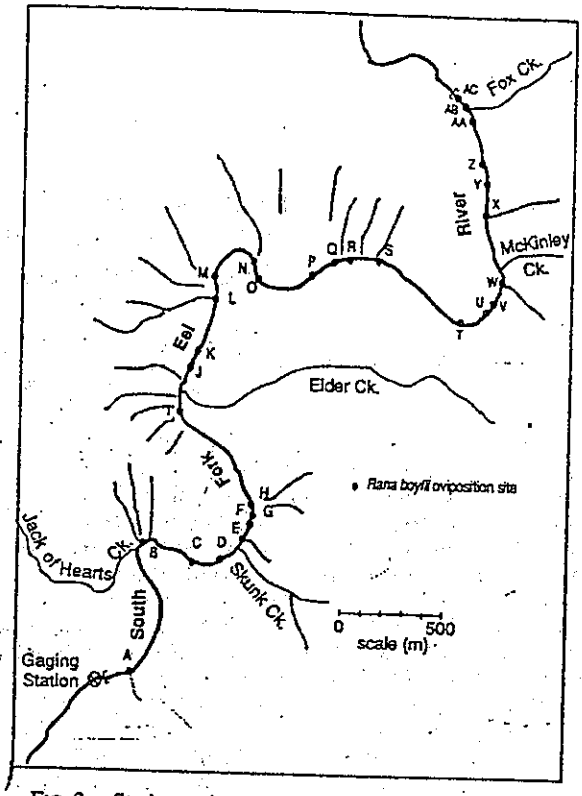

FIG. 2. Study reach and *Rana boylii* breeding sites (points on heavy solid line enclosed by small brackets). The frogs occur, but do not breed, in tributaries (thin solid lines). Shaded thick lines indicate drainage patterns of rivulets that flow in early spring. Letter placement indicates breeding site location on the left or right bank. Site use ranged from regular to sporadic. Site name (no. clutches in 1992, 1993, and 1994; . . . indicates sites not censused in 1992): A (. . ., 37, 44); B (23, 23, 43); C (. . ., 0, 4); D (. . ., 0, 12); E (0, 3, 9), F (48, 26, 37); G (22, 23, 26); H (7, 0, 12); I (22, 27, 33); J (47, 41, 38); K (0, 0, 8); L (18, 0, 1); M (11, 23, 22); N (20, 29, 26); O (. . ., 0, 1); P (. . ., 0, 6); Q (. . ., 0, 3); R (. . ., 7, 10); S (. . ., 43, 55); T (. . ., 0, 2); U (10, 19, 10); V (6, 13, 60); W (26, 11, 32); X (32, 27, 40); Y (. . ., 4, 2); Z (. . ., 8, 19); AA (. . ., 43, 29), AB (. . ., 0, 4), AC (. . ., 0, 5).

boylii (Moyle 1973, Hayes and Jennings 1986, Kupferberg 1996), and invasion by fish either nonindigenous to the drainage basin (Sacramento squawfish, *Ptychocheilus grandis*) or the region (bass, *Micropterus* sp., and green sunfish, *Lepomis cyanellus*) (M.E. Power and S.J. Kupferberg, *unpublished data* from Ten Mile Creek and South Fork Eel River below confluence with Ten Mile Creek). These simultaneous stresses make the causes of ranid decline difficult to untangle (Hayes and Jennings 1986). This study focuses on the links between habitat quality and reproduction of *R. boylii* by quantifying the physical conditions necessary for eggs to survive to hatching.

To maintain viable populations, organisms that live in highly variable environments, such as rivers, must be able to withstand or recover from disturbance. Here, I present observations that yellow-legged frogs lessen the effects of hydrologic disturbance during breeding by using sites with geomorphic and hydraulic conditions that minimize adverse effects of discharge fluctuation. Specifically, I address the following questions: (1) Is the distribution of breeding sites random, in proportion to availability, with respect to tributary confluences and geomorphic units (pools, riffles, and bars)? (2) Within breeding sites, do frogs oviposit according to depth, distance to shore, flow velocity, and substrate? (3) What are the major causes of egg mortality, and how frequently do they occur? (4) Is survival of eggs related to the shape of the channel and date of oviposition? (5) Do frogs initiate oviposition in relation to discharge and temperature? I address these questions for a stable population of *R. boylii* in a relatively pristine river reach, and discuss implications for engineered channel design and flow regime.

NATURAL HISTORY AND STUDY SITE

This research was conducted at the South Fork Eel River, within the Angelo Coast Range Reserve (formerly the Northern California Coast Range Preserve), Mendocino County, California (39°44′ N, 123°39′ W) (Fig. 1). I chose the 5.3-km study reach (marked by brackets in Fig. 2) because of accessibility and the absence of nonindigenous bullfrogs and fish relative to downstream reaches near Ten Mile Creek, where they

are present. The study reach is typical of streams and rivers inhabited by *R. boylii*, being characterized by partial shade, shallow riffles, and substrates cobble-sized or greater (Hayes and Jennings 1988). The watershed is sparsely settled and dominated by old-growth mixed coniferous forest. Within the study area, the channel is fourth order and the gradient is 0.44%. The river has cut a narrow canyon lacking a floodplain, and active channel width is ≈30 m.

Although *R. boylii* are common along tributaries, they congregate at the same sites in the main stem each spring to breed. In 1992, I located 15 discrete sites along 2.6 km of noncontiguous river channel. In 1993 and 1994, I expanded the survey to 5.3 contiguous kilometres and located 14 additional sites (Fig. 2). I define these discrete sites as breeding sites, and the location of a given egg mass as an oviposition site. Breeding sites range in size from 2 × 10 m to 5 × 70 m, and are separated from other breeding sites by up to several hundred metres. For ≈1 mo beginning in mid-April to early May, mating and egg-laying occur. Egg incubation lasts ≈2 wk, depending on water temperature and position in a clutch, with eggs at the perimeter hatching first and those at the center and close to the rock hatching last (S. J. Kupferberg, *personal observation*). The number of egg masses indicates reproductive female population size, because one female lays one clutch of 1000–2000 eggs (Zweifel 1955). During the three study years the mean (±1 SE) reproductive output was 92.8 ± 10.2 clutches/km, or 18.8 ± 1.9 clutches per breeding site. For the 15 breeding sites sampled in all three years, among-year differences in this estimate of population size were not significant (multivariate repeated-measures ANOVA: Wilks' $\lambda = 0.68$; $F_{2,13} = 3.02$; $P = 0.08$).

Methods

Breeding site distribution

I mapped the distribution of breeding sites during spring 1992–1994 and measured the distance from each breeding site to the nearest tributary (temporary and permanent), using a hip chain in the field and topographic maps. At mid-April 1994 discharge (flow volume per unit time) levels, I characterized each breeding site by noting whether or not it was at a bar, and by classifying the adjacent channel according to depth and turbulence: riffle (water surface turbulent, depth <1 m); shallow pool (smooth water surface, depth <1 m); medium pool (1 m ≤ depth < 2 m); or deep pool (depth ≥2 m). I measured the length of each channel type with a hip chain and calculated the proportion of the study reach in each channel type. To determine whether or not distribution of breeding sites indicated selectivity, I compared observed to expected frequencies with chi-square tests. Expected frequencies were calculated under the null hypothesis that the proportion of breeding sites in each channel type would equal the proportion of the study reach in each channel type.

Egg survival

Over the survey period, April–June 1992–1994, I monitored survival to hatching by marking individual egg masses with numbered flags or popsicle sticks placed nearby. I visually estimated the percent of clutch remaining from week to week, and finally the percent hatching. I gave each clutch a rank with respect to desiccation and scour. For stranding: 1, egg mass completely exposed to air; 2, egg mass partially exposed; and 3, egg mass completely submerged. For scouring: 1, egg mass completely gone from substrate; 2, egg mass partially removed; and 3, egg mass intact. If markers were not relocated, clutches were not included in analyses. I also noted the presence or sign of predators and fungal disease. Effects of scour were visually distinctive from predation. A portion missing indicated a large predator, whereas frayed jelly and loose connections among eggs indicated partial scour. I attributed empty egg cases to small predators, such as limnephilid caddisflies, which can penetrate jelly to consume embryos (Stein 1985). I did not observe empty jelly cases in recently oviposited egg masses. I used log-linear analysis to assess associations among the mortality sources, Kruskal-Wallis tests to compare survival among breeding sites, and Spearman's rank correlations to assess the correspondence among oviposition date, stranding/scouring index, and hatching success.

Historical analysis of stranding and scouring event frequency

To determine how representative the three study years were in terms of rainfall and discharge, I consulted USGS records of daily and peak discharge measured at the study site from 1946 to 1970 (EarthInfo 1994). Recording of river stage (elevation of water surface in relation to an arbitrary datum) was resumed in 1990 by M. E. Power at the same staff gage. The gaging station is near the most upstream breeding site (Fig. 2). In spring 1993, base flow (discharge in between storm events) was estimated from discharge monitored on Elder Creek (EarthInfo 1994), because sediment clogged the stilling well at the South Fork Eel gaging station. At base flow, the float measuring stage was resting on sediment, but measurements at peak flows were accurate. In 1994, gaps in the record due to technical problems with the data logger were filled in by extrapolation from data gathered at a temporary gage at breeding site X (Fig. 2) (A. Lind, U.S. Forest Service, *unpublished data*). I estimated discharge from stage height using a low-flow rating curve (M. E. Power, *unpublished data*) in conjunction with a rating curve provided by the U.S. Geological Survey (K. Markham, USGS, Ukiah, California, *unpublished data*). A rating curve is an empirical relationship developed by mea-

suring the cross-sectional area of flowing water and the velocity at several stages; the product of area and velocity is discharge.

The frequencies of large spring spates and dewatering rates were assessed by calculating the recurrence intervals of such events during the oviposition period, 15 April–15 June, 1946–1970. Recurrence interval = $(N + 1)/(M)$, where N is the number of years of record and M is the rank order of the discharge, with the largest discharge ranked first (Leopold 1974). Dewatering rate of the channel was calculated as the percent decrease in discharge over the oviposition period.

Physical conditions at clutches

I measured water depth, distance to shore, and substrate (bedrock, boulder ≥ 256 mm, cobble ≥ 64 mm, pebble ≥ 2 mm, or vegetation) at recently (within 0–3 d) laid clutches throughout the 1992 and 1994 breeding seasons. Between-year differences in depth and distance to shore were compared using t tests. At seven breeding sites on 7 May 1992 (discharge: Q = 0.44 m³/s at gaging station), I measured velocity with a current meter, holding the rotor adjacent to the center of recently laid clutches. Velocity was then measured several centimetres horizontally away from eggs at depths equivalent to the centers of the egg masses. These ambient velocities therefore reflect flow conditions of the near-bank breeding area, not the entire channel. A two-way ANOVA tested for differences between velocity at the egg mass and ambient velocity, as well as for differences among breeding sites. Location of velocity measurement, at egg mass vs. ambient, was treated as a fixed factor and was crossed with breeding site, which was also treated as a fixed factor because sites are often historical.

Channel geometry in relation to breeding site selection and egg survival

During April 1994, I established staff gages (metre sticks wired to steel rebar pounded into the river bed) and measured channel cross sections with a surveyor's rod and level at the approximate center of 15 breeding sites and at 11 nonbreeding sites. I chose nonbreeding sites by dividing the study reach into 15 equal-length segments; within each segment, I used 10-sided dice (Kotanen 1992) to generate the digits of longitudinal distances for the origin of each cross section. Four cross sections were eliminated because they fell within or only a few metres away from breeding sites. Between breeding and nonbreeding sites, I compared hydraulic radius (the ratio of cross-sectional area to wetted perimeter, about equal to the mean depth) and wetted cross-sectional area at discharge Q = 0.20 m³/s at the gaging station. To test the hypothesis that good breeding sites have geometries in which stage and velocity are relatively insensitive to changes in discharge, I compared four descriptors of channel shape: (1) cross-sectional area; (2) wetted width to depth ratio; (3) wetted perimeter, which is the distance along the varying topography of the channel bottom rather than width of the water surface; and (4) hydraulic radius. For each variable, I used Mann-Whitney U tests to compare breeding to nonbreeding sites, and to compare sites with above-average survival to sites with below-average survival. To illustrate how channel shape interacts with changes in discharge, I used HEC-2 computer simulations of water surface profiles (U.S. Army Corps of Engineers 1991) in a typical low-survival channel (site W) and a high-survival channel (site X). To determine if the survival consequences of channel shape were consistent under conditions of decreasing and increasing discharge, I used Pearson's r to test for survival correlation in a dry and a wet year. All statistics were calculated with SYSTAT (Wilkinson 1992).

Timing and duration of breeding

To evaluate whether or not frogs began oviposition at the same discharge each year and whether or not the length of breeding activity was influenced by discharge fluctuations, I superimposed a cumulative frequency distribution of clutches over time onto the April–May hydrographs.

To evaluate whether or not frogs began oviposition at the same temperature each year, I compared daily mean water and air temperature during the week preceding and the week following the appearance of the first egg mass. Means were calculated from hourly data logged from thermistors at the gaging station. Air temperature at a given hour may vary among breeding sites according to canyon wall slope and aspect, but I assume that differences in daily means are minimal. Water temperatures are likely to be uniform across sites and to mirror values of the thermistor, located ≈10 cm above the river bed. Most clutches were laid ≤10 cm above the bed, at depths of ≈20 cm, where the effects of surface warming would be minimal. In the early spring, variation in water temperature due to ground water seeps, regions of upwelling, and tributary confluences are also minimal (S. J. Kupferberg, *personal observation*).

RESULTS

Geomorphic distribution of breeding sites and physical characteristics of egg attachment sites

Breeding sites tended to be located near tributary confluences (Fig. 2, Table 1) in shallow reaches (Table 2). Typically, breeding site channels were asymmetrical and eggs were deposited on the less steeply sloping side, indicating that these sites provide shallow, low-velocity habitats close to shore, over a range of river stages. Of the surveyed channels, those with eggs were wider and shallower than non-egg channels chosen at random (Fig. 3). Twenty of 29 breeding sites were at cobble/small boulder bars. At the April 1994 stage,

TABLE 1. Landscape patterns of *Rana boylii* oviposition at the South Fork Eel River, California. Most clutches are in closer proximity to confluences with side drainages than would be expected by chance.

Year	Distance to nearest tributary (m)	Proportion of study reach	Observed no. clutches	Expected no. clutches	χ^2†	P
1992	<100	0.57	292	166	224	<0.001
	≥100	0.43	0	126		
1993	<100	0.57	399	233	274	<0.001
	≥100	0.43	12	178		
1994	<100	0.57	553	337	320	<0.001
	≥100	0.43	42	258		

† df = 1.

TABLE 2. Nonrandom distribution of *Rana boylii* breeding sites (n = 29) with respect to geomorphic features of the South Fork Eel River, based on a 3.6-km longitudinal survey (χ^2 = 8.1, df = 3, P < 0.05).

Feature	Proportion of reach	Observed no. sites	Expected no. sites
Riffle	0.16	3	4.6
Shallow pool (depth < 1 m)	0.46	21	13.4
Medium pool (1 m ≤ depth < 2 m)	0.13	1	3.8
Deep pool (depth ≥ 2 m)†	0.25	4	7.3

† Breeding sites were at bars near the outlets of these pools, not at the deepest part of the profile.

emergent rocks were a common feature at breeding sites (15 out of 15 surveyed channels) but not at random sites (3 out of 11 channels).

Individual egg attachment sites occurred within a narrow depth range and a more variable range of distances from shore. Depth ranged from 4 to 43 cm, with consistent yearly means (±1 SD) and coefficients of variation ($\bar{X}_{1992}$ = 19.7 ± 5.4, CV_{1992} = 27.4%, n = 225; $\bar{X}_{1994}$ = 19.7 ± 7.3, CV_{1994} = 36.5%, n = 293; t = 0.05, P = 0.96). To achieve consistent egg depth, frogs oviposited at highly variable distances from shore, ranging from 0 to 1250 cm. In 1994 when base flow discharge was low, frogs oviposited farther from shore than they did in 1992 ($\bar{X}_{1992}$ = 220.3 ± 184.3, CV_{1992} = 83.6%, n = 216; $\bar{X}_{1994}$ = 280.5 ± 260.1, CV_{1994} = 92.72%, n = 290; t = 3.0, P = 0.003). The most commonly used substrates were cobbles (53.6%) and boulders (34.4%). Bedrock and vegetation were used much less frequently (9.6% and 1.2%, respectively).

Frogs selected attachment sites on lee sides of rocks and beneath overhangs within a narrow velocity range (3.2 ± 0.19 cm/s, mean ± 1 SE; range = 1.1–13.5 cm/s). Flow velocities at egg masses were significantly lower than mean ambient velocities within the breeding site (Fig. 4).

Hatching success in relation to hydrology and channel geometry

The main causes of mortality were hydrologic: desiccation (in 1992) or scour (in 1993 and 1994) (Figs. 5A, 6). In 1992, a drought year, survival was relatively high (89.7 ± 10.2%, mean ±1 SE) and stranding was the major cause of mortality. During the oviposition period, 3 cm of rain fell and discharge decreased 53% (from 0.60 to 0.28 m³/s) in the 5 wk between appearance of the first clutches and hatching of most of the eggs. In 1993, survival could not be estimated accurately because of late-season rainstorms (24.7 cm total rainfall) when most larvae were emerging, constituting a >300% increase in discharge (from 4.8 to 20.8 m³/s). After the water receded and visibility improved, most egg masses had been swept off their substrates and markers were also gone, making an accurate census impossible. Subsequent tadpole censusing later in the summer indicated that survival was indeed very low (S. J. Kupferberg, *unpublished data*). In 1994, survival was 79.8 ± 12.4% and the major cause of mortality

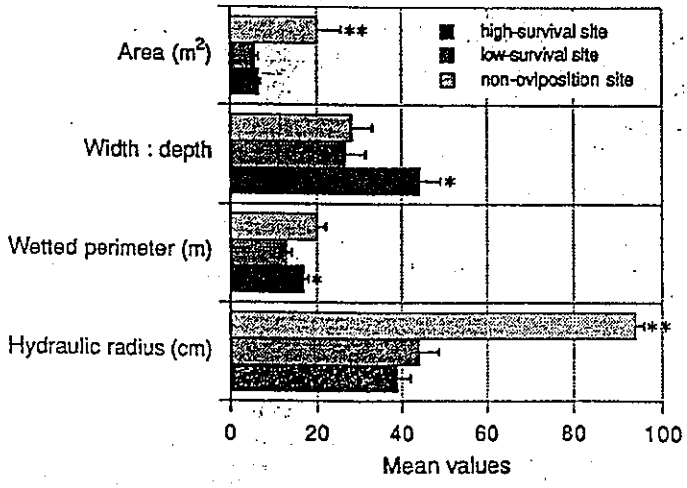

FIG. 3. Mean values (+1 SE) of cross-sectional geometry variables for nonbreeding (non-oviposition) sites, breeding sites (n = 11) with high survival (n = 10), and low-survival sites (n = 5). Measurements refer to the wetted channel in mid-April 1994, when oviposition began. * indicates significant (P < 0.05) differences between high- and low-survival breeding sites ($U_{\text{width:depth}}$ = 46.5, $U_{\text{wetted perimeter}}$ = 46.5); ** indicates significant ($P \leq 0.01$) differences between nonbreeding and breeding sites (Mann-Whitney $U_{\text{hydraulic radius}}$ = 140, U_{area} = 141).

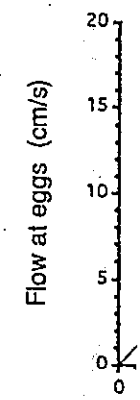

FIG. 4. *Rana* microsites (F_{location} Each point is the clutches (y) and 5- ing sites. Line x = were not microsit higher velocities t 0.001). A signific measurement (nea ($F_{\text{location} \times \text{site}}$ = 11. increasing differe ambient velocity i

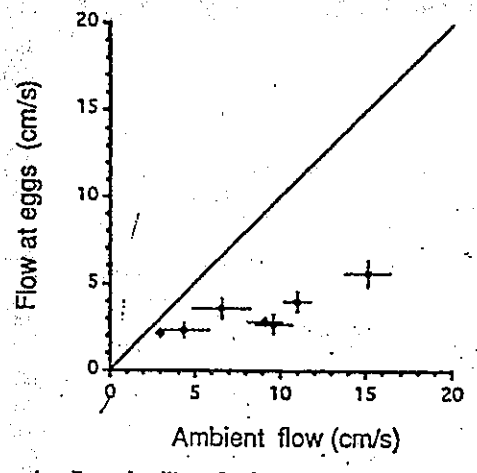

FIG. 4. *Rana boylii* prefer low-velocity egg attachment microsites ($F_{\text{location, egg vs. ambient}} = 140$; df = 1,170; $P \ll 0.001$). Each point is the mean (±1 SE) flow velocity measured at clutches (y) and 5–10 cm away from eggs (x), for seven breeding sites. Line $x = y$ indicates expected flow at eggs if frogs were not microsite selective. Some sites had significantly higher velocities than others ($F_{\text{site}} = 27.6$; df = 6, 170; $P \ll 0.001$). A significant interaction between location of flow measurement (near or away from egg mass) and breeding site ($F_{\text{location} \times \text{site}} = 11.2$; df = 6, 170; $P \ll 0.001$) indicates the increasing difference between egg and ambient velocity as ambient velocity increases.

was scour, associated with 14.3 cm total rainfall over the breeding season. Debris marks on staff gages indicated that river stage rose an average of 40 cm during peak flows, and stage height was, within an average of 1 cm, the same at hatching as at initial egg-laying. Stranding was, therefore, minimal. In both 1992 and 1994, eggs laid later experienced less variation in discharge and had less chance of being scoured or stranded than eggs laid earlier (Figs. 5B and 6).

Mortality was also specific to breeding site (Fig. 5A). The correlation between survival in years with and without spring rain (Fig. 7) suggests that, for some channel shapes, stage and velocity are relatively insensitive to discharge changes and, thus, allow higher survival to hatching (Fig. 8). There were significant differences between the above-average, and below-average survival sites, with respect to wetted perimeter and width to depth ratio (Fig. 3), but no significant differences in cross-sectional area or depth.

Stranding, a consequence of discharge fluctuation and channel geometry, interacted with predation but not with fungal-associated mortality (Table 3). In 1992, stranding increased predation by exposing eggs to surface-dwelling hemipterans and terrestrial predators such as ants, in addition to fully aquatic predators such as limnephilid caddis fly larvae (41% of exposed clutches had predators present, whereas 14% of submerged clutches had predators present). Stranding did not alter risk of fungal attack (23% of exposed clutches had fungus vs. 25% of submerged clutches). Moreover, risks of predation and fungal attack were independent.

Historically, eggs face scouring conditions more often than stranding. The proportion of one stranding to two scouring years resembles the longer term record, in which there were eight years with no rain during the oviposition period and 16 years with rain. The 1992–1994 study period was representative of historical breeding season conditions with respect to peak discharge (Fig. 9A), but the late May–early June 1993 storms were anomalous with respect to dewatering of the channel (Fig. 9B). Although the 1993 flood has a recurrence interval of ≈10 yr, or a 10% chance of occurring in any given year's breeding season, it represents a much rarer event in terms of dewatering (Fig. 9B).

Seasonality of breeding

In low base-flow discharge years, oviposition occurred earlier than in high discharge years (Fig. 5). The duration of breeding activity corresponded to rain during the oviposition period. In the absence of appreciable spring rain during 1992, 75% of clutches were laid in 11 d. In the presence of rain in 1994, 75% of clutches were laid in 39 d. Peaks on the 1994 hydrograph correspond to flat regions of the cumulative percentage of clutches curve, whereas the receding limbs after peaks correspond to regions of steep increase in oviposition.

Initiation of oviposition was also associated with warming (Fig. 10). Daily mean air and water temperatures were significantly warmer during the first week of oviposition than during the preceding week, in all three years. There were significant among-year differences in pre-oviposition water temperature, but no differences in postoviposition temperature, as indicated by the significant interaction term in the ANOVA.

DISCUSSION

The reproductive strategy of *R. boylii* appears well-suited to rivers with predictable winter–flood, summer–drought hydrographs. Breeding was completed in a shorter period of time and earlier in a drought year compared to two years with rainy oviposition periods. Successful *R. boylii* selected historically used breeding sites associated with tributary confluences, with distinctive channel morphologies, and with boulders that created microhabitats with below-ambient flow velocity. In combination, these behaviors enhanced egg and early larval survival by decreasing the risk of desiccation and concomitant exposure to predators, and by mitigating the likelihood of scour off rocks.

When rivers are modified by channelization, gravel mining, damming, or diversion, the characteristics of channel morphology and hydrology important to *R. boylii* recruitment become decoupled from the climatic patterns that regulate breeding. Latitudinal variation in *R. boylii* breeding season, in which southern populations breed earlier than northern populations (Zweifel 1955), suggests that these frogs wait for warm temperatures and the cessation of winter rains to initiate

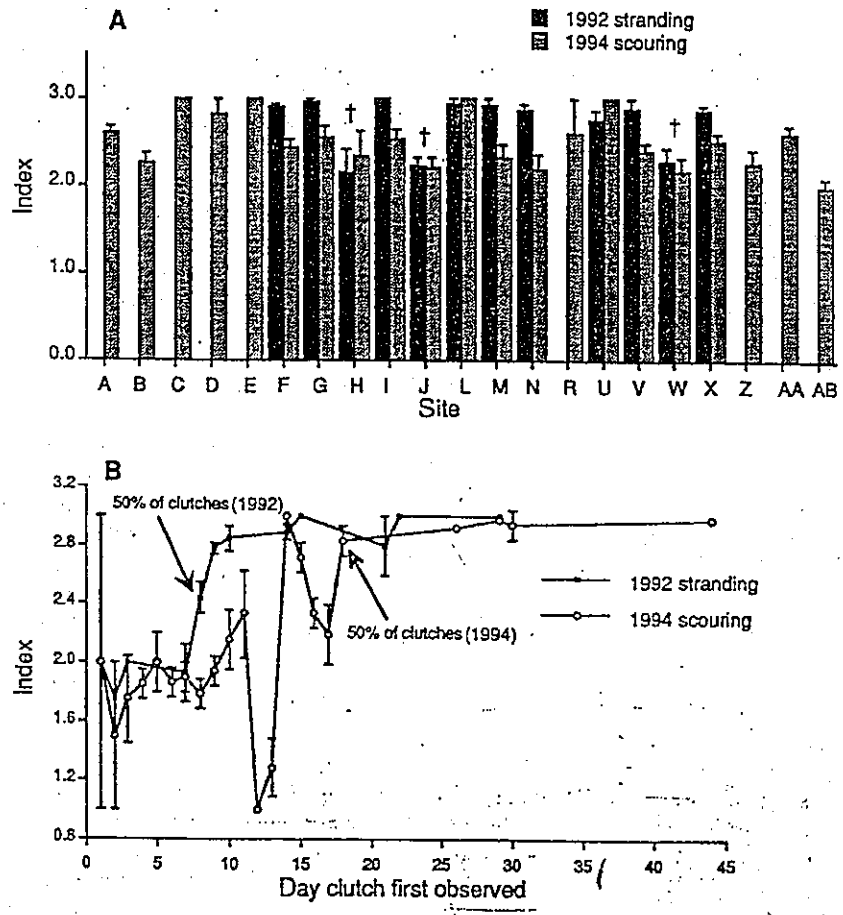

FIG. 5. Mean (+1 SE) scouring and stranding indices of *R. boylii* egg masses were significantly different among breeding sites (A), and were significantly correlated with oviposition date (B) and survival. For 1992: $r_{\text{stranding index} \times \text{survival}} = 0.62$, $P < 0.001$; between-site differences, Kruskall–Wallis $\chi^2 = 87.3$, df = 11, $P < 0.001$; $r_{\text{stranding index} \times \text{date}} = 0.28$, $P < 0.01$; $n = 280$ clutches at 12 sites. For 1994: $r_{\text{scour index} \times \text{survival}} = 0.89$, $P < 0.001$; between-site differences, Kruskal–Wallis $\chi^2 = 60.8$, df = 22, $P < 0.001$; $r_{\text{scour index} \times \text{date}} = 0.70$, $P < 0.001$; $n = 476$ clutches at 23 sites. Daggers indicate sites that had significantly more losses in both years. Index of stranding fate: 1, egg mass completely exposed to the air; 2, partially exposed; and 3, completely submerged. Index for scouring: 1, egg mass completely gone from substrate; 2, partially removed; and 3, intact. Breeding sites A–E, R, and Z–AB were not monitored for survival in 1992.

breeding. The specific proximal cues that *R. boylii* use to initiate breeding, such as air and water temperature, insolation, and discharge, are currently being compared in regulated and unregulated rivers across a latitudinal gradient in six northern California watersheds (A. Lind, U.S. Forest Service, *personal communication*). This forthcoming information plus an understanding of breeding site selection and mortality sources within a single, relatively pristine system (from this study of the South Fork Eel River watershed) may allow us to manage rivers in ways that do not continue to threaten *Rana boylii*.

Spatial scales of habitat preference

The choice of appropriate boundaries for a conservation project is particularly important for riverine organisms, because rivers are highly heterogeneous environments (Ward 1989) in which habitats are nested hierarchically (Frissel et al. 1986, Hawkins et al. 1993). Factors controlling the distribution and abundance of river organisms span many orders of magnitude in space and time (Minshall 1988, Crowl and Schnell 1990, Biggs and Gerbaux 1993), from climate, geology, land use, and hydrologic regime (Benda et al. 1992, Poff and Allan 1995), to water velocity (Rabeni and Minshall 1977, Biggs and Gerbaux 1993), substrate (Minshall 1984, Power 1992*b*), food abundance, and predation (Peckarsky 1984, Power 1987, Crowl and Schnell 1990). To determine what habitats must necessarily be included in a project focused on maintaining *R. boylii* populations, I consider both the largest and smallest scales (extent and grain, sensu Wiens 1989) of spatial heterogeneity to which these frogs respond, in terms of reproductive behavior.

The largest scale of *R. boylii* selectivity was at the sub-basin level (1000s of square metres). Breeding

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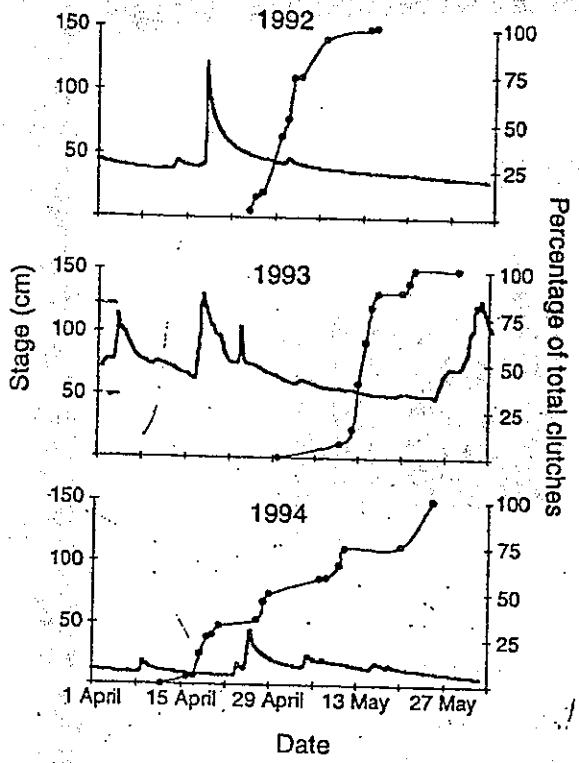

FIG. 6. Spring hydrographs 1992–1994 (bold line) and cumulative frequency distribution of *R. boylii* clutches (thin line).

sites were associated with drainage patterns of the subbasins and were close to confluences with tributaries. This result may be explained by the disadvantages of tributaries for breeding, but relative advantages for adult overwintering. Tributaries are dark and cool with low algal food production, conditions not conducive to tadpole growth. Although *R. boylii* overwintering behavior is not known, adults are commonly found in the tributaries in the early spring before they are abundant in the mainstem (S. J. Kupferberg, *personal observation*). It is also not known whether or not *R. boylii* leave water channels for the forest margins, but they are rarely seen more than a few metres away from water (S. J. Kupferberg, *personal observation*). It is thus likely that they leave the active channel of the mainstem to avoid scour, and move to low-order tributaries, some of which may only flow during the rainy season. Adults may then migrate downstream to the main stem to breed, congregating at the gravel/boulder bars closest to the tributary confluences. An alternative explanation for this result is that sediment from tributaries may contribute to local maintenance of the coarse sediment patches that cover the main stem's bedrock channel. The availability of coarse sediment enables frogs to find rocks that can shield egg masses from high flow velocities. An analogous sediment supply link between tributaries and main stems is exemplified in the Pacific Northwest, where the supply of salmonid spawning gravels in larger streams is affected by logging practices (Hartman et al. 1987) as well as by natural erosion processes in low-order tributaries (Benda et al. 1992).

At the scale of reaches (e.g., pools and riffles, 10–100 m²), frogs selected broad, shallow channels. Breeding sites with greater than average width to depth ratios had above-average survival. One explanation for this result is that the two variables critical to eggs being swept off rocks or desiccated, current velocity and stage, are less sensitive to discharge fluctuation in broad, shallow channels than in deep, narrow channels. Velocity increases more slowly with increasing discharge in wide channels than in narrow channels because of greater channel roughness (Dunne and Leopold 1978). Under conditions of declining discharge, stage decreases less in a broad channel than in a narrower channel. Alternatively, frogs may have avoided deep pools because substrates there were too small for egg attachment, there was predation risk from fish (Holomuzki 1995), or algal food resources needed by tadpoles were absent. Chemicals released by algae, which stimulate spawning in another ranid (Savage 1961), may be at low concentration in deep pools.

At the finest scale (e.g., individual cobbles and boulders, 0.1–1 m²), frogs attached eggs to microsites with lower than ambient flow velocities. High velocities can

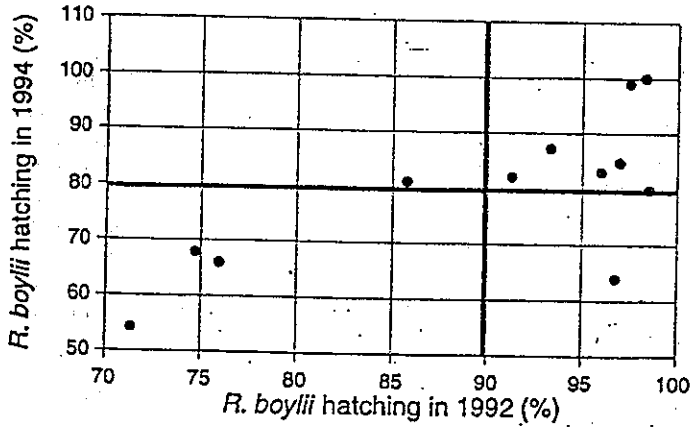

FIG. 7. Correlation between *R. boylii* hatching success in a drought year, 1992, and a flood year, 1994 (Pearson $r = 0.73$, $P = 0.007$). Vertical and horizontal lines represent mean survival in 1992 and 1994, respectively.

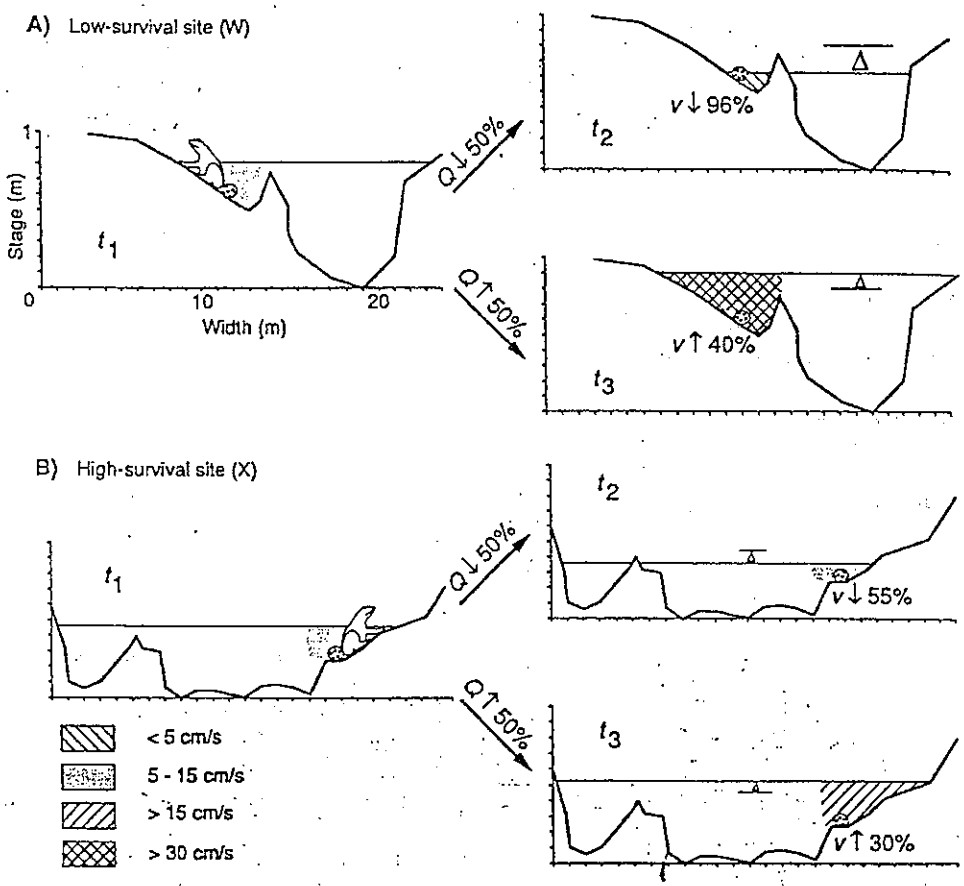

FIG. 8. Sensitivity of stage and velocity to discharge fluctuation at *R. boylii* breeding sites with different channel shapes. Frogs (not drawn to scale) are ovipositing at equal depths in (A) a low-survival channel cross section (1:10 vertical exaggeration), and (B) a high-survival channel, at discharge $Q_1 = 3$ m³/s. At subsequent times (t), discharge can decrease ($Q_2 = 1.5$ m³/s) or increase ($Q_3 = 4.5$ m³/s). Changes in stage (indicated by Δ) and velocity (v, indicated by fill pattern; percentage change in velocity is also shown) are relatively smaller in the wider, shallower channel. Eggs become exposed to air in the narrower channel when Q decreases by 50%.

limit fertilization (Pennington 1985, Denny and Shibata 1989, Levitan 1991). Although sperm density and viscosity can counteract diffusion caused by velocity and turbulence, as has been shown for marine invertebrates (Thomas 1994), current velocity must be slow enough to allow external fertilization. Interestingly, the tailed frog (*Ascaphus truii*), one of the few frogs with internal fertilization and the only frog with an intromittant organ, breeds in the steep gradient, and high velocity, tributary creeks at the site.

High velocities also sweep away clutches. I have observed clutches that were oviposited at low velocity remaining attached as velocities rose >20 cm/s, but not for sustained periods. When returning to a site that had experienced 20 cm/s flow for a few days, I usually found that all but a few of the eggs in the clutch had washed away. Thus, it appears that there is a threshold velocity and duration of exposure beyond which the egg jelly loses adhesion. If velocities were high at the time of oviposition, however, frogs concealed their clutches in low flow microsites underneath overhanging portions of large boulders.

Oviposition timing and historic site use in relation to discharge and temperature

R. boylii breed early during the transition between the wet and dry seasons, despite the likelihood of highly variable discharge that can cause egg mortality. Discharges equaling those of late May 1993 (20.8 m³/s), which swept most clutches away, recur at an interval of ≈9 yr during the breeding season, based on 25 years of records. Although longer term data are not available, it is reasonable to assume that breeding later would minimize exposure to variable conditions. Accordingly, frogs commence ovipositing later when base flow is high, and earlier in low-flow years, but this plasticity may be driven by temperature cues as well as by precipitation. At the South Fork Eel, oviposition appeared to begin once mean water temperatures reached ≈12°C.

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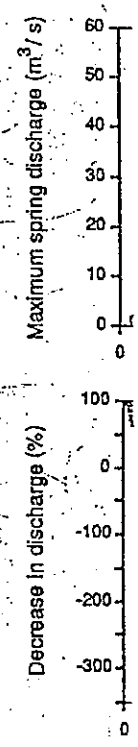

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TABLE 3. Multidimensional contingency analysis examining associations among three sources of mortality for *Rana boylii* egg masses: stranding (S), fungal attack (F), and predation (P) in 1992.

Null hypothesis	df	γ^2 (likelihood ratio χ^2)
P independent of F at all levels of S	2	0.39
P independent of S at both levels of F	2	22.2***
F independent of S at both levels of P	2	0.16
P independent of F and S	3	22.5***
F independent of P and S	3	0.41
S independent of P and F	3	22.4***

*** $P < 0.001$.

although *R. boylii* eggs have been found in water ranging from 9° to 21.5°C at other sites (Zweifel 1955). Unlike hylid pond frogs, in which breeding is positively correlated with both warm temperatures and rain (Ritke et al. 1992), breeding of rhacophorid and ranid frogs in first and second order Japanese mountain streams is positively correlated with water temperature but negatively correlated with rain (Kusano and Fukuyama 1989, Fukuyama and Kusano 1992). These behaviors may explain why, during 1994, *R. boylii* breeding started earlier and continued >2 wk longer than in previous years.

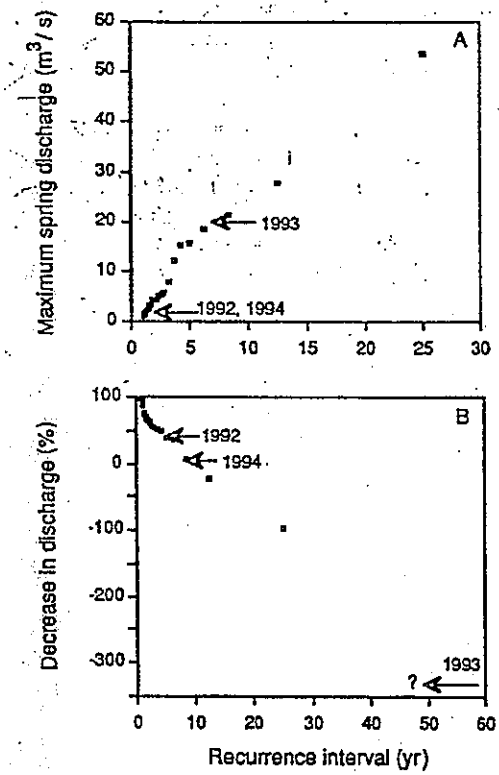

FIG. 9. Frequency of spring discharge (1946–1970) recorded at the South Fork Eel River near Branscomb, California, by the USGS. (A) Maximum mean daily discharge during the approximate oviposition period of *R. boylii*, 15 April–1 June. (B) Channel dewatering rate during the same period. Arrows indicate magnitude of discharge and dewatering during 1992–1994. The extrapolated recurrence interval for the 1993 increase in discharge is indicated by a question mark.

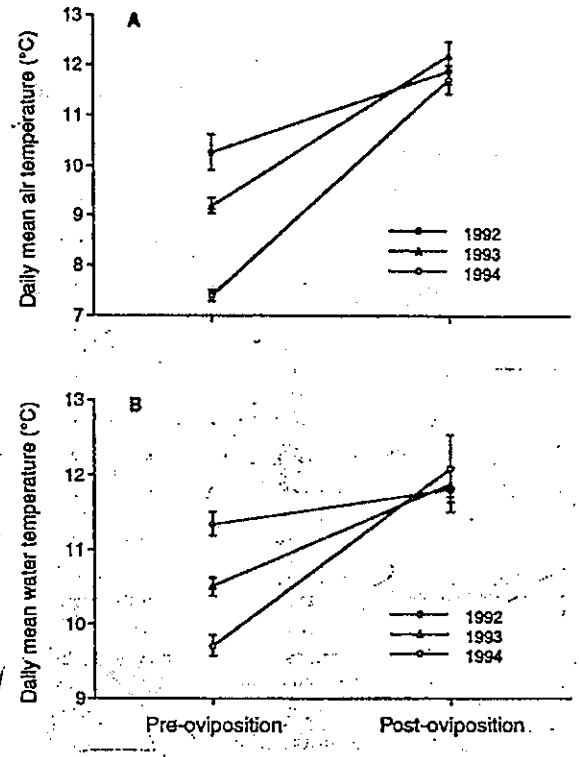

FIG. 10. Daily mean (±1 SE) temperature in the week preceding and following the appearance of the first *R. boylii* egg mass. Two-way ANOVA results for (A) air: $F_{year} = 3.3$; df = 2, 36; $P = 0.05$; $F_{pre\text{- vs. post-oviposition}} = 34$; df = 1, 36; $P \ll 0.001$; $F_{year \times pre\text{- vs. post-oviposition}} = 2.5$; df = 2, 36; $P = 0.1$; (B) water: $F_{year} = 3.6$; df = 2, 36; $P = 0.04$; $F_{pre\text{- vs. post-oviposition}} = 42$; df = 1, 36; $P \ll 0.001$; $F_{year \times pre\text{- vs. post-oviposition}} = 6.7$; df = 2, 36; $P = 0.003$.

Despite the results in 1992 and 1994 that the first 50% of clutches had greater losses to stranding and scouring than the second 50%, early breeding may be maintained because of priority advantages accrued by early breeders. For example, late-arriving males risk finding that all gravid females have already mated and laid their eggs (Wells 1977). Offspring of early-mating frogs also have priority advantages with respect to size and, hence, competitive ability as tadpoles (Wilbur and Alford 1985, Morin et al. 1990). Moreover, the phenology of algal blooms in spring and summer (Power 1992*a*) may create a situation in which food resources are less abundant for tadpoles not yet metamorphosed in the fall. There also may be insufficient time for late-metamorphosing juveniles to forage and grow in the fall before winter dormancy must begin. These conflicts among selection pressures, when superimposed on years of varying rainfall and temperature, may serve to maintain variation in oviposition timing.

Historic site use appears to be maintained, despite annual variation in river stage and breeding season. The heavily used sites in this study have been used for ≥25 yr (P. Steel, Angelo Coast Range Reserve manager, *personal communication*), suggesting that these sites have appropriate habitat at a range of river stages. It is also likely that these sites have been morphologically stable during this period. The large boulders dominating these sites do not move at bank-full discharge, i.e., at 1–2 yr recurrence intervals. The force, or critical shear stress, necessary to move the large rocks probably occurred last during storm events of 1964 (W. E. Dietrich, *unpublished data*).

Conservation and restoration implications

Amphibians and fish are important components of biodiversity. Amphibians constitute 28% of all U.S. animal species that are ranked as extinct, possibly extinct, critically imperiled, imperiled, or rare; fish constitute 34% (Master 1990). In rivers, this diversity is maintained, in part, by variation in hydrologic regime, as has been shown for fish assemblages (Grossman et al. 1982, Moyle and Vondracek 1985, Poff and Allan 1995). Under natural flow regimes, conditions favoring recruitment of one species, or set of species, fluctuate with states favoring recruitment of other species (Starrett 1951, Seegrist and Gard 1972, McElravy et al. 1989). Management strategies should therefore be dynamic to respond to species differences in links between the physical structure and flow regime of a river, and the population processes of the target organisms. Most efforts to manage physical conditions in the rivers of California and Oregon for wildlife benefit have focused on optimizing habitat and discharge for salmonids (Shirvell 1990, Flosi and Reynolds 1991, Nickelson et al. 1992). Additions of spawning gravels and high-volume releases in the spring (to trigger spring spawning runs or to get smolts out to the ocean) may be at cross-purposes to conservation of other species vulnerable to late-season floods, as is shown here for *R. boylii*.

If rivers are to be restored, enhancement plans should contain a heterogeneity of habitats and flow regimes that can sustain diverse populations. To achieve this goal, we need data that relate hydrology and channel morphology to population processes for a broad array of taxa (algae, insects, turtles, snakes, salamanders, etc.). Just as the availability of spawning gravels is recognized as essential for conservation of river-breeding salmonids, availability of frog breeding sites, i.e., broad, shallow channels with stable, large-boulder substrates that do not move under bank-full conditions, are necessary for *R. boylii* conservation. Censuses of adult frogs conducted in midsummer (Moyle 1973, Hayes and Jennings 1988) may yield a partial picture of the necessary physical conditions if the availability of breeding habitat is overlooked.

Specific recommendations for *R. boylii* conservation follow from observations of this study. Plans regarding the scale of any project should incorporate the fact that breeding habitats are embedded within the drainage network of the watershed, with heavily populated breeding sites located near tributaries that may be important adult habitats. Channel restoration plans should include the appropriate heterogeneity of elevations, grain size, and flow velocities present at repeatedly used, high-survival breeding sites. Specifically, these channels should mimic the asymmetrical cross-sectional profiles of egg sites, and should have large boulders that are stable under bank-full conditions. To provide protection from discharge fluctuation and to create oviposition sites at a range of stages, relatively low-slope benches elevated above the thalweg (main conveyance channel) should be included. In addition to sloping toward the thalweg, benches should be graded to elevate the surface of the water higher at the upstream end of the benches, so that tadpoles will follow the receding water line and end up in the low-flow channel. Instream aggregate (gravel) mining, which typically removes bars and creates a wide, flat channel, might be particularly harmful to *R. boylii* recruitment. To minimize loss of breeding habitat, mining should occur in parts of rivers not used for oviposition, such as deeper pools or reaches with few tributaries, and at times of year when frogs are more common in tributaries, i.e., fall and winter. At least in some years, releases of water from dams during the breeding season (April–June) should be timed to minimize stranding and scouring mortality, because extreme fluctuation in discharge can lead to the loss of a cohort of tadpoles, as occurred naturally during the late May flood of 1993. The absolute magnitude of peak discharge is also important, because the lowest peak discharge year, 1992, had the highest survival.

As amphibians decline (Wake 1991), we rarely know whether or not sensitive species, such as *R. boylii*, are strong interactors possessing unique traits with ramifications for other trophic levels. *R. boylii* tadpoles can enhance macroalgal standing stock on cobbles by removing diatom epiphytes, have negative competitive effects on benthic invertebrate grazers (Kupferberg 1996), and are important prey for juvenile aquatic garter snakes (*Thamnophis atratus*) (Lind and Welsh 1994; S. J. Kupferberg, *personal observation*). Because of these interactions, as well as this frog's susceptibility to displacement by non-native bullfrogs (Kupferberg 1996), conservation of *R. boylii* has implications for other components of river food webs.

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