BULLFROG (*RANA CATESBEIANA*) INVASION OF A CALIFORNIA RIVER: THE ROLE OF LARVAL COMPETITION

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Abstract. I studied the invasion of *Rana catesbeiana* (the bullfrog) into a northern California river system where bullfrogs are not native. Native yellow-legged frogs, *Rana boylii,* a species of special concern, were almost an order of magnitude less abundant in reaches where bullfrogs were well established. I assessed the potential role of larval competition in contributing to this displacement in a series of field manipulations of tadpole density and species composition. The impact of *R. catesbeiana* on native tadpoles in the natural community agreed with the outcome of more artificial experiments testing pairwise and three-way interactions. In 2-m^2 enclosures with ambient densities of tadpoles and natural river biota, bullfrog tadpoles caused a 48% reduction in survivorship of *R. boylii,* and a 24% decline in mass at metamorphosis. Bullfrog larvae had smaller impacts on Pacific treefrogs, *Hyla regilla,* causing 16% reduction in metamorph size, and no significant effect on survivorship. Bullfrog tadpoles significantly affected benthic algae, although effects varied across sites. Responses to bullfrogs in field settings were similar qualitatively to results seen in smaller-scale experiments designed to study size-structured competition among disparate age/size classes of species pairs and trios. Competition from large overwintering bullfrog larvae significantly decreased survivorship and growth of native tadpoles. Competition from recently hatched bullfrog larvae also decreased survivorship of *R. boylii* and *H. regilla.* Native species competed weakly, both interspecifically and intraspecifically. The only suggestion of a negative impact of a native species on bullfrogs was a weak effect of *H. regilla* on recent hatchlings. Competition appeared to be mediated by algal resources, and there was no evidence for behavioral or chemical interference. These results indicate that, through larval interactions, bullfrogs can exert differential effects on native frogs and perturb aquatic community structure.

Key words: algae; biological invasions; California; grazing; Hyla regilla; Rana boylii; Rana catesbeiana; *rivers; size-structured competition.*

INTRODUCTION

Biological invasion poses a serious threat to freshwater biodiversity (Allan and Flecker 1993). Invasions have been implicated in 68% of the forty North American fish extinctions that have occurred since the turn of the century (Miller et al. 1989). A high proportion of endemic aquatic animals are at risk relative to terrestrial fauna (Master 1990). Amphibians are of particular concern because of their apparent global population declines (Blaustein and Wake 1990, Wake 1991), their sensitivity to a wide array of environmental stressors (Harte and Hoffman 1989, Carey 1993, Pounds and Crump 1994, Blaustein et al. 1994*a*), and their susceptibility to local and global extinctions (Blaustein et al. 1994*b*).

Declines of native ranid frogs in western North America have coincided with introductions and subsequent range expansions of the bullfrog, *Rana catesbeiana* (Moyle 1973, Bury and Luckenbach 1976,

Green 1978, Hammerson 1982, Clarkson and DeVos 1986, Clarkson and Rorabaugh 1989). Bullfrogs, although native to North America, are alien west of the Rocky Mountains (Stebbins 1985). They have been introduced around the world, including Europe (Albertini and Lanza 1987, Stumpel 1992), South America, and Asia (M. J. Lannoo, *unpublished report*, Declining Amphibian Task Force, IUCN). In California, bullfrogs were first introduced in 1896 (Heard 1904) for human food after populations of native frogs, particularly *Rana aurora,* the red-legged frog, were overharvested (Jennings and Hayes 1985). The role of bullfrogs in native ranid declines is unclear because there have often been concurrent alterations of aquatic habitats, changes in land use of adjacent terrestrial habitats, and introduction of non-native fishes (Hayes and Jennings 1986), which can devastate populations by predation on tadpoles (Bradford 1989, Bradford et al. 1993).

I studied bullfrog impacts in a watershed where invasion has only recently occurred and which remains relatively pristine. Here I present observations that where bullfrogs are well established in otherwise unaltered river habitats, breeding populations of the native ranid are much lower than populations upstream
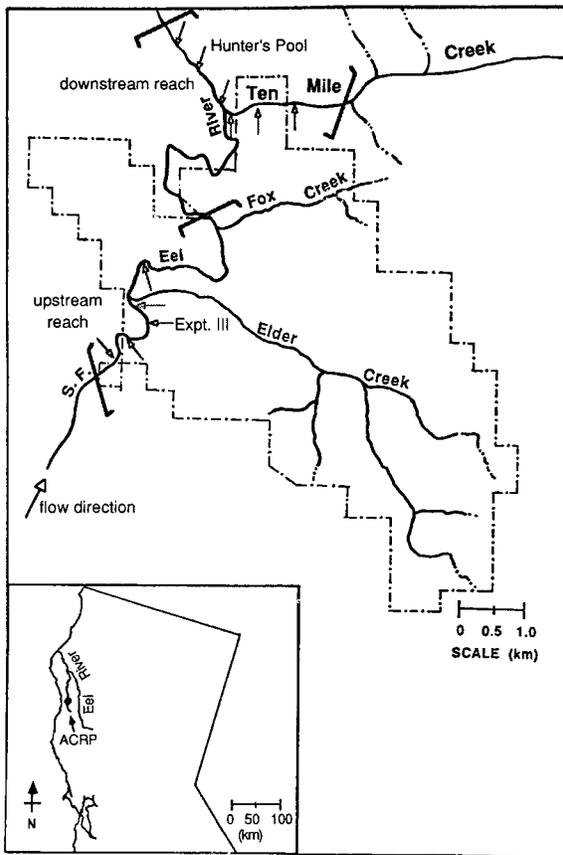
FIG. 1. Location of the Angelo Coast Range Reserve in northern California. Brackets mark the upstream native-frog and downstream bullfrog study reaches on the South Fork Eel River and Ten Mile Creek. Arrows indicate location of transects and experimental sites.

of the invasion front. I also present experimental evidence that bullfrog tadpoles have negative impacts on native frogs. To determine what role larval competition may play in the exclusion of native frogs by bullfrogs, I investigated: (1) The relative competitive abilities of different size classes of native and invading tadpoles; (2) The impact of bullfrogs on native frogs and algal food resources in larger enclosures in the natural river; and, (3) The potential role of chemical interference or feces-borne pathogens as mechanisms of competition.

Natural History and Study System

This research was conducted in two rivers at the Angelo Coast Range Reserve, Mendocino Co., California (39°44′ N, 123°39′ W) (Fig. 1). The watershed of the South Fork Eel River is sparsely populated by humans and is dominated by mixed coniferous forest and oak–madrone woodland. Ten Mile Creek, a tributary of similar drainage area, flows through grazed pastures. Stock ponds and recreational fishing ponds along these rivers are possible sources of invading bullfrogs, which began to appear on the reserve coincident

with a multi-year drought in the late 1980s (Kupferberg 1996*a*). The native anurans include the foothill yellow-legged frog, *Rana boylii,* a California Species of Special Concern (Jennings and Hayes 1994) and the Pacific treefrog, *Hyla regilla.*

I investigated larval competition rather than predation by adult bullfrogs (Moyle 1973) because adults did not exhibit the same degree of habitat and resource overlap as larvae. *R. boylii* commonly occurred along shaded steep gradient tributaries and *Hyla* were widely dispersed throughout the forests and meadows of the surrounding watershed, habitats not used by bullfrogs. Gut contents of adult and juvenile bullfrogs collected on site did not include native frogs (C. Bailey, *unpublished data*). All three species were found to use the main stem South Fork Eel River and Ten Mile Creek to breed. Larval competition was suggested because feces of the three tadpole species contained similar diatoms, algae, and detritus.

As is typical for rivers experiencing the winter flood–summer drought hydrologic conditions of a mediterranean climate, algal blooms occurred in the late spring when discharge declined and the rock bedded river was clear and sunlit. In this system the dominant alga is *Cladophora glomerata,* a periphytic filamentous green alga. The growth of *Cladophora* turfs on rock substrates is controlled by both hydrologic and trophic conditions including limited nitrogen availability (Power 1992*a*). When *Cladophora* is overgrown by taxa not susceptible to nitrogen limitation, such as the cyanobacteria *Nostoc* and diatoms in the genus *Epithemia,* the algae slough off and float to the surface. The abundance of floating algae therefore indicates tadpole food quality. The epiphytes can completely cover the filaments of host algae, and tadpoles can effectively remove diatoms from *Cladophora* (Kupferberg 1997). Diatoms increase the nutritional value of *Cladophora* because the most common epiphytes, *Epithemia* spp., contain nitrogen fixing cyanobacterial endosymbionts. The protein content of *Cladophora* with epiphytes is 11.3% of dry mass vs. 5.8% without (Kupferberg et al. 1994). In addition, epiphytes store excess photosynthate as lipid rather than carbohydrate so *Cladophora* with epiphytes has higher fat than *Cladophora* without epiphytes. *Hyla regilla* (Kupferberg et al. 1994) and *R. boylii* (Kupferberg 1996*a*) tadpoles fed diets rich in diatoms had enhanced growth, development, and survival to metamorphosis.

Differences among the three species in size, seasonal timing of oviposition, and time to metamorphosis set the stage for size-structured competition (Werner 1994, Wilbur 1984). Maximum total lengths are 4.4 cm for *H. regilla* tadpoles, 5 cm for *R. boylii,* and 16.2 cm for *R. catesbeiana* (Stebbins 1985). *Hyla* bred from early spring to late summer, beginning in wet meadows and ponds and then using the river as the dry season progressed. *R. boylii* oviposited in the river during the first few weeks of May. *R. catesbeiana* oviposited in July

TABLE 1. Treatments in small scale competition experiments comparing tadpoles of different species at different densities (Experiments I, with large bullfrog tadpoles; and II, with small bullfrog tadpoles). Treatment names are the initials of the species stocked, with a subscript indicating the number of individuals.

| | Total tadpole density (inds./bucket) | | | |
Species	0	2	4	6
No tadpoles	control			
Hyla regilla (native)		Hr_2	Hr_4	
Rana boylii (native)		Rb_2	Rb_4	
Rana catesbeiana (invader)		Rc_2	Rc_4	
H. regilla + R. boylii			Hr_2Rb_2	Hr_3Rb_3
H. regilla + R. catesbeiana			Hr_2Rc_2	Hr_3Rc_3
R. boylii + R. catesbeiana			Rb_2Rc_2	Rb_3Rc_3
H. regilla + R. boylii + R. catesbeiana				$Hr_2Rb_2Rc_2$

in the river and tadpoles had to overwinter to metamorphose. Early in the summer, recently hatched *R. boylii* overlapped temporally with large bullfrog larvae. Later in the summer, recently hatched bullfrogs overlapped temporally with 7–9 wk old *R. boylii* tadpoles. Both ranids encountered a wide age/size range of *Hyla* tadpoles.

METHODS

Patterns of distribution

To document the spatial distribution of native and invading frogs along the invasion front I conducted censuses along 9.3 km of river. From 1991 to 1995, I censused second-year bullfrog tadpoles along permanent 1 m wide cross-river transects ($n = 6$ downstream bullfrog sites, and $n = 5$ upstream non-bullfrog sites) (Fig. 1). I also censused eggmasses of *R. boylii* from 1992 to 1996. In the upstream reach, I searched 3.25 km in 1992, 4.9 km in 1993, and 5.3 km in subsequent years. In the downstream reach I searched 2 km in 1992 and 4 km in each of the subsequent years of the study. *R. boylii* congregated at the same breeding sites each spring to breed. Breeding sites were located in the margins of wide shallow channel reaches and ranged in size from 2 × 10 m to 5 × 70 m, were separated from other breeding sites by up to several hundred meters, and contained a range of 2 to 60 clutches per site. Because each female laid one discrete clutch of eggs, these counts indicate reproductive female population sizes.

Competition experiments

Experiment I: Bullfrog size advantage, small scale enclosures.—This experiment, designed following the recommendations of Underwood (1986: Table 11.2), assessed the relative competitive status of recently hatched *R. boylii* and *H. regilla,* and of overwintered *R. catesbeiana* tadpoles. Treatments (Table 1) included each species alone at two tadpoles per enclosure (28 individuals/m²), single species and species pairs at four tadpoles per enclosure (56 individuals/m²), and species pairs and trios at six tadpoles per enclosure (84 indi-

viduals/m²). A control treatment, with respect to algal consumption, contained no tadpoles. Each treatment was replicated four times, and treatments were assigned randomly among 56 enclosures. Enclosures were 12.7-L, 30 cm diameter plastic flow-through buckets with two windows, each 23 × 31 cm, and lids, of 1-mm fiberglass mesh. The experiment ran 13 Jun–11 Jul 1992.

R. catesbeiana tadpoles that had overwintered were caught in the South Fork Eel near the confluence with Ten Mile Creek and transported to the site of the enclosures. Native tadpoles were collected as egg masses and recently hatched tadpoles at the experiment site. Bullfrog and *R. boylii* tadpoles were weighed in batches on an Ohaus Port-o-gram balance to the nearest 0.1 g and per capita mass calculated (bullfrog = 19.5 ± 3.1 g, *R. boylii* = 0.05 ± 0.009 g). Groups of *Hyla* tadpoles were too light for accurate measurement but were visually similar in size. Tadpoles were randomly assigned to treatments and buckets. No significant differences among treatments in starting tadpole size were detected.

Tadpole mortality was monitored weekly for 4 wk. Dead individuals were replaced with tadpoles of similar size held in replacement buckets for that purpose. Replacement was necessary to maintain the same density conditions in all replicates of a treatment. If each replicate is considered as a potential ''sink'' habitat (sensu Pulliam 1988) with an arbitrary number of tadpoles equal to the treatment density, then replacements represented individuals moving in from a ''source'' population. To determine whether patches dominated by bullfrog tadpoles were greater ''sinks'' than patches dominated by conspecifics or native competitors, I compared the rates at which patches depleted sources of new individuals.

I calculated tadpole loss rate as the number of tadpoles added to a replicate each week divided by the initial number for that treatment. One-way ANOVAs tested for treatment effects on arcsine (proportion replaced). Twenty-two comparisons of treatment means were planned for the native species as targets of com-

TABLE 2. ANOVA of tadpole loss, arcsine (proportion tadpoles replaced per week), in Experiment I (described in Table 1).

ANOVA

Target species	Source of variation	MS	df	F	P
Hyla regilla	Treatment	0.24	6	8.7	<0.0001
	Plus-bullfrog treatments vs. natives only	1.2	1	44.7	<0.0001
	Error	0.571	21		
Rana boylii	Treatment	0.37	6	10.3	<0.0001
	Plus-bullfrog treatments vs. natives only	0.15	1	4.2	0.05
	Error	0.036	21		

Pairwise treatment comparisons†

	Hyla regilla as target		*Rana boylii* as target	
Effects of	Comparison	P	Comparison	P
1) Intraspecific competition	Hr_4 vs. Hr_2	0.69	Rb_4 vs. Rb_2	0.92
2) Interspecific competition with:				
a) Native	Hr_2Rb_2 vs. Hr_2	0.58	Hr_2Rb_2 vs. Rb_2	0.07
b) Native in presence of invader	$Hr_2Rb_2Rc_2$ vs. Hr_2Rc_2	0.02	$Hr_2Rb_2Rc_2$ vs. Rb_2Rc_2	0.06
c) Invader	Hr_2Rc_2 vs. Hr_2	0.03	Rb_2Rc_2 vs. Rb_2	0.08
d) Invader in presence of native	$Hr_2Rb_2Rc_2$ vs. Hr_2Rb_2	0.0004	$Hr_2Rb_2Rc_2$ vs. Hr_2Rb_2	0.07
e) Invader and native combined	$Hr_2Rb_2Rc_2$ vs. Hr_2	0.0001	$Hr_2Rb_2Rc_2$ vs. Rb_2	0.001
3) Inter- vs. intraspecific competition				
a) Native vs. self	Hr_2Rb_2 vs. Hr_4	0.58	Hr_2Rb_2 vs. Rb_4	0.08
b) Invader vs. self	Hr_2Rc_2 vs. Hr_4	0.015	Rb_2Rc_2 vs. Rb_4	0.1
4) Interspecific competition with:				
a) Invader relative to native	Hr_2Rc_2 vs. Hr_2Rb_2	0.1	Rb_2Rc_2 vs. Hr_2Rb_2	0.9
	Hr_3Rc_3 vs. Hr_3Rb_3	0.0008	Rb_3Rc_3 vs. Hr_3Rb_3	<0.0001
b) Invader and native combined relative to native alone	$Hr_2Rb_2Rc_2$ vs. Hr_3Rb_3	0.0001	$Hr_2Rb_2Rc_2$ vs. Hr_3Rb_3	0.0008

Notes: Pairwise comparisons test the null hypothesis that the difference between treatment means is zero. Effects are significant if P values are below the Bonferroni-adjusted $\alpha = 0.0023$.

† Treatment names are the initials of the species stocked, with a subscript indicating the number of individuals.

petition (Table 2). The Bonferroni-adjusted $\alpha = 0.0023$.

Enclosures were also stocked with 100 g of *Cladophora* (damp mass). To obtain uniform water content, algal turfs were harvested from rocks and spun 50 revolutions in a salad spinner to reduce superficial water (Hay 1986, Power 1990). Algae were weighed weekly. Buckets and screens were scrubbed to remove periphyton and prevent tadpoles from grazing on anything but the allocated algae. Thirty grams of algae were added to each bucket during week three, when some treatments had very little algae remaining. Repeated-measures ANOVA tested for bullfrog effects on algal depletion.

All analyses were conducted using SYSTAT (Wilkinson 1992).

Experiment II: Native species size advantage, small scale bullfrog enclosures.—To mimic the natural hatching priority conditions, Experiment I was repeated with different size classes of competitors, and ran from 27 Jul to 10 Aug 1992. Recently hatched *R. catesbeiana* larvae (mass = 0.38 ± 0.14 g) were paired with older larvae of *R. boylii* (1.14 ± 0.26 g) and *H. regilla* (0.1 ± 0.04 g). At initiation of the experiment, tadpoles and algae were randomly assigned to treatments and each

treatment was replicated four times. There were no significant size differences among treatments. Buckets received cobbles covered with attached turfs of *Cladophora*, because loose *Cladophora* was not abundant at that time. After 2 wk, tadpole survival was measured. No mortality replacement occurred. I measured length of *Cladophora* turf to the nearest 0.5 cm at three evenly spaced intervals on each cobble.

The overall effects of competition between native species and between natives and invaders were assessed using Kruskal-Wallis tests, due to non-normality and heteroscedasticity. Data for *Hyla* and *R. boylii* in treatments with bullfrogs were pooled and contrasted with means from treatments with only native competitors. For bullfrog data, contrasts were made between bullfrog-only treatments and treatments in which *Hyla* or *R. boylii* were present. One-way ANOVA tested for treatment effects on algae.

Experiment III: Natural community bullfrog enclosures.—To determine the impact of bullfrog invasion within the context of the resident benthic community, I manipulated tadpole species composition and density in screened pens enclosing two square meters of natural river substrate. Treatments were ambient densities of native tadpoles with or without bullfrog tadpoles (*n* =

6 enclosures/treatment). The experimental site, a reach ≈70 m long between two riffles, was used for oviposition by both native frog species. Space constraints required that half of the enclosures be placed in a portion of the pool that, as flows declined during the summer, became separated from the main channel of the river by a berm of sedges and boulders. Treatments were randomly assigned to enclosures. The experiment ran 60 d: 16 Jul–13 Sep 1992.

1. *Enclosures.*—Wood frame boxes (1 × 2 m) were covered with 1-mm fiberglass mesh stapled on the sides. The mesh extended 30 cm beyond the bottom of the frame, forming a skirt that was folded out to the exterior, thereby minimizing disturbance to the enclosed substrate. Rocks and gravel anchored the skirt to prevent escape of tadpoles. A horizontal flap of 20 μm thick (8 mil) clear plastic 25 cm wide was glued on to the top perimeter of each enclosure to prevent treefrogs from entering to oviposit, to prevent escape of recent metamorphs, and to keep snakes out. Previous experience indicated that snakes and frogs could not negotiate such overhangs. Each enclosure served as a large sampling device. When an enclosure was placed in the river, native tadpoles were enclosed; few were observed to be laterally displaced during installation. Tadpoles were removed from enclosures by hand. Then fish were caught with an electroshocker. There were, on average, less than one fish ≥5 cm standard length per enclosure, so any fish that large was released outside the enclosure. Smaller fish were not manipulated. Other infrequently observed vertebrates like newts, salamanders, and snakes were also removed. Tadpoles were then pooled and equally redistributed among enclosures. *H. regilla* larvae were stocked at 8.5 individuals/m² and *R. boylii* at 10 individuals/m². Recently hatched and overwintered bullfrog tadpoles were stocked at densities of 16.5 and 2 individuals/m², respectively, densities within the natural range observed.

2. *Sampling regimes.*—I measured foraging behavior, survival to metamorphosis, and size at metamorphosis. I made focal animal observations (sensu Altmann 1974) of tadpole activity and feeding behavior at each enclosure 12 d after the experiment began. After approaching an enclosure, I stood still for 10 min allowing animals to return to normal activity patterns. I watched three individuals of each species for 1–3 min, and noted time spent actively feeding and time spent resting. I observed all enclosures on the same day around the middle of the day when all enclosures were in full sun, thus minimizing confounding effects of date or time of day. Pens were checked daily for metamorphs. When tail reabsorption was complete, metamorphs were caught, weighed, and released outside the enclosure.

I sampled standing stocks of benthic algae and detritus three times: before treatments were established, at the midpoint, and at the end of the experiment. Each enclosure was sampled using a 13 cm diameter corer,

with two subsamples on boulders where algal turfs grew and two in sediment. The logistics of placing the hard framed pens onto the uneven topography of the river bed resulted in each enclosure having a couple of similarly sized boulders surrounded by less coarse sediment. Six 2-m² open areas adjacent to the enclosures were sampled as controls. Samples were preserved in ethanol. After removing benthic invertebrates from preserved samples, ash free dry mass (AFDM) was measured by drying samples at 60°C for 24 h and then incinerating in a muffle furnace at 510°C for 1 h. Data from each core type were averaged for each enclosure. At the start of the experiment there were no significant differences in biomass of algal turfs or detritus in sediment among treatments. Floating algae were harvested when blooms occurred, not at regular intervals. At the end of the experiment, each enclosure was sampled using a 6 cm diameter rubber gasket and scraping algae off the rocks within the sealed area (10 subsamples per enclosure and adjacent control areas). Samples from this final harvest were not preserved, but processed fresh for AFDM.

Before bullfrog tadpoles were added to enclosures, temperature was monitored hourly for 48 h using a multiplex array of thermistors connected to a data logger. Thermistors placed in shallow and deep ends of enclosures and adjacent open river sites indicated similar temperatures in all three categories.

Screens were scrubbed weekly to prevent fouling. Dead tadpoles were removed daily to prevent spread of diseases. One second-year bullfrog tadpole died within a few days of the start of the experiment and was replaced, otherwise dead tadpoles were not replaced.

The experiment concluded when no native tadpoles remained in either treatment. Bullfrog tadpoles were caught by hand. Enclosures were then electroshocked until there were two passes with no bullfrogs detected.

3. *Statistics.*—Nested ANOVAs tested for bullfrog effects on tadpoles. Data from individual tadpoles were nested within enclosures, as is appropriate when "experimental treatment is replicated on several batches of animals" (Underwood 1981:550). Proportion of time spent feeding was arcsine transformed. Size at metamorphosis data was natural log transformed. Two-way ANOVAs tested for effects of location (main stream channel vs. side pool) and treatment × location interactions on algal mass and tadpole production (ln total metamorph mass per replicate). Because of the prediction that bullfrogs would decrease native tadpole performance, multiple tests of bullfrog effects were treated as one-tailed tests, $\alpha = 0.1$, using a sequential Bonferroni adjustment (Rice 1989).

Path analysis (Sokal and Rohlf 1981, Hayduk 1987) determined the relative importance of direct and indirect effects. I hypothesized that there was a direct path from bullfrogs to native frogs as well as an indirect path from bullfrogs through algae to native frogs. Vari-

ables in the path analysis were: (1) presence vs. absence of bullfrogs; (2) location of enclosures in side-pool or main channel; (3) production of *H. regilla*; (4) production of *R. boylii* (sum of the masses of each species of native metamorph leaving an enclosure); (5) high food quality algal production (rank transformations [Conover and Iman 1981] of floating algal biomass consisting of senescing, heavily epiphytized *Cladophora,* and *Nostoc,* both of which taxa are high in protein and lipids and enhance tadpole growth and development [Kupferberg et al. 1994]; and (6) production of lower food quality attached algae (biomass at experiment midpoint, which indicates bullfrog-modified conditions). A predicted correlation matrix among these variables was derived from the hypothesis. The predicted correlation between any two variables was calculated as the sum of the path coefficient associated with the direct path between the two variables and the products of the path coefficients in the indirect paths. I compared the predicted and observed correlations using a chi-square goodness of fit test (Wootton 1994: Appendix I).

Experiment IV: Fecal pathogen or waterborne chemical interference.—To determine whether waterborne pathogens or allelopathic chemicals could be responsible for the bullfrog effect, I conducted a ''cages within cages'' experiment in 1993 (19 Jul–23 Sep). I focused on *R. boylii* because it was the native species with the strongest response to bullfrogs in the previous summer's experiments. *R. boylii* tadpoles were stocked in plastic wading pools (four tadpoles per 0.8-m² pool) that were placed in shallow water along a gravel bar. This density was lower than the previous summer but accurately reflected ambient density in 1993. Wading pools were left with solid walls as enclosed systems because exchange with the open river might dilute any pathogen or chemical. A smaller enclosure, a screened bucket of the type described for Experiments I and II, with the bottom replaced by 6.4-mm plastic Vexar mesh, was placed in the center of the pool elevated a few centimeters off the bottom by small rocks. Each small enclosure and each pool was stocked with 50 g (damp mass) epiphytized *Cladophora.* Half of the small enclosures were randomly chosen to receive five bullfrog tadpoles. Bullfrog feces fell through the mesh and deposited in the wading pool. First-year tadpoles were used because second-year bullfrogs were scarce after heavy flooding during the preceding winter. Dead tadpoles were replaced to maintain equivalent densities in all replicates. Replacements came from replicates maintained for that purpose. Tadpoles were weighed at the start of the experiments (*R. boylii* = 0.39 ± 0.03 g, bullfrogs = 1.36 ± 0.06 g), 28 Aug, and at the end. The experiment concluded when the first *R. boylii* metamorphosed. Repeated-measures ANOVA, with initial size as a covariate, tested for treatment effects on growth.

Tadpole density estimates

To compare large bullfrog tadpole densities in Experiments I and III with the ranges of densities occurring naturally, I converted bullfrog transect data from 14 and 18 Jun and 30 Jul 1992 into number of tadpoles per unit area. To convert the results of cross stream snorkel transects to density I distinguished how frequently tadpoles occurred in a habitat (i.e., near shore or mid-channel) from how closely tadpoles were packed when they were present. Since competition occurs only where the tadpoles are, I did not average in zeroes from routinely unoccupied habitats, such as deep areas and areas with high flow velocity.

To compare small bullfrog tadpole densities with experimental densities, bullfrogs were also observed at their breeding location, Hunter's Pool (Fig. 1). Bullfrog tadpole densities were observed there on 18 Jun, 16 Jul, and 30 Jul. Overwintering bullfrog tadpoles densities were estimated by observation from shore because their skittishness made counting difficult while snorkeling. When startled they disappeared into visually impenetrable mats of vegetation, so the number basking at the surface was counted. This likely underestimated density as those below the surface could not be seen. A 1-m² white PVC (polyvinyl chloride plastic) quadrat was placed at the surface of a vegetation mat for reference. I measured densities of young of the year bullfrog tadpoles, which occupied more open areas, by counting the number of tadpoles in 0.25-m² quadrats while snorkeling.

To count native tadpoles at the 70 m long site of Experiment III I used a stratified random sampling scheme. For each ten meters in length of the site, I randomly chose a distance for a cross stream transect using ten sided dice (Kotanen 1992), for a total of seven transects. On 15 Jun 1992 I censused these transects at 1-m intervals using a bottomless bucket enclosure as a sampling device. On 15 Jul, densities were again measured when all tadpoles in the large enclosures were caught and redistributed.

RESULTS

Frog distributions along the invasion front

Where bullfrogs were well established in Ten Mile Creek, and in the South Fork Eel River below its confluence with Ten Mile Creek, the native foothill yellow-legged frog, *Rana boylii,* was rare relative to uninvaded areas upstream from the confluence. In the downstream study reaches, I counted 9.6 ± 6.3 tadpoles per transect (*n* = 5 yr). Upstream I did not see any bullfrogs during regular surveys but caught two or three large bullfrog tadpoles each summer. *Rana boylii* were rare where bullfrogs were common. I found almost an order of magnitude fewer clutches per unit length of river course in bullfrog reaches (Fig. 2a). It is possible that there are fewer geomorphically appropriate breeding sites per unit length of the river as it increases in flow and
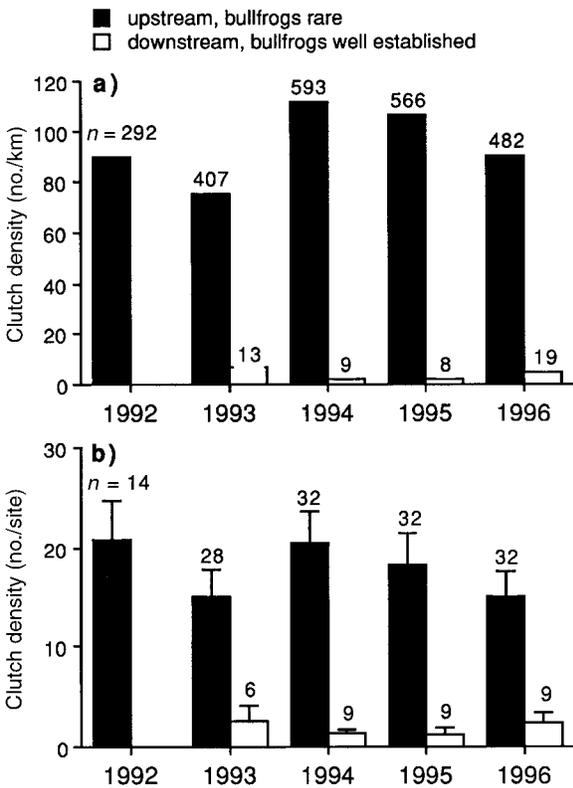
Fig. 2. Abundance of *Rana boylii* eggmasses in the absence and presence of invading bullfrogs on two bases: (a) per unit length of river course, and (b) per breeding site (mean + 1 SE). Sample sizes indicate (a) total number of clutches found, and (b) number of breeding sites. Downstream reach not censused in 1992.

channel width downstream, but the number of clutches per site was also much lower in bullfrog reaches (Fig. 2b).

Experiment I: Bullfrog size advantage, small-scale enclosures

Species relations.—Bullfrog tadpoles had strong effects on native tadpole mortality, as shown by the significant difference between treatments with bullfrogs and those with natives only (Table 2). In contrast, native tadpoles did not compete heavily with each other (Table 2, comparisons 1, 2a, 2b). Native tadpoles had no effect on bullfrog tadpoles; all survived. The combined effects of bullfrogs and a native interspecific competitor (comparison 2e, Table 2) were highly significant. Bullfrogs plus *R. boylii* caused a six-fold increase in *Hyla* loss. Similarly, bullfrogs plus *Hyla* increased *R. boylii* loss 4.75-fold. In most cases the loss of *Hyla* and *R. boylii* tadpoles was greater when both bullfrogs and native interspecific competitors were present than when only native competitors were present (Fig. 3). The effect of bullfrogs on *Hyla* in the presence of *R. boylii* was significant but the effect of bullfrogs on *R. boylii* in the presence of *Hyla* was not statistically

significant (Table 2, comparison 2d). The effects of bullfrogs and natives combined compared to the effects of the native competitors at equal density were significant for both *Hyla* and *Rana* (Table 2, comparison 4b). These results indicate that native species survival was higher when they competed with each other at high density than when they competed with each other plus the invader. Although the density of *Hyla* and *R. boylii* is different between the treatments compared in 4b, any possible effects can be ignored because the comparisons above indicated that native inter- and intraspecific competition was negligible.

Algae.—Bullfrog tadpoles significantly reduced algal mass (Fig. 4, Table 3). Algae in controls grew relative to all tadpole treatments during the first week but then began to senesce as the algal mass had become overgrown with epiphytes and infested with midges (Chironomidae), known to be effective grazers in this system (Power 1990). Bullfrog larvae significantly diminished algal resources relative to native-tadpole treatments and no-tadpole controls.

Experiment II: Native tadpole size advantage, small-scale enclosures

Species relations.—Loss of native tadpoles in the presence of recently hatched bullfrog tadpoles was sim-
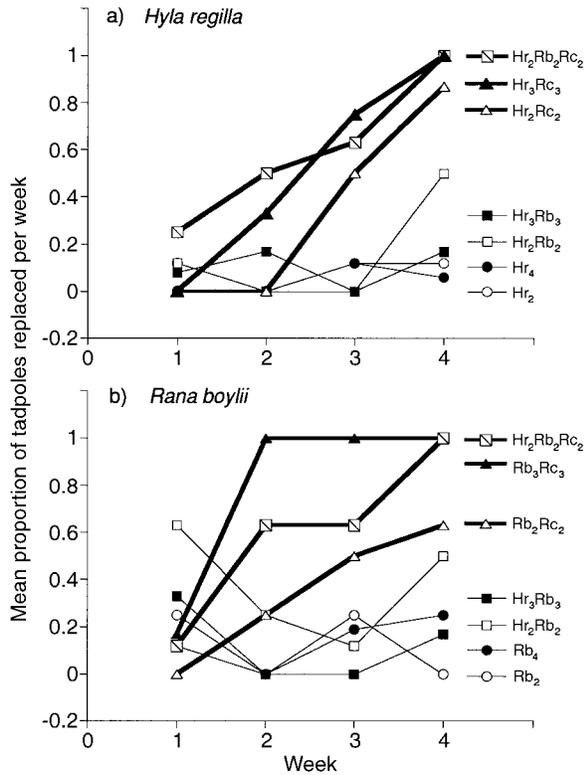

Fig. 3. Replacement of (a) *Hyla* and (b) *Rana boylii* tadpoles in the presence of bullfrogs (bold lines) and with native competitors (thin lines) in Experiment I. Treatment names are the initials of the species stocked with a subscript indicating the number of individuals. Comparisons of means are reported in Table 2.
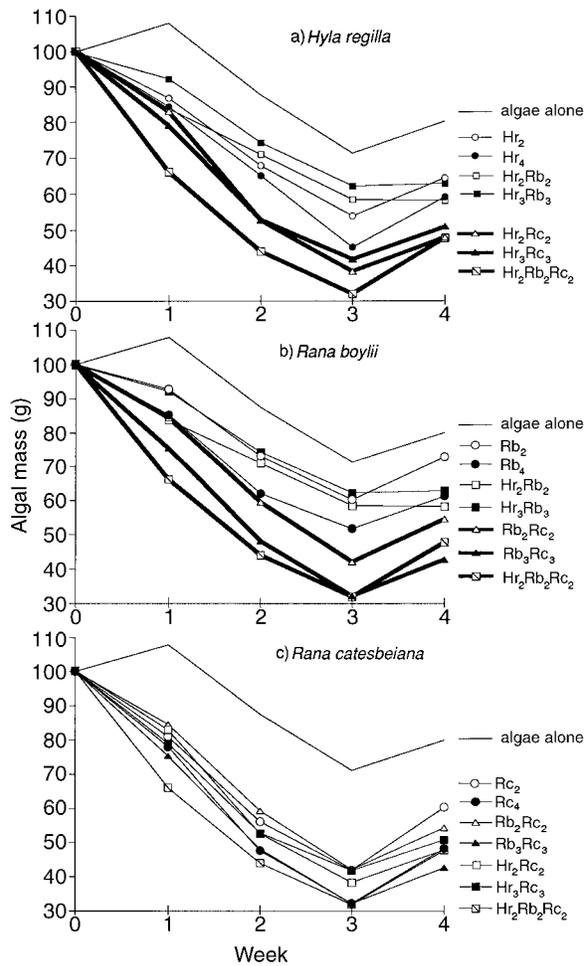
FIG. 4. Damp algal mass (Experiment I) in the presence of (a) *Hyla,* (b) *R. boylii,* and (c) *R. catesbeiana.* Treatment names are the initials of the species stocked, with a subscript indicating the number of individuals. Some treatments are repeated. Algal resources were significantly lower in the presence of bullfrog larvae (thick lines), relative to treatments with native tadpoles (thin lines).

ilar to the response to large bullfrog tadpoles (Fig. 5). Overall treatment effects, however, were not significant, so data from ''plus bullfrog'' and ''natives only'' treatments were pooled. Because inter- and intraspecific competition between the native species was weak in the previous experiment, this pooling is reasonable. For bullfrogs the collapsed treatments were: bullfrogs alone, bullfrogs with *Hyla,* and bullfrogs with *R. boylii.* Bullfrog effects were significant for *Hyla* and *R. boylii* (Table 4). The decrease in survival of *R. catesbeiana* in the presence of *Hyla* suggests interspecific competition but the effect is not statistically significant.

Algae.—No effect of treatment on periphyton abundance was observed (one-way ANOVA of mean algal turf length, $F_{13,42} = 0.95$, $P = 0.51$).

Experiment III: Impacts of bullfrogs in natural community enclosures

Metamorphosis.—Bullfrog tadpoles had adverse effects on the metamorphosis of *R. boylii* but not *Hyla* tadpoles from 2-m^2 enclosures of natural river substrate (Fig. 6 and Table 5). *R. boylii* survival was 48% lower in the presence of bullfrogs, whereas *Hyla* survival was almost equal between treatment and control. Mass at metamorphosis was 24% lower in bullfrog enclosures for *R. boylii* and 16% for *Hyla. R. boylii* metamorphs caught in the open river were very similar in mean size to those raised in enclosures without bullfrogs: mass$_{open}$ = 1.16 ± 0.14 g (mean ± 1 SE), $n = 7$ individuals vs. mass$_{-bullfrog}$ = 1.18 ± 0.16 g, $n = 87$ individuals. Location of enclosures did not influence native metamorph production (for *R. boylii,* $F(location)_{1,8} = 2.3$, $P = 0.17$, $F(treatment \times location)_{1,8} = 0.6$, $P = 0.62$; for *Hyla,* $F(location)_{1,8} = 1.5$, $P = 0.26$, $F(treatment \times location)_{1,8} = 0.32$, $P = 0.59$.

Behavior.—Bullfrog tadpoles did not significantly change the proportion of time spent feeding by *Hyla* and *R. boylii. Hyla* foraged 28.9 ± 11.8% of the time (mean ± 1 SE) in the absence of bullfrogs vs. 17.3 ±

TABLE 3. Repeated-measures analysis of *Cladophora* consumption by tadpoles in Experiment I (described in Table 1).

Source	Mean square	Wilks' lambda	df	F	P
Analysis of differences (MANOVA)					
Time		0.046	4, 39	200	1×10^{-14}
Time × Treatment		0.28	52, 153	1.16	0.24
Analysis of totals (ANOVA)					
Treatment	1 493.8		13	3.6	0.0008
Plus-bullfrog vs. no-tadpole control	11 692.0		1	28.2	0.4×10^{-5}
Plus-bullfrog vs. native-only treatments	8 487.8		1	20.5	0.5×10^{-5}
Natives only vs. control	35 548.2		1	8.57	0.005
Error	414		42		

Notes: For the four univariate tests of treatment effects on *Cladophora* mass totaled across weeks 0–4, the Bonferroni-adjusted $\alpha = 0.0125$.
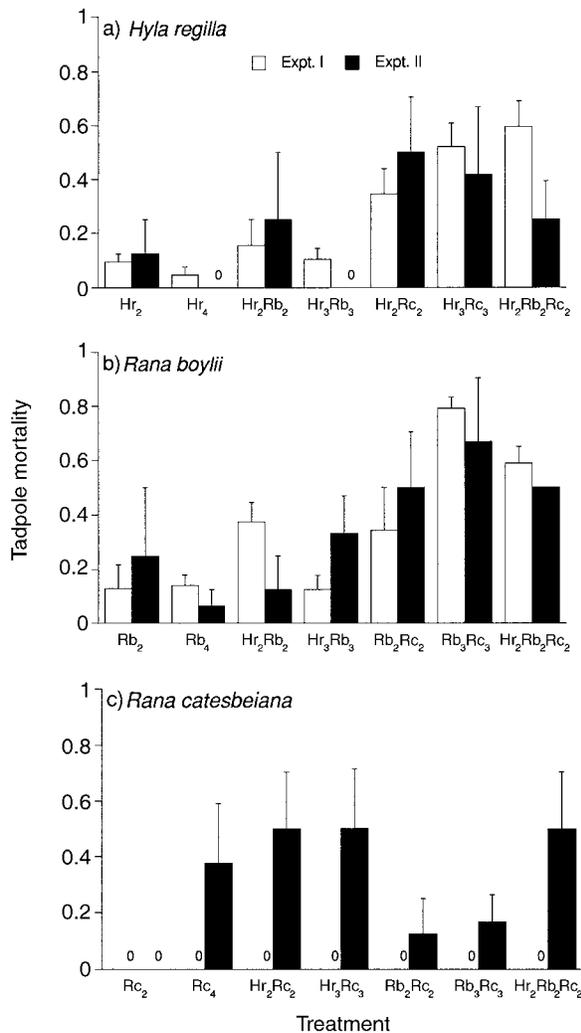
FIG. 5. Tadpole mortality (means and 1 SE) in Experiment II (dark bars). The proportions of tadpoles replaced in Experiment I are plotted with light bars. Treatment names are the initials of the species stocked, with a subscript indicating the number of individuals. See Table 4 for significance of treatment effects.

7.1% of the time in the presence of bullfrogs (ANOVA of arcsine proportional activity: $F_{1,10} = 0.697$, $P = 0.42$). *R. boylii* foraged $9.1 \pm 3.7\%$ without bullfrogs and $12.1 \pm 4.9\%$ with bullfrogs ($F_{1,10} = 0.2$, $P = 0.67$). Recently hatched bullfrog tadpoles fed $35 \pm 8.0\%$ of the time and large bullfrog tadpoles were less active, feeding $13.5 \pm 8.6\%$ of the time. When activity levels among these four groups of tadpoles are compared with ANOVA ($F_{3,32} = 2.7$, $P = 0.06$) the only difference near statistical significance was that between first-year bullfrog tadpoles and *R. boylii* ($P = 0.056$).

Algae.—By the end of the experiment, there were differences in the abundance of attached algae between bullfrog enclosures, native-tadpole enclosures, and adjacent open river sites (Fig. 7). In the absence of bullfrogs algal standing stock in enclosures mirrored the unenclosed areas. In bullfrog enclosures, however, algal abundance was higher than ambient in the main channel and lower than ambient in the sidepool. This response is represented by the significant interaction between treatment and location: $F(\text{treatment})_{2,12} = 0.43$, $P = 0.66$; $F(\text{location})_{1,12} = 0.22$, $P = 0.65$; $F(\text{treatment} \times \text{location})_{2,12} = 5.3$, $P = 0.02$. There was no significant relationship between *Cladophora* abundance and the total mass of either native tadpole metamorphosing from enclosures (Table 6).

There were also differences in AFDM of floating algae between treatments. Less was harvested in bullfrog enclosures (0.046 ± 0.026 g) than in enclosures without bullfrogs (0.33 ± 0.18 g). Although the treatment effect on floating algae was not significant (Mann-Whitney $U = 28$, χ^2 approximation $= 2.56$, df $= 1$, $P = 0.11$), there was a significant correlation between ranked mass of floating algae, taken as a measure of algal quality (Q), and the total mass of *R. boylii* metamorphosing from the enclosures (B) (Table 6).

There was no treatment effect on biomass sampled from sediments at the end of the experiment. There was a significant location effect, with 0.96 ± 0.17 mg/cm^2 in the side pool and 0.51 ± 0.12 mg/cm^2 in the main channel (ANOVA of ln(AFDM): $F(\text{treatment})_{2,12} = 2.5$, $P = 0.12$; $F(\text{location})_{1,12} = 6.9$, $P = 0.02$; $F(\text{treatment} \times \text{location})_{2,12} = 0.96$, $P = 0.41$)

Path analysis.—The relative importance of direct and indirect effects in causing the bullfrog effect was determined from the hypothesized web of interactions in Fig. 8. The only significant interactions in the web are those among bullfrogs, native *R. boylii* tadpoles, and algal quality. Most of the variation in *R. boylii* production was explained by the multiple regression on *R. catesbeiana* presence or absence, algal quality, and *Cladophora*. The interaction strengths associated with the direct and indirect paths between bullfrogs and *R. boylii* were approximately equal. The correlation matrix among all variables predicted by the model is not significantly different from the observed matrix ($\lambda^2 = 2.97$, df $= 7$, $P > 0.5$), and the correlation between observed and expected values was $R^2 = 0.96$. For example, the predicted correlation coefficient between bullfrogs and *R. boylii* production is the sum of the direct path between *R. catesbeiana* and *R. boylii*, and the products of the path coefficients in the indirect paths through algal quality and *Cladophora*. The predicted correlation is, therefore, $-0.34 + (-0.49 \times 0.64) + (-0.1 \times 0.21) = -0.67$ vs. $r_{\text{observed}} = -0.63$.

Experiment IV: Fecal or waterborne chemical interference

R. boylii growth was not influenced by water conditioned with bullfrog excretions. Tadpole mass before bullfrog exposure (0.39 ± 0.03 g [mean $\pm$ 1 SE]), was used as a covariate in a repeated-measures ANOVA of post-exposure tadpole mass (on 28 Aug 0.95 ± 0.04 g with bullfrogs and 0.88 ± 0.02 g without bullfrogs; on

TABLE 4. Kruskal-Wallis one-way ANOVAs of treatment effects on tadpole mortality in Experiment II, competition with small bullfrog tadpoles (described in Table 1).

Target species	Source of variation	χ^2 approxi- mation	df	P
Hyla regilla	Treatment†	7.8	6	0.25
	Plus-bullfrog treatments vs. natives only§	5.8	1	0.02‡
Rana boylii	Treatment†	9.5	6	0.15
	Plus-bullfrog treatments vs. natives only§	7.6	1	<0.01‡
Rana catesbeiana	Treatment†	9.0	6	0.18
	Plus *H. regilla* vs. *R. catesbeiana* alone‖	3.7	1	0.054
	Plus *R. boylii* vs. *R. catesbeiana* alone¶	0.65	1	0.42

Notes: For the four tests of bullfrog effects, ‡ indicates significance of one-tailed tests, α = 0.1, adjusted with a sequential Bonferroni technique.

† Tests for differences among the 7-treatment subset of 14 treatments in which a given species of tadpole was present.

§ Tests for a difference between treatments with bullfrogs vs. treatments with only native tadpoles.

‖ Tests for differences between treatments where bullfrogs were in the presence of *H. regilla* vs. treatments with only bullfrogs.

¶ Tests for differences between treatments where bullfrogs were in the presence of *R. boylii* vs. treatments with only bullfrogs.

23 Sep 0.87 ± 0.06 g with bullfrogs and 1.04 ± 0.06 g without bullfrogs. Slopes were homogenous: F(treatment × initial mass)$_{1,10}$ = 0.02, P = 0.36. Between subjects effects were not significant: F(initial mass)$_{1,11}$ = 0.19, P = 0.68; and, F(treatment)$_{1,11}$ = 0.91, P = 0.36. Within subjects, only the time × treatment interaction was significant: F(time)$_{1,11}$ = 0.02, P =

0.89; F(time × initial mass)$_{1,11}$ = 0.03, P = 0.86; and F(time × treatment)$_{1,11}$ = 11.03, P = 0.007.

Tadpole densities

Overwintered bullfrog tadpoles.—Densities of large bullfrog tadpoles in Experiment I, of 28, 42, and 56 individuals/m², were higher than mean early summer density, but not greatly beyond the range observed. On 18 Jun the density of overwintering bullfrogs at Hunter's Pool where they occurred near the surface of floating vegetation ranged from 1 to 52 individuals/m² (mean ± 1 SD = 18.2 ± 13.1 individuals/m², n = 17 quadrats). By 30 Jul, when Experiment III was under-way and bullfrog transects were censused, density had decreased to 1.4 ± 1.2 individuals/m² (n = 6 transects, range 1–4 individuals/m²). Densities in the large pens, 2 individuals/m² for overwintered tadpoles, therefore mimicked field densities in mid-late summer when the most mature tadpoles have commenced metamorphos-ing.

Young of the year bullfrog tadpoles.—Densities of small bullfrog tadpoles in Experiment II, of 28, 42, and 56 individuals/m², did not exceed average natural den-sities. On 16 Jul 1992, mean ± 1 SD density was mea-sured as 90.9 ± 97.7 tadpoles/m², range = 0–310 tad-poles/m², n = 20 quadrats. On 30 Jul, density was 42.2 ± 46.8 individuals/m², range 4–120 tadpoles/m², n = 5 quadrats.

Native tadpoles.—At the site of Experiment III, on 15 Jun 1992, *R. boylii* density was 57.6 ± 75.12 in-dividuals/m² [mean ± 1 SD], range = 0–350 individ-uals/m², n = 27 samples. *Hyla* density was 16.25 ± 7 individuals/m², range = 0–350 individuals/m², n = 27 samples. Densities in the small-scale experiments, where the density of each species was 28 or 42 indi-viduals/m² and the total densities in buckets holding 2
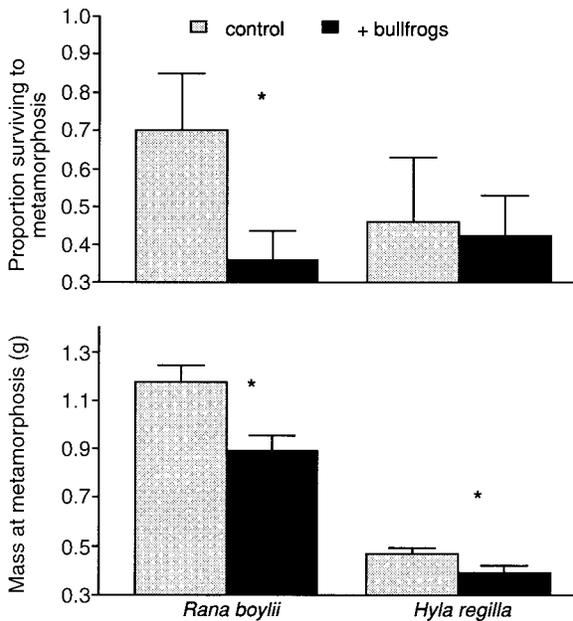

FIG. 6. Survival to and mass at metamorphosis for native tadpoles in the presence (dark bars) or absence (light bars) of bullfrog tadpoles in 2-m² enclosures of natural river sub-strate (means and 1 SE; Experiment III). Asterisks indicate significance (P < 0.05). For *R. boylii*: control n = 85 me-tamorphs; treatment n = 41. For *Hyla*: control n = 35 me-tamorphs; treatment n = 32.

TABLE 5. Nested ANOVAs of enclosure and bullfrog effects on native tadpoles in 2-m² enclosures placed in the river margins (Experiment III).

Species	Response variable	Source of variation	df	MS	F	P
Hyla regilla	Survival (no. of metamorphs)	Bullfrog treatment	1	0.013	0.017	0.899
		Error	10	0.754		
	Size at metamorphosis (ln body mass)‡	Bullfrog treatment	1	0.405	7.243	0.023†
		Enclosure	10	0.056	0.946	0.499
		Error	55	0.059		
Rana boylii	Survival (no. of metamorphs)	Bullfrog treatment	1	3.144	4.946	0.050†
		Error	10	6.356		
	Size at metamorphosis (ln body mass)‡	Bullfrog treatment	1	1.883	6.336	0.031†
		Enclosure	10	0.297	5.472	<0.001
		Error	114	0.054		

Notes: Data on individual metamorphs are nested within enclosures and enclosures within treatments. For the four tests of bullfrog effects, † indicates significance of one-tailed tests, $\alpha = 0.1$, adjusted with a sequential Bonferroni technique.
‡ Body mass was measured in grams.

or 3 species ranged from 56 to 84 individuals/m², were thus well within the range of natural early summer densities. One month later when the site was sampled with the 12 2-m² enclosures, 240 *R. boylii* and 204 *Hyla* were caught, thus yielding Experiment III's densities of 10 and 8.5 tadpoles/m², respectively.

DISCUSSION

The outcome of the small-scale experiments indicates that bullfrog tadpoles can have strong effects on native tadpoles and that native tadpoles have weak effects on bullfrogs. Both overwintering and young of the year bullfrog tadpoles significantly increased native tadpole mortality above levels observed when the native species were raised together (Experiments I and II). Additionally, intraspecific and interspecific competition among native tadpoles was negligible (Experiments. I and II). The outcome of the larger scale experiment similarly indicates strong bullfrog effects. The effect of bullfrog tadpoles on native tadpoles ap-

FIG. 7. Ash free dry mass of attached algae, mostly *Cladophora glomerata,* harvested from tadpole enclosures and adjacent open river sites at the end of Experiment III.

peared to be mediated by algal resources (Experiment I and III). Additionally there was little evidence of behavioral interference (Experiment III) or water borne interference (Experiment IV).

These manipulations, although all done in the field, represent different ends of the spectrum between realism and control. The large pen experiment (Experiment III), tested the magnitude of bullfrog effects in a natural setting at mid-summer ambient native tadpole density. In Experiment III, I doubled the total density of tadpoles by adding bullfrog larvae. With only two treatments I overlooked the most important question regarding competition: Would observed effects be a result of increased density or the identity of the tadpoles added? More precisely, was interspecific competition with bullfrogs greater than intraspecific competition? Was interspecific competition with the non-native species greater than interspecific competition between the native species? To address these questions I examined interactions between size classes and among several combinations of species pairs and trios in artificial enclosures (Experiments I and II). I reasoned that if I observed minimal effects of intraspecific and native inter-specific competition in these experiments, then I could conservatively ignore these processes in the larger pens where logistical constraints prohibited the use of numerous treatments. With some treatments higher than mean field densities, the lack of effects provides conservative tests. Because investigation at each scale reveals different aspects of the nature and strengths of competition, the results of these separate experiments should be considered in toto.

Experimental densities were within the ranges observed in the open river. Determining an "average" field density, however, is problematic. Bullfrog and native tadpole densities vary from year to year due to hydrologic disturbance, and within one season due to dispersal, predation, competition, etc. In 1992, how-
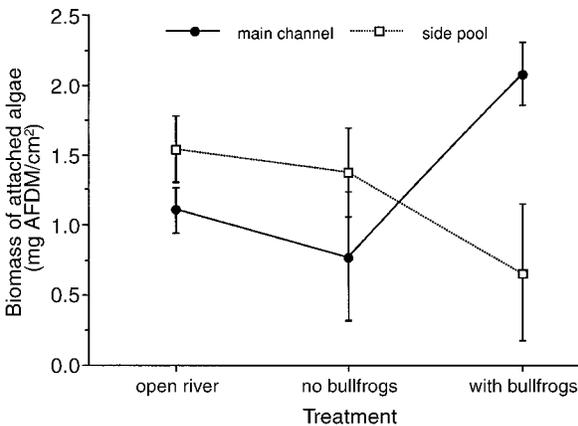
TABLE 6. Observed correlations and descriptive statistics of variables used in the path analysis of bullfrog manipulations in the river-margin enclosures (Experiment III).

	C	H	B	A	Q	Mean	SD	SS
C = *Rana catesbeiana* presence vs. absence (1 vs. 0)						0.5	0.52	2.8
H = *Hyla regilla* total metamorph biomass (g)	−0.15					2.58	2.14	50.3
B = *Rana boylii* total metamorph biomass (g)	−0.63*	0.53				11.7	7.9	688.6
A = Algal standing stock ash free dry mass (g)	0.18	−0.12	0.07			24.7	16.7	3050.2
Q = Quality of algae as tadpole food (rank)	−0.48	0.51	0.75**	−0.07		6.5	3.6	142.0
L = Location of enclosures sidepool or main channel (1 vs. 0)	0	0.36	0.27	−0.25	0.46	0.5	0.52	2.8

Notes: n = 12 enclosures, * $P < 0.05$, ** $P < 0.01$.

ever, both bullfrogs and natives were at the high end of their densities. The winter storms were not severe and there was little spring precipitation (hydrograph data in Kupferberg 1996*a*). So, the large bullfrog tadpoles that are susceptible to scouring floods and the hatchling native tadpoles that are susceptible to late spring spates (Kupferberg 1996*b*) were abundant. Because there is a substantive difference between the success of an invasion and its impact, it is justifiable to conduct investigations at densities reached in the absence of abiotic disturbance. In this case, invasion success is likely determined by interactions with the abiotic environment while invasion impact is determined by interactions with native biota. Establishment appears to depend on a number of sequential low rainfall winters allowing tadpoles to reach metamorphosis thus creating local recruitment in addition to emigration from ponds in the watershed. Alternatively, invasion impact, as reported here, is measured in terms of the lower abundance of breeding yellow-legged frogs in bullfrog reaches and decreased production of new metamorphs with bullfrog competition. The findings of Experiment III, conducted under as similar to field conditions as possible, document how larval bullfrog exploitation of algal resources effects native tadpoles.

Mechanisms of competition: exploitation vs. interference

Food limitation has often been implicated as the mechanism for density dependent effects on anuran life history traits and survivorship (Brockelman 1969, DeBenedictis 1974, Wilbur 1980, Travis 1984). Food quantity (Wilbur 1977*a*, *b*, Seale 1980, Alford and Harris 1988, Berven and Chadra 1988, Johnson 1991) and quality (Steinwascher and Travis 1983, Kupferberg et al. 1994) significantly influence tadpole growth and timing of metamorphosis. In my experiments, exploitative competition is suggested as a mechanism of bullfrog effects when the results of the small and large enclosure manipulations are considered together. In Experiment I, algal depletion was much greater in bullfrog treatments than native only treatments. In Experiment II, no treatment effects on algae were detected, but this may have been due to the short duration of the experiment. In Experiment III, there was no significant correlation between native frog production and total algal biomass, but lumping all potential food into a pooled biomass category, although common, is not well justified (Mittelbach and Osenberg 1994). When resources were partitioned into attached and floating algae, di-
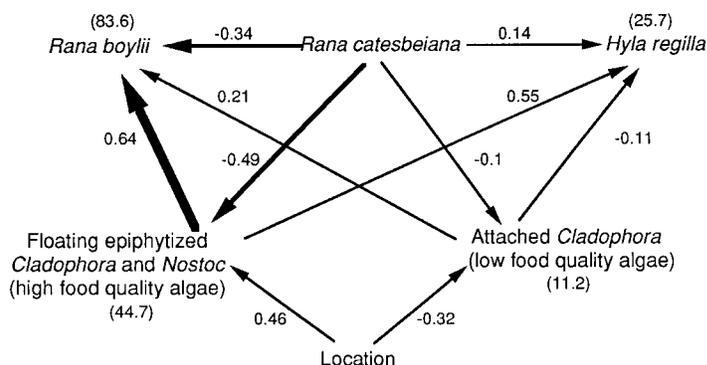

FIG. 8. Path diagram of interactions among variables in a study of species interactions on natural river substrate in California (Experiment III). Arrow thickness corresponds to statistical significance of paths from multiple regression analysis (thin $P > 0.1$, medium $0.05 < P \leq 0.08$, and thick $P < 0.01$). Path coefficients are adjacent to paths. Percentage of total variance explained for each endogenous variable is in parentheses.

minished food quality in the large bullfrog enclosures, as indicated by the decreased abundance of floating algae, explained much of the variation in native tadpole production. The floating algae comprised a combination of senescing *Cladophora* heavily covered with epiphytes containing cyanobacterial endosymbionts and *Nostoc,* also a cyanobacterium, which shows dramatic biomass expansion when nitrogen becomes limiting. A diet rich in epiphytes enhances growth, development, and survivorship of tadpoles (Kupferberg et al. 1994). In the path analysis, there was an important negative path from bullfrogs to algal quality, despite site differences in bullfrog effects. A small impact of bullfrogs on algal quality resulted in a large impact on *R. boylii* because there was such a strong correlation between algal quality and the biomass of *R. boylii* metamorphosing from the enclosures.

Very little of the variation in *Hyla* survival in the large enclosures was explained by algal quality. *Hyla* may be good response competitors (sensu Goldberg 1990), able to extract low quality or low availability resources not measured with my sampling regimes. For example, I observed *Hyla* tadpoles swimming on their backs at the surface grazing epineustic films of diatoms. In the small-enclosure studies, bullfrogs did significantly decrease *Hyla* survival. This discrepancy could be due to the absence of alternative foods or the overall higher density of tadpoles in the small enclosures.

There was no evidence of direct behavioral interference effect of bullfrog tadpoles on native tadpoles, but species specific differences in activity level and body size may explain the disparate responses of the native species to bullfrog tadpoles. *R. boylii,* which was more negatively affected by bullfrogs, had lower activity levels than *Hyla.* Tadpoles with higher activity levels are competitively dominant (Werner 1992). In addition to being less active, *R. boylii* is larger. Net energy gain is also thought to scale with body size such that large size classes are at a disadvantage under low resource conditions (Werner 1994). To maintain equal consumption rates when high quality food is scarce, tadpoles would have to increase their feeding rate, thereby increasing costs. If smaller tadpoles, i.e., *Hyla,* have lower metabolic costs than the larger *R. boylii,* they are less likely to show a response to changes in resource levels. Under low quality resource conditions, as indicated by the decreased mass of floating algae in bullfrog enclosures, native tadpoles feeding for equal amounts of time spent would have lower food (nutrient) intake rates. Therefore a combination of increased cost and decreased return may explain the more negative response by *R. boylii.*

Growth inhibition among tadpoles has long been documented (Richards 1962, Licht 1967), but I did not detect waterborne interference competition by first-year bullfrog tadpoles on *R. boylii* in my ''cage within a cage'' manipulation (Experiment IV). There is conflicting evidence whether chemical interference is important under natural conditions and in field experiments (Petranka 1989, Griffiths 1991, Biesterfeldt et al. 1993). Fecally borne unicellular algae, *Prototheca* sp., known growth inhibitors in the laboratory (Beebee 1991), do not proliferate when tadpoles are enclosed outdoors or when laboratory temperature regimes resemble natural conditions (Biesterfeldt et al. 1993). Similarly, conditions in my experiment may have been insufficient to produce interference, e.g., algal foods in addition to feces were available and tadpoles were stocked at low densities. High food levels, however, have been shown not to ameliorate negative effects of *Prototheca* (Griffiths et al. 1993). In fact, inferior tadpole competitors may forego high quality foods due to the attractive properties of *Prototheca* in feces (Beebee and Wong 1993).

If chemical interference is due to hormones associated with metamorphosis, rather than *Prototheca,* then first-year bullfrog tadpoles would not be able to produce an effect. Studies on intraspecific interactions in toads show that tadpoles secrete and absorb steroid and thyroid hormones that decrease survival, growth, and size at metamorphosis (Hayes et al. 1993, Hayes and Wu 1995). Chemical interference due to hormones is suggested by the result that large overwintered bullfrog tadpoles had strong adverse impacts (Experiment I) and that the negative effects on native tadpole survival increased as the bullfrog tadpoles lost body mass in approach to metamorphosis.

Implications of a bullfrog invasion

Native species may decline if bullfrogs tighten their recruitment bottlenecks. Decreased recruitment because of competitive interactions at an early life stage has often had population dynamics consequences for fishes (Werner 1986, Persson and Greenberg 1990, Osenberg et al. 1992). An empirical example of an invader causing a bottleneck is seen in the southwestern U.S., where convict cichlids (*Cichlasoma nigrofasciatum*) have had a negative impact on recruitment of native White River springfish (*Crenichthys baileyi*) (Tippie et al. 1991). Amphibian populations are also strongly influenced by changes in recruitment (Smith 1987, Semlitsch et al. 1988, Berven 1990). The negative effects of bullfrog larvae on *R. boylii* recruitment observed in these experiments may explain the pattern of low *R. boylii* abundance in dense bullfrog reaches.

Consequences of bullfrog tadpole grazing could extend to changes in primary production and habitat heterogeneity as structured by the abundance of the dominant macroalga, *Cladophora.* Because bullfrog larvae do not metamorphose in one season, their effects extend beyond the normal season for tadpole grazing. In September after all natives had metamorphosed, *Cladophora* standing stock in bullfrog enclosures was 121% greater than the open river in the main channel habitat. Bullfrogs may have enhanced standing stock of the relatively inedible macroalgae by removing ed-

ible diatom epiphytes that harm their macroalgal host. Previous grazing experiments conducted at the same site with native tadpoles indicated the importance of epiphyte removal to *Cladophora* growth (Kupferberg 1997). Werner (1994) similarly found a significant positive correlation between tadpole mass and the mass of macro-vegetation (macrophytes and filamentous algae) in pond enclosures. In the river's side pool, however, algal biomass was 55% lower in bullfrog enclosures than in the open. *Cladophora* may not respond similarly to epiphyte removal in the side pool because nutrients are more limiting there than epiphytes (S. Gresens, *unpublished water chemistry data*). The habitat heterogeneity created by *Cladophora* turfs has implications for other components of the aquatic food web, such as the susceptibility of aquatic insects to predation (Power et al. 1992), and the functional importance of fish as top predators in trophic cascades (Power 1992*b*).

The possible impacts of terrestrial bullfrogs as predators and competitors are considerable, but difficult to quantify. Adult bullfrogs are generalist consumers with a broad taxonomic spectrum of prey (Korschgen and Moyle 1955, Korschgen and Baskett 1963, Corse and Metter 1980, Clarkson and DeVos 1986), notably including other amphibians (Cohen and Howard 1958, Stewart and Sandison 1972, Smith 1977, Hayes and Warner 1985). Bullfrogs could eat native tadpoles and metamorphs, as they are known to cannibalize their own (Schwalbe and Rosen 1988). Bullfrog invasion has coincided with declines of their prey populations, such as Mexican garter snakes (*Thamnophis eques*) in the Southwest (Rosen and Schwalbe 1995) and western pond turtle (*Clemys marmorata*) hatchlings in Oregon (Milner 1986). It is difficult to assess the impact of invading bullfrogs as predators, because there may be only a brief window of time in which sensitive native species have high enough relative abundances to be detected in a diet study. With respect to competition, Morey and Guinn (1987) found a high degree of diet overlap of arthropod taxa between juvenile terrestrial bullfrogs dispersing around vernal pools in the Central Valley of California and the adult native frogs breeding there. It is not known though, whether insect resources limit frog populations.

The conservation implications of this study are both general and specific. Small-scale manipulations of pairwise interactions yielded qualitatively, if not quantitatively, correct predictions of the impact of an invader in a broader community context. To uncover the mechanisms of an invader's impact, however, I had to manipulate species composition at a larger scale and measure other community variables, like algal production. Populations of the more tolerant species in these experiments, *H. regilla,* are more likely to withstand bullfrog invasions than populations of *R. boylii. Hyla* are better larval competitors, have a broader range of physical tolerances, and reproduce in ephemeral habitats unsuitable for bullfrogs. *R. boylii* are limited to breeding in the river and are not as strong larval competitors. The ultimate test of the usefulness of small-scale experiments in predicting interactions at natural scales will rely on continued monitoring of native populations and bullfrog establishment.

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