

POND PERMANENCE AND THE EFFECTS OF EXOTIC VERTEBRATES ON ANURANS

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Abstract. In many permanent ponds throughout western North America, the introduction of a variety of exotic fish and bullfrogs (*Rana catesbeiana*) correlates with declines in native amphibians. Direct effects of exotics are suspected to be responsible for the rarity of some native amphibians and are one hypothesis to explain the prevalence of amphibian declines in western North America. However, the prediction that the permanent ponds occupied by exotics would be suitable for native amphibians if exotics were absent has not been tested. I used a series of enclosure experiments to test whether survival of northern red-legged frog (*Rana aurora aurora*) and Pacific treefrog (*Hyla regilla*) larvae is equal in permanent and temporary ponds in the Puget Lowlands, Washington State, USA. I also examined the direct effects of bullfrog larvae and sunfish. Survival of both species of native anuran larvae was generally lower in permanent ponds. Only one permanent pond out of six was an exception to this pattern and exhibited increased larval survival rates in the absence of direct effects by exotics. The presence of fish in enclosures reduced survival to near zero for both native species. An effect of bullfrog larvae on Pacific treefrog larval survival was not detected, but effects on red-legged frog larvae were mixed. A hypothesis that food limitation is responsible for the low survival of native larvae in some permanent ponds was not supported. My results confirm that direct negative effects of exotic vertebrates on native anurans occur but suggest that they may not be important to broad distribution patterns. Instead, habitat gradients or indirect effects of exotics appear to play major roles. I found support for the role of permanence as a structuring agent for pond communities in the Puget Lowlands, but neither permanence nor exotic vertebrates fully explained the observed variability in larval anuran survival.

Key words: amphibian declines; anura; competition; environmental gradients; exotic species, effects on native species; *Hyla regilla*; *Lepomis*; pond amphibian communities vs. pond permanence; pond permanence vs. effects of exotic species; predation; *Rana aurora aurora*; *Rana catesbeiana*.

INTRODUCTION

Lentic communities in western North America have been greatly altered by species introductions (Mooney and Drake 1986). Besides vegetative changes, a variety of exotic fish have been introduced into most permanent waters (Moyle 1986), and in lowland areas the bullfrog (*Rana catesbeiana*) now occupies many permanent ponds and streams (Bury and Whelan 1984, Stebbins 1985). Together, exotic introductions represent a significant and widespread disturbance to the freshwater systems of western North America, but the extent to which current conservation problems are related to exotics has not been well established.

Negative associations between the distribution of bullfrogs and a variety of animals native to western North America are well quantified (Moyle 1973, Hayes and Jennings 1988, Schwalbe and Rosen 1988, Fisher and Shaffer 1996) and recent experimental studies suggest that direct negative effects of bullfrogs on native

anurans in Oregon and California are occurring (Kiesecker and Blaustein 1997, Kupferberg 1997, Lawler et al. 1999). Inverse associations between exotic fish and native anurans suggest that fish could also be causing declines in native lowland amphibians (Moyle 1973, Hayes and Jennings 1988, Fisher and Shaffer 1996, Kiesecker and Blaustein 1998). Exotic fish and bullfrogs tend to be sympatric in the relatively deep, structurally simple, permanent ponds that are increasingly common on the landscape (Hayes and Jennings 1986). However, it has not been demonstrated that native anurans were ever as abundant at such sites as they are at more ephemeral ponds (Hayes and Jennings 1988, Adams et al. 1998). Because pond permanence can affect the distributions of both exotic and native species (Skelly 1995a, Wellborn et al. 1996), the regional effects of exotics should be examined in the context of the pond-permanence gradient.

I used a series of enclosure experiments to examine the larval survival of two anurans native to the Puget Lowlands of Washington State, USA (defined by Omerik 1987): the northern red-legged frog (*Rana aurora aurora*, hereafter red-legged frog) and the Pacific treefrog (*Hyla regilla*, hereafter treefrog). I tested the hypothesis that direct effects of exotic fish and bullfrog

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TABLE 1. Characteristics of temporary (T) and permanent (P) pond study sites.

Characteristic	T1, Chambers Pond	T2, Lost Marsh	T3, Shaver Marsh	P1, Hamilton Marsh	P2, Hardhack Marsh	P3, Chambers Lake	P4, Vietnam Marsh†	P5, Spanaway Marsh	P6, East Watkins Pond
Captures per trap night‡									
Red-legged frog	0.70 (1.312)	3.00 (3.857)	3.00 (3.333)	0.04 (0.044)	0.13 (0.119)	0.22 (0.269)	N	0.30 (0.403)	0 (0)
Pacific treefrog	2.87 (13.209)	13.67 (94.095)	0	0	0.44 (0.893)	0	N	0	0
Northwestern salamander	0	0	0.1 (0.100)	0	0.826 (2.787)	0.043 (0.043)	N	0.652 (1.146)	0.036 (0.036)
Rough-skinned newt	0	0	0.1 (0.100)	0	0	0	N	0	0.5 (1.444)
Presence data§									
Dytiscidae	Y	Y	Y	Y	Y	Y	Y	Y	Y
Odonata	N	N	N	N	Y	Y	Y	Y	Y
Bullfrogs	N	N	Y	Y	Y	Y	Y	Y	Y
Exotic fish	N	N	Y	Y	Y	Y	Y	Y	Y

† Pond P4 was not trapped in a comparable manner to other sites, and only presence is indicated.

‡ Captures per trap night (mean with 1 SE in parentheses) are given for native amphibians from funnel trapping around the enclosures over 3 yr ($N = 20-28$ trap nights).

§ Presence data (Y/N) are a combination of funnel trap, dip net, visual encounter, and call surveys (see Adams [1999] for details).

larvae could explain differences in abundance of native larval anurans observed between temporary and permanent ponds (Adams et al. 1998). Specifically, I tested the predictions that native larval survival will be lower in the presence of exotics and that, when direct effects by exotics are excluded, native larval survival will be comparable in permanent and temporary ponds. I also examined the role of food availability in this system.

METHODS

The system

Three experiments were conducted on the 27 000-ha Fort Lewis Military Reservation located at the southern tip of the Puget Sound, Washington State, USA. Fort Lewis contains a diverse array of ponds and wetlands, and native anurans are most common in temporary ponds (Adams 1999). Bullfrogs and exotic fish are more common in the deepest permanent waters that lack extensive emergent vegetation, but bullfrogs also overlap with native anurans in some broad, shallow margins of large permanent ponds (Adams 1999). Permanent ponds chosen for study had few or no native anurans and had bullfrogs and exotic fish present, offering a possible explanation for the lack of natives (Table 1). The same three temporary ponds were used in all three experiments and were chosen to represent ponds with a high density of native anurans. Most ponds were deliberately selected to represent extreme conditions, but the three permanent ponds used in Experiment 3 were randomly chosen from five potential ponds that had not been used in Experiment 1.

Experiment 1: Effects of exotic fish and bullfrog larvae

In 1995 four experimental enclosures were set 1 m apart (perpendicular to shore) in the margins of six ponds (Table 1: T1-3, P1-3), three temporary and three permanent (Fig. 1). Enclosures were 182-cm-long \times 91-cm-wide \times 122-cm-tall wooden frames covered on all sides except the top with fiberglass window screen (1.5-mm mesh measured diagonally). Initial water depth in the enclosures averaged 80 cm with the deep end about 15 cm deeper than the shallow end. Final

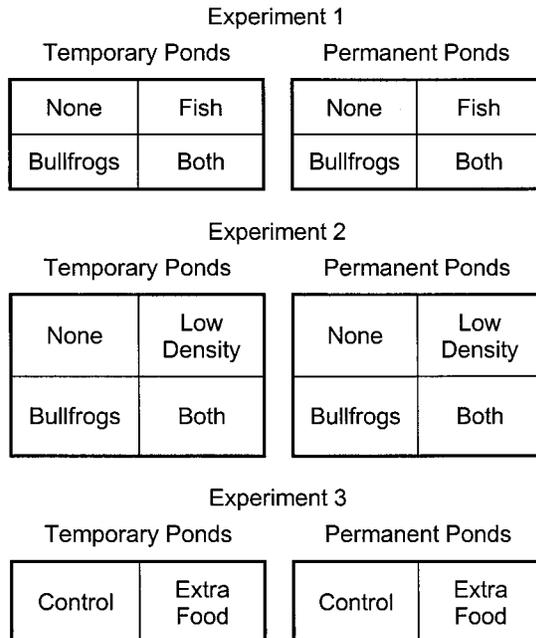


FIG. 1. Experimental design. Three permanent and three temporary ponds were used in each experiment. Cells correspond to enclosure. See *Methods: Expt. 1, Expt. 2, and Expt. 3* for descriptions of treatments.

depths averaged 20 cm (range: 4–36 cm), with permanent ponds tending to have a deeper final depth. Water depths were kept approximately equal among sites throughout most of the experiment by repositioning enclosures as water levels changed. Thus, drying was not a mortality factor and other potential effects of permanence were tested. These ponds typically hold water long enough for larvae to reach metamorphosis so desiccation is not often a major mortality factor.

The remains of the previous year's emergent vegetation (mostly reed canarygrass, *Phalaris arundinacea*) were gathered from the marsh bottom around the enclosures and piled into the bottom of the enclosures in a dense layer (~20 cm). This layer provided cover for the larvae not easily penetrated by fish and resembled the natural substrate layering. An array of aquatic invertebrates that were present at each site, both planktonic and pelagic, colonized the enclosures (including copepods, cladocerans, odonates, leeches, belostomatids, ephemeropterans, and others). Colonization was facilitated by laying the enclosures on their sides for a few days prior to installation so that organisms in the water column could enter. Invertebrates provided alternative prey for the fish and some were potential predators of larval anurans.

Anuran eggs from temporary (~70%) and permanent (~30%) ponds were combined and added to each enclosure (permanent ponds had exotic fish and bullfrogs). All of the ponds where eggs were collected were within 500 m of permanent ponds containing exotics. Eggs were held in aerated aquariums in the laboratory at room temperature. The experiment began when 100 treefrog and 100 red-legged frog larvae (3–8 d post-hatching) were added to each enclosure from 29 March to 10 April. Initiation of the experiment and the subsequent addition of bullfrog larvae and fish always proceeded in pairs of ponds consisting of one permanent and one temporary site. Native larvae were counted into plastic bags using a turkey baster and were gradually acclimated to the pond water temperature over a period of 30 min prior to release. I chose an initial density of 100 larvae because it was a convenient number between egg density and the density of larvae 3 wk after hatching (determined by dip-net sweeps) at a temporary pond with moderate to high densities compared to other ponds on Fort Lewis.

The presence or absence of sunfish and of bullfrog larvae was crossed in a fully factorial design within each pond (Fig. 1). Fifteen bullfrog larvae (total length = 35–85 mm) were added to randomly chosen enclosures at pairs of ponds from 14 to 21 April. This number is near the high end of second-year larval densities I have found on Fort Lewis (*unpublished data*). A single fish (mostly bluegill sunfish, *Lepomis gibbosus*, but I also used two that appeared to be hybrids with *L. macrochirus*; 9–13 cm total length) was placed in two randomly selected enclosures at each pond on 5 May. Fish were split into three size categories that were randomly

assigned to permanent and temporary pond pairs to prevent a size bias in the permanence treatment.

Experiment 2: Effects of bullfrog larvae and native larval density

Experiment 2 repeated Experiment 1 the following year (1996) with two modifications. First, one of the permanent ponds from Experiment 1 (P2) was replaced with a different permanent pond (P6) to see if larval survival rates at another permanent pond would be similar to the ponds used in Experiment 1. P2 was chosen to be replaced because it was dredged over the winter. Second, the fish treatment was replaced with a native larval density treatment (50 or 100 larvae of each species; Fig. 1). All other aspects of this experiment were the same as in Experiment 1.

Experiment 3: Effects of supplemental food

In 1996 two 61-cm-long × 61-cm-wide × 91-cm-tall enclosures were placed in each of six ponds (three permanent, three temporary; Fig. 1). A randomly chosen enclosure at each site received two handfuls of rabbit feed (~60 g) about every 7 d. This treatment was designed to test if food is limiting native larval survival in permanent ponds. Smaller enclosures were used so that fewer larvae would be needed and enclosures could be placed at sites where thick terrestrial vegetation precluded access with the large enclosures. The temporary ponds used were the same as Experiment 1, but three new permanent ponds (P4–6) were randomly chosen (P6 was also used in Experiment 2). This experiment started with 25 treefrog and 15 red-legged frog tadpoles (5–10 d old) in each enclosure. All other aspects were the same as Experiments 1 and 2 (Fig. 1).

Data collection and analysis

All enclosures were checked every 2–4 d in 1995 (Experiment 1) and once per week in 1996 (Experiments 2 and 3). Any transforming frogs (stage 42+; Gosner 1960) were caught with a small dip net and preserved in formalin within 12 h. Experiments were terminated site by site when all larvae had died or transformed or, in one case (Experiment 1: T3), the experiment was ended when the marsh dried (most larvae had already died or transformed). After preservation, frogs were transferred to alcohol and measured. Size at metamorphosis was measured as the volume (in milliliter) of water displaced in a graduated cylinder. Size and age (in days) at metamorphosis of larvae were adjusted for the stage at which they were collected (i.e., coefficients from regressions of size or age on stage were used to adjust the measurements to a standard stage; Adams 1997) and summary statistics are presented to facilitate comparisons among treatments. A statistical analysis was not conducted for size and age data because zero survival in some enclosures resulted

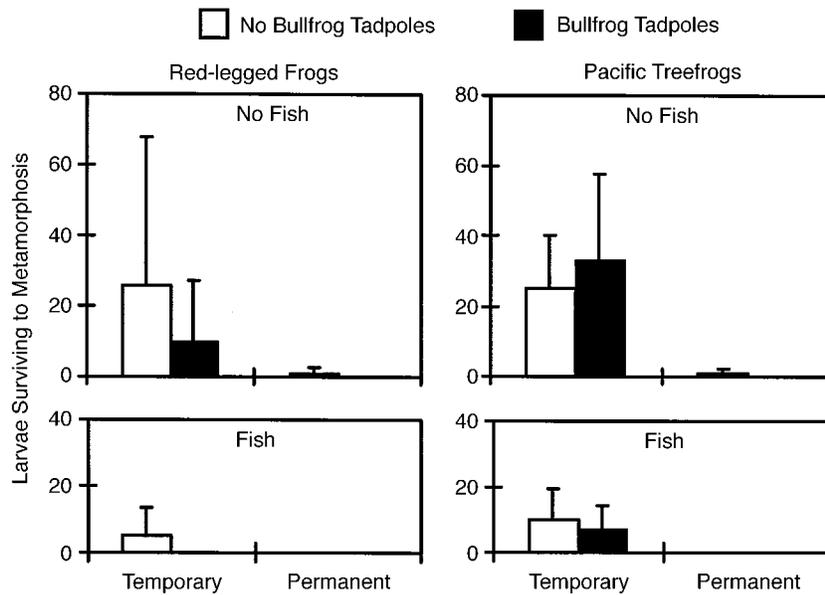


FIG. 2. Number of larvae surviving to metamorphosis (mean and 1 SD) at three permanent and three temporary ponds in Experiment 1.

in a highly unbalanced design for the responses of size and age.

Analysis of deviance (ANODEV), using GLIM 4.0 (Green and Payne 1993), compared survival of larvae to metamorphosis among treatment combinations for all experiments. Number surviving to metamorphosis was treated as a binomial response and the model was made linear using a logistic transformation (Aitkin et al. 1989, McCullagh and Nelder 1989). The initial number of larvae stocked was the binomial denominator. All models treated permanence as a whole-plot factor and, depending on the experiment, treated bullfrog larvae, exotic fish, initial density, or supplementary food as split-plot factors. The two split-plot factors in Experiments 1 and 2 were fully factorial. The significance of split-plot factors was evaluated at $\alpha = 0.05$. The whole-plot factor (permanence) or interactions between split-plot factors and permanence were considered significant at $\alpha = 0.10$. Increasing α was a conservative approach in this case because the hypothesis that bullfrogs or exotic fish were suppressing native anurans in permanent ponds would be supported by a failure to detect an effect of permanence, and power is inherently lower to detect whole-plot compared to split-plot effects.

To assess the importance of whole-pond effects in the absence of direct effects by exotics, larval survival inside the enclosures was compared to the relative abundance of native larvae outside the enclosures and pond permanence. Larval survival in the enclosures should have been roughly correlated with relative abundance outside the enclosures if the enclosures adequately mimicked environmental attributes important to larval survival. The hypothesis that exotics were

responsible for the low abundance of native anurans at permanent ponds predicts that larval survival in the enclosures lacking exotics at permanent ponds should be higher than predicted by relative abundance (outside enclosures) and that both relative abundance and permanence should be poor predictors of larval survival. This analysis used results from all three experiments, but only control enclosures were analyzed from Experiments 1 and 3 because of strong main effects. Deviance attributable to the three experiments and, in the case of Experiment 2, the density treatment, was removed from the total deviance in survival prior to analysis. Relative abundance was measured twice per year for 2–3 yr using five wire funnel traps at each of the nine ponds (Adams 1999). Trapping was conducted in June and July before metamorphosis began. The mean number of captures per trap night was used as an index of abundance in the analysis.

RESULTS

Experiment 1: Effects of exotic fish and bullfrog larvae

A total of 125 red-legged frogs (5%) and 227 treefrogs (9%) survived to metamorphosis. Both species had low survival with fish and zero survival in enclosures with fish in permanent ponds (Fig. 2). A trend towards lower survival in permanent ponds was not significant for either species but, for treefrogs, a significant interaction between fish and permanence (Table 2) was due entirely to a negative effect of permanence in enclosures without fish (Fig. 2). In other words, very low survival with fish negated the effects of permanence when fish were present. Bullfrog larvae signifi-

TABLE 2. Results of analysis of deviance for the number of Pacific treefrog larvae surviving to metamorphosis in Experiment 1.

Source of deviance	df	Deviance	F	P
Permanence, (Perm.)	1, 4	82.750	2.803	0.169
Bullfrog larvae, (Bull.)	1, 12	1.132	0.774	0.396
Fish	1, 12	314.100	214.8	<0.001
Perm. × Bull.	1, 8	4.292	2.303	0.168
Perm. × Fish	1, 8	1.188	3.604	0.094
Bull. × Fish	1, 12	5.471	3.741	0.077
Perm. × Bull. × Fish	1, 12	0.003	0.002	0.965
Residual				
Site (Perm.)	4	118.100		
Bull. × Site (Perm.)	4	14.910		
Fish × Site (Perm.)	4	2.637		
Bull. × Fish × Site (Perm.)	4	0.0004		

Notes: Permanence is a whole-plot treatment. Bullfrog larvae and fish are fully factorial split-plot treatments.

icantly lowered survival of red-legged frog larvae (Table 3), but not of treefrog larvae. Red-legged frog larvae averaged 1.3 mL smaller and 15.7 d younger at metamorphosis in permanent ponds (Table 4). Treefrogs averaged 0.1 mL smaller and 22 d younger at metamorphosis in permanent ponds. Also, red-legged frogs were 0.5 mL smaller at metamorphosis when bullfrog larvae were present.

Experiment 2: Effects of bullfrog larvae and native larval density

All of the enclosures were vandalized at one temporary pond (T2) and the effect of permanence was not analyzed, but results of this experiment are included in the combined analysis. A total of 17.7% of red-legged frog and 23.1% of treefrog larvae at the remaining five ponds survived to metamorphosis. Bullfrog effects depended on density for both native larvae (Table 5), but there was little evidence of intra- or interspecific competition. Bullfrog larvae only lowered red-legged frog survival at low densities and did not lower the survival of treefrogs at either density (Fig. 3). Both species tended to be smaller in temporary ponds, at high densities, and with bullfrogs (Table 4).

Experiment 3: Effects of permanence and supplemental food

Fifty-five red-legged frog larvae (30.5%) and sixty treefrog larvae (20%) survived to metamorphosis. Both species showed nonsignificant trends toward lower survival in permanent than in temporary ponds (Fig. 4). Treefrogs showed a marginally significant trend towards higher survival in the supplemental-food treatment, but the interaction predicted by the hypothesis that food is limiting in permanent ponds was not present for either species (Table 6). Red-legged frog and treefrog size averaged 1.4 and 0.1 mL longer, respectively, with supplemental food (Table 4).

Combined Analysis

Red-legged frog survival inside enclosures was related to mean trap rate outside enclosures ($F_{1,17} = 3.660$, $P = 0.072$). Moreover, East Watkins Pond (P6) was an outlier (mean Cook's distance = 8.3; Fig. 5) and, when it was removed, red-legged frog survival was strongly associated with mean trap rate ($F_{1,14} = 70.703$, $P < 0.001$) and was also negatively associated with permanence ($F_{1,14} = 4.272$, $P = 0.058$). The trap

TABLE 3. Results of analysis of deviance for the number of red-legged frog larvae surviving to metamorphosis in Experiment 1.

Source of deviance	df	Deviance	F	P
Permanence, (Perm.)	1, 4	85.520	1.188	0.337
Bullfrog larvae, (Bull.)	1, 12	38.550	17.559	0.001
Fish	1, 12	158.500	72.193	<0.001
Perm. × Bull.	1, 8	7.716	32.047	<0.001
Perm. × Fish	1, 8	0.648	0.212	0.657
Bull. × Fish	1, 12	1.654	0.753	0.403
Perm. × Bull. × Fish	1, 12	0.0002	<0.001	0.993
Residual				
Site (Perm.)	4	287.900		
Bull. × Site (Perm.)	4	1.926		
Fish × Site (Perm.)	4	24.420		
Bull. × Fish × Site (Perm.)	4	0.0002		

Notes: Permanence is a whole-plot treatment. Bullfrog larvae and fish are fully factorial

TABLE 4. Size and age at metamorphosis of larvae in experimental enclosures.

Treatment	Red-legged frog			Pacific treefrog		
	Count	Size (mL)	Age (d)	Count	Size (mL)	Age (d)
Experiment 1						
T	77	2.4 (0.22)	142 (41)	74	0.4 (0.02)	124 (179)
TB	30	1.8 (0.18)	144 (13)	100	0.4 (0.02)	131 (46)
TF	3	2.1 (0.13)	151 (177)	3	0.5 (0.003)	132 (225)
P	15	0.8 (0.07)	130 (51)	29	0.3 (0.01)	108 (100)
PB	0	21	0.3 (0.01)	106 (47)
Experiment 2						
TL	17	1.6 (0.08)	130 (20)	3	0.6 (0.07)	114 (103)
TLB	0	11	0.5 (0.03)	123 (59)
TH	4	1.6 (0.56)	155 (0)	3	0.5 (0.003)	121 (16)
THB	51	1.3 (0.11)	125 (72)	11	0.4 (0.01)	120 (36)
PL	27	3.9 (0.88)	117 (172)	0
PLB	25	3.7 (0.60)	121 (184)	21	0.7 (0.03)	108 (32)
PH	59	3.0 (0.50)	110 (132)	20	0.6 (0.04)	112 (179)
PHB	83	2.8 (0.5)	112 (95)	12	0.6 (0.01)	105 (19)
Experiment 3						
T	19	2.1 (0.44)	120 (135)	7	0.4 (0.006)	105 (39)
TS	23	2.4 (1.91)	117 (99)	35	0.5 (0.07)	108 (65)
P	10	1.6 (0.10)	115 (31)	4	0.6 (0.02)	95 (163)
PS	3	4.0 (0.75)	114 (56)	13	0.7 (0.05)	96 (16)

Notes: Data are means with 1 SE in parentheses; SE is based on the number of individuals that survived to metamorphosis (Count). Treatment combinations are represented by letters: P = permanent pond, T = temporary pond, B = bullfrog larvae present, F = sunfish present, H = high initial density, L = low initial density, S = supplemental food added.

rate of larvae outside the enclosures accounted for 83% of the residual deviance after removing deviance attributable to differences among experiments. Treefrog survival had a weak quadratic relationship to mean trap rate ($F_{1,15} = 3.038, P = 0.102$). When East Watkins Pond was removed, survival of treefrogs was significantly lower in permanent than in temporary ponds ($F_{1,14} = 5.678, P = 0.032$).

DISCUSSION

This experiment was the first to compare suitability, for red-legged frogs and Pacific treefrogs, of the permanent ponds occupied by exotic fish and bullfrogs to temporary ponds with larger populations of native anurans. The hypothesis that direct effects of exotics are reducing the abundance of natives predicts that excluding exotics will increase the survival of natives.

TABLE 5. Results of analysis of deviance for proportion of larvae surviving to metamorphosis in Experiment 2. Pond is a blocking variable.

Source of deviance	df	Deviance	F	P
Pacific treefrog				
Pond	4	144.900	21.54	<0.001
Density (Den.)	1	4.005	2.382	0.149
Bullfrog larvae (Bull.)	1	12.430	7.392	0.019
Den. × Bull.	1	21.030	12.507	0.004
Residual	12	20.178		
Red-legged frog				
Pond	4	667.000	57.652	<0.001
Density	1	14.180	4.903	0.047
Bullfrog larvae	1	22.500	7.779	0.016
Den. × Bull.	1	50.520	17.467	0.001
Residual	12	34.708		

My results were not consistent with this prediction. Instead, environmental variables associated with pond permanence (including native predators) or indirect effects of exotics may reduce native anurans at ponds occupied by exotics.

Survival of native larvae in enclosures was highly variable, but several patterns were apparent. Treefrog larval survival was generally lower in permanent than in temporary ponds when direct effects by exotics were excluded. The interacting effect of fish and permanence on treefrog survival in Experiment 1 was due to a permanence effect in enclosures without fish (Fig. 2). Power to detect whole-plot effects was necessarily low for individual experiments, but the combined analysis suggests that East Watkins Pond was the only site that supported the hypothesis that direct effects of exotics were responsible for the low abundance of treefrogs at permanent ponds. Survival of red-legged frog larvae was best explained by the abundance of red-legged frogs outside the enclosures, suggesting that direct effects of exotics were not necessary to produce the distribution and abundance patterns of red-legged frogs observed in this region (Fig. 5). East Watkins Pond was the only permanent pond where, in the absence of direct effects by exotics, native larval survival rates were relatively high.

The discrepancy between results for East Watkins and other permanent ponds should not be discounted, but, rather, suggests that the suitability of permanent ponds for red-legged frogs and treefrogs is variable. Some red-legged frog populations can be found in permanent ponds in the Puget Lowlands, but these tend to be in large, structurally complex wetlands (Richter

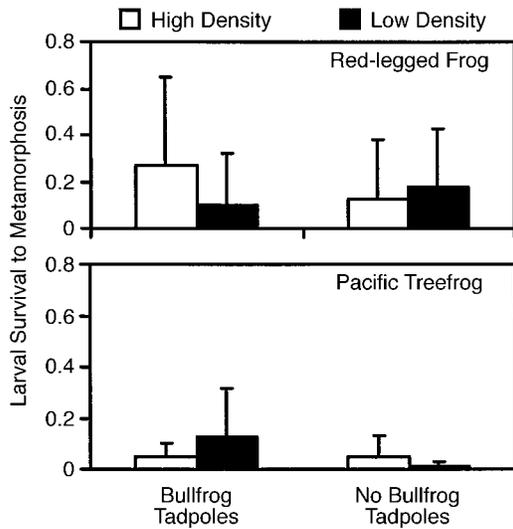


FIG. 3. Proportion of larvae surviving to metamorphosis (mean and 1 SD) at three permanent and three temporary ponds in Experiment 2.

and Azous 1995, Adams 1999). While experimental error likely contributed to the high variability in larval survival, the among-pond variability appears to reflect real differences because, at four ponds where enclosures were set in both years, survival rates were correlated between years ($r_s = 0.816$ and $r_s = 0.949$ for red-legged frogs and treefrogs, respectively), indicating that results were consistent over time for individual ponds.

Several hypotheses could explain the low survival of native larvae in most permanent ponds. First, a reduction in activity by larvae in response to a perceived threat from exotics (Petranka et al. 1987, Lawler 1989, Skelly and Werner 1990, Lefcort 1996) could lower growth rates and increase predation rates by invertebrate predators inside the enclosures (Skelly 1992). Red-legged frog larvae exhibited such a response to bullfrogs and smallmouth bass in experiments in Oregon (Keisecker and Blaustein 1997, 1998). It seems unlikely that a behavioral response could fully explain my results because one temporary pond (T3) was invaded by exotic fish and bullfrogs each year via a permanent stream and thus had exotics present outside the enclosures (Table 1). This site had relatively high survival of native larvae in the enclosures despite the potential for indirect effects from exotics.

A second hypothesis is that a trophic cascade initiated by exotic fish reduced the food available for larvae. Larger fish might limit zooplanktivorous fish and invertebrates, causing a decrease in phytoplankton and periphyton availability (Vanni et al. 1997). However, most of the exotic fish appeared to be very small *Lepomis gibbosus*, *L. macrochirus*, and *Perca flavescens* (total length: <5 cm). These primarily ingest zooplankton and aquatic insect larvae (reviewed by Wydoski and Whitney [1979]), theoretically increasing food

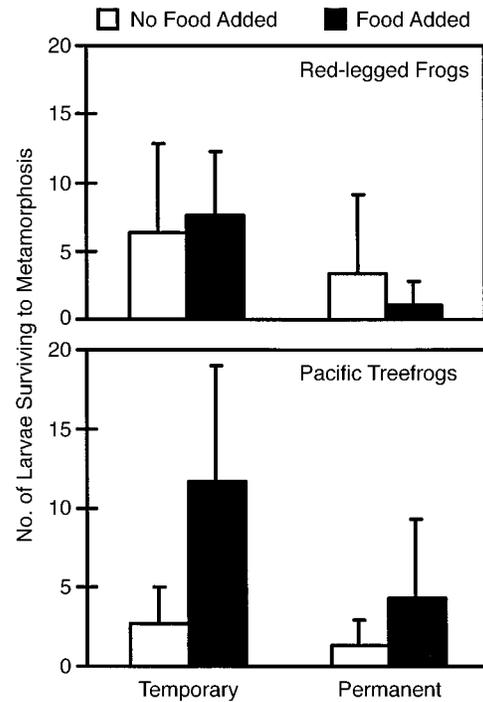


FIG. 4. Number of larvae surviving to metamorphosis (mean and 1 SD) at three permanent and three temporary ponds in Experiment 3.

availability for larvae (Andersson et al. 1978, Mazumder et al. 1988, Vanni and Layne 1997). Moreover, food limitation in permanent ponds was not supported by the feeding experiment.

While indirect effects of exotics outside the enclosures cannot be ruled out, it seems likely that some other feature of the ponds occupied by exotics may have been at least partially responsible for the low survival of native larvae. This leads to two additional hypotheses: food limitation and predation by native predators. Food limitation was not supported, but such an effect would likely be variable because productivity

TABLE 6. Analysis of deviance table for proportion of larvae surviving to metamorphosis in Experiment 3.

Source of deviance	df	Deviance	F	P
Pacific treefrog				
Permanence, (Perm.)	1	14.470	2.641	0.179
Food	1	30.000	5.687	0.075
Perm. × Food	1	0.803	0.152	0.717
Residual				
Site (Perm.)	4	21.920		
Food × Site (Perm.)	4	21.100		
Red-legged frog				
Perm.	1	22.880	1.301	0.318
Food	1	0.269	0.154	0.715
Perm. × Food	1	5.060	2.900	0.164
Residual				
Site (Perm.)	4	70.340		
Food × Site (Perm.)	4	6.980		

Note: Permanence is a whole-plot factor.

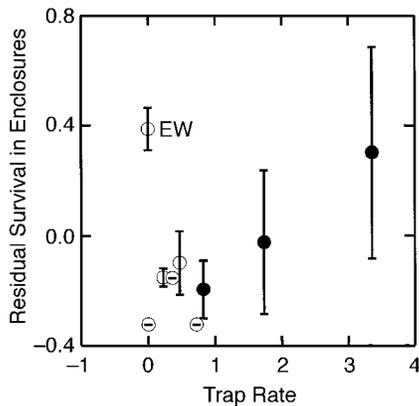


FIG. 5. Relationship between survival of red-legged frog larvae in enclosures and relative abundance outside enclosures ($N = 9$ ponds). The y-axis is residual survival after deviance attributable to differences among the experiments is removed. The x-axis is the number of red-legged frog larvae caught per trap night. Survival data are means ± 1 SD (the sample size for each pond ranged from 1 to 6 enclosures). Solid circles are temporary ponds; open circles are permanent ponds. Circles without error bars (and with short horizontal lines) represent single observations. EW = the data point for East Watkins Pond.

can be influenced by many factors other than permanence (Gosselink and Turner 1978). The native northwestern salamander (*Ambystoma gracile*) and rough-skinned newt (*Taricha granulosa*) are predators of native larvae (Calef 1973, Licht 1974), but were not in the enclosures. However, invertebrate predators appeared abundant inside the enclosures early in the experiment and could have been an important source of mortality. Moreover, predation by invertebrate larvae has been shown to be limiting for other amphibian larvae (Smith 1983, Werner and McPeck 1994) and can be associated with pond permanence (reviewed by Wellborn et al. [1996]).

Predation rates by fish on native larvae in enclosures may have been enhanced by cage effects (e.g., the tendency for larvae to aggregate along walls and in the corners). However, the enclosures did offer some cover for larvae and alternative prey for the fish. The strength of the fish effect suggests that, even in a more complex and natural environment, sunfish can be a major predator of native anuran larvae. Moreover, this experiment did not address predation immediately after the anuran larvae hatch when they aggregate around the egg mass and do not swim well. Exclusion of the early hatching stage in the experiment might have increased larval survival compared to natural levels. Adaptations to predaceous fish include unpalatability, small size, low activity levels, and overwintering ability (Woodward 1983, Wellborn 1994, Werner and McPeck 1994, Skelly 1995a, Smith and Van Buskirk 1995). Although these potential adaptations are poorly studied in red-legged frogs and Pacific treefrogs, this study suggests that larvae of these species lack adaptations for coexistence

with fish, but cannot rule out the possibility that larvae would fare better in a more natural environment (i.e., outside the enclosures).

There was no evidence of competition between bullfrog and treefrog larvae, but evidence of competition between bullfrog and red-legged frog larvae was mixed. The discrepancy between the results of Experiments 1 and 2 may be due to an apparent change in conditions from 1995 to 1996 that resulted in significantly higher overall survival in Experiment 2 ($F_{3,13} = 6.140$, $P = 0.028$). An increase in food resources could explain the higher survival and lack of competition in Experiment 2 and is consistent with the lack of an effect from supplemental food in Experiment 3. Competition between bullfrog and other ranid larvae has been previously reported (Werner 1994, Kupferberg 1997, Lawler et al. 1999), but my results suggest that variable conditions in ponds affect the importance of competitive interactions (e.g., Wiens 1977). Competition has also been reported between ranids and hylids (Wilbur and Alford 1985), but the lack of an effect at the high densities used in this study is consistent with the conclusion that *Rana-Hyla* competition is often weak under field conditions (Skelly 1995b).

In lowland areas of western North America, the freshwater lentic habitats available to amphibians increasingly are permanent and lack the extensive emergent vegetation common to more ephemeral waters (Kentula et al. 1992, Lannoo et al. 1994, Holland et al. 1995). This conversion is likely facilitating the spread of exotic fish and bullfrogs, which require permanent waters for overwintering (Kentula et al. 1992, Lannoo et al. 1994), but may also affect other limiting factors for native anuran larvae (Skelly 1996). Pond permanence appears to be an important gradient structuring pond communities in eastern North America (Wellborn et al. 1996). Its role as a structuring gradient in western pond communities has not been examined. My results were consistent with the finding that red-legged frog occurrence and amphibian species richness were more closely associated with permanence and other habitat variables than with the presence or abundance of exotic vertebrates in the Puget Lowlands (Richter and Azous 1995, Adams et al. 1998, Adams 1999).

My results did not support the hypothesis that direct effects of exotic fish and bullfrogs are responsible for the low abundance of native anurans at many permanent ponds, but some direct effects likely occur. For example, fish predation in permanent ponds can clearly have a strong negative effect on larvae not adapted to fish (Kats et al. 1988, Werner and McPeck 1994), but is only important to the extent that native anurans rely on the sites where exotic fish occur. Behavioral adaptations of larvae may allow coexistence with introduced predators in some situations, but with consequences for fitness that may affect population viability (Kiesecker and Blaustien 1997). Such indirect effects have been shown to be important in other

pond systems (e.g., Werner and McPeck 1994, Werner and Anholt 1996) and deserve further study in western North America. I did not examine the role of adult bullfrogs, which can be major predators on juvenile anurans (Bury and Whelan 1984, Werner et al. 1995), but strong negative effects of fish and habitat on survival of native larvae could limit the potential for interaction between bullfrogs and native juveniles. Moreover, other studies suggest that larvae appear minor in bullfrog diets (Bury and Whelan 1984, Werner et al. 1995). Although all studies in the Puget Lowlands to date have failed to support the hypothesis that bullfrogs are a major factor affecting the occurrence of native amphibians (Richter and Azous 1995, Adams et al. 1998, Adams 1999), other evidence suggests bullfrogs can be detrimental in some regions (Kiesecker and Blaustein 1997, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999). My study should not diminish concern over bullfrog introductions in western North America and worldwide, but suggests exotic-fish introduction and habitat alterations are also of concern and could be more detrimental to native anurans in some areas.

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