Local and Landscape Effects of Introduced Trout on Amphibians in Historically Fishless Watersheds

David S. Pilliod* and Charles R. Peterson

Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007, USA

ABSTRACT

Introduced trout have often been implicated in the decline of high-mountain amphibian populations, but few studies have attempted to understand whether fish stocking also influences the distribution and abundance of amphibians throughout entire mountain basins, including the remaining fishless lakes. We examined this relationship using the relative abundance of long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) in fish-containing and fishless lentic sites in basins with varying levels of historic fish stocking. All lentic waters were surveyed for fish and amphibians in 11 high-elevation basins in the Frank Church–River of No Return Wilderness, Idaho, between 1994 and 1999. We found introduced trout (*Oncorhynchus clarki, O. mykiss, O. m. aguabonita*) in 43 of the 101 sites, representing 90% of the total surface area of lentic water bodies available. At the scale of individual water bodies, after accounting for differences in habitat characteristics between fish-containing and fishless sites, the abundance of amphibians at all life stages was significantly lower in lakes with fish. At the basin scale, densities of overwintering life stages of amphibians were lower in the fishless sites of basins where more habitat was occupied by trout. Our results suggest that many of the remaining fishless habitats are too shallow to provide suitable breeding or overwintering sites for these amphibians and that current trout distributions may eventually result in the extirpation of amphibian populations from entire landscapes, including sites that remain in a fishless condition.

Key words: *Ambystoma macrodactylum*; amphibian; extinction; fish stocking; introduced trout; metapopulation; persistence; *Rana luteiventris*; wilderness.

INTRODUCTION

For over a century, trout and other sport fishes have been introduced into historically fishless, high-elevation lakes in western North America to provide recreational fisheries for backcountry anglers (Bahls 1992). Recent concern over the decline in amphibian populations has led researchers to assess the role of fish stocking in the loss of amphibian populations from high-elevation watersheds. Although several recent studies have documented the negative effects of introduced trout on amphib-

ians at the scale of individual water bodies (Hayes and Jennings 1986; Bradford 1989; Fisher and Shaffer 1996; Bradford and others 1998), few studies have examined the consequences of introduced fish on amphibian distributions at broader spatial scales (but see Bradford and others 1993; Knapp and Matthews 2000).

Numerous local-scale studies have documented that, in general, amphibians are less likely to exist and to breed successfully in lakes with predatory, nonnative fish (Bradford 1989; Brönmark and Edenhamn 1994; Braña and others 1996; Gamradt and Kats 1996; Hecnar and M'Closkey 1997; Bradford and others 1998; Goodsell and Kats 1999; Knapp and Matthews 2000). In part, amphibian

breeding success is lower in sites containing predatory fish because female amphibians avoid laying their eggs (Resetarits and Wilbur 1989; Kats and Sih 1992; Hopey and Petranka 1994). If egg-laying does take place, fish prey upon the embryonic and larval stages (Hayes and Jennings 1986; Gamradt and Kats 1996; Resetarits 1997; Tyler and others 1998a, b).

Further, the negative effects of introduced fish on amphibians may be magnified in mountain lakes, as compared to low-elevation waters, because many mountain lakes have less habitat structure (greater exposure to predation), lower productivity (reduced prey resources), and shorter productive periods. At high elevations, amphibians usually require more time to reach metamorphosis than lower-elevation conspecifics (Anderson 1967; Licht 1975; Howard and Wallace 1985), increasing their probability of predation during the vulnerable larval period. In some circumstances, larvae may overwinter for several years; thus, they are restricted to permanent, deeper bodies of water, most of which now contain fish (Bradford 1989; Knapp and Matthews 2000). Furthermore, postmetamorphic amphibians that overwinter in lentic sites may have to share with fish the few areas that do not freeze or become anoxic beneath surface ice.

The effects of introduced fish at broader spatial scales have not been adequately addressed and, to our knowledge, are restricted to two hypotheses. Bradford and others (1993) suggested that fish introductions have caused the loss of mountain yellow-legged frog (*Rana muscosa*) populations from entire drainages (including fishless lakes) as a result of fish predation on frogs in stocked lakes and the increased isolation of frog populations in the remaining fishless lakes. Knapp and Matthews (2000) suggested that the extirpation of this species from entire drainages could also be the result of fish occupying the most suitable habitats (deep lakes), restricting frogs to marginal habitats where extinction rates are high.

The objective of this study was to evaluate how introduced trout influence the distribution and abundance of amphibians at two spatial scales: individual lakes (local scale) and drainage basins (landscape scale). To accomplish this, we first tested the hypothesis that introduced trout have important local effects by comparing amphibian densities in sites with and without trout after controlling for habitat differences between fish-containing and fishless sites. Although the local effects of introduced fish on amphibians have been documented in numerous studies, our study is unique in that we examined the local effects of introduced trout on two amphibian species, the long-toed salamander

(*Ambystoma macrodactylum*) and the Columbia spotted frog (*Rana luteiventris*), each of which has a different life history and thus potentially different responses to introduced trout. Long-toed salamander larvae overwinter twice before metamorphosing into a terrestrial adult, whereas spotted frog tadpoles complete their larval stage in a single summer (Pilliod and Fronzuto forthcoming; Reaser and Pilliod forthcoming). To evaluate the effects of introduced trout on these amphibian species at the basin scale, we tested the hypothesis that within drainage basins, amphibian densities in fishless sites would decline with increasing levels of trout occupancy.

METHODS

Study Area

Between 1994 and 1999, we repeatedly surveyed all lentic habitats (lakes, ponds, flooded meadows) in a 90 km^2 area of the Bighorn Crags, a region of the Salmon River Mountains along the eastern boundary of the Frank Church–River of No Return Wilderness, Lemhi County, Idaho (Figure 1). The study area encompassed the headwater areas of five major drainages forming tributaries of the Middle Fork and Main Salmon rivers. These drainages contained two to three glacial cirque basins at 2300–2800 m. Each basin contained one to 15 permanent lakes or ponds and up to 10 ephemeral ponds and flooded meadows. The basins were separated from each other by headwall ridges of 500–1000 m and steep, cascading outlets dropping 500 to 1000 m into drainage tributaries. In total, we surveyed all 101 lentic sites in 11 basins, including 74 permanent lakes and ponds, 14 permanently flooded meadows, and 13 ephemeral ponds.

The climate of the study area is typical of the Rocky Mountains. Winters are long (8 months), and most precipitation falls as snow (more than 85% of approximately 80 cm average annual precipitation) (Finklin 1988). The dominant vegetation is subalpine fir (*Abies lasiocarpa*) and grouse whortleberry (*Vaccinium scoparium*), with Engelmann spruce (*Picea engelmanni*), alpine rhododendron (*Rododendrous altiflorum*), and sedges (*Carex* sp.) along riparian areas and shorelines of lakes.

The study area is entirely within federally designated wilderness and is relatively free from most anthropogenic disturbance. The area is 4–32 km from the nearest unpaved road and is accessible only by trail. Some recreational impacts appeared to be associated with packstock (for example, horses, llamas), which was mostly localized around a few
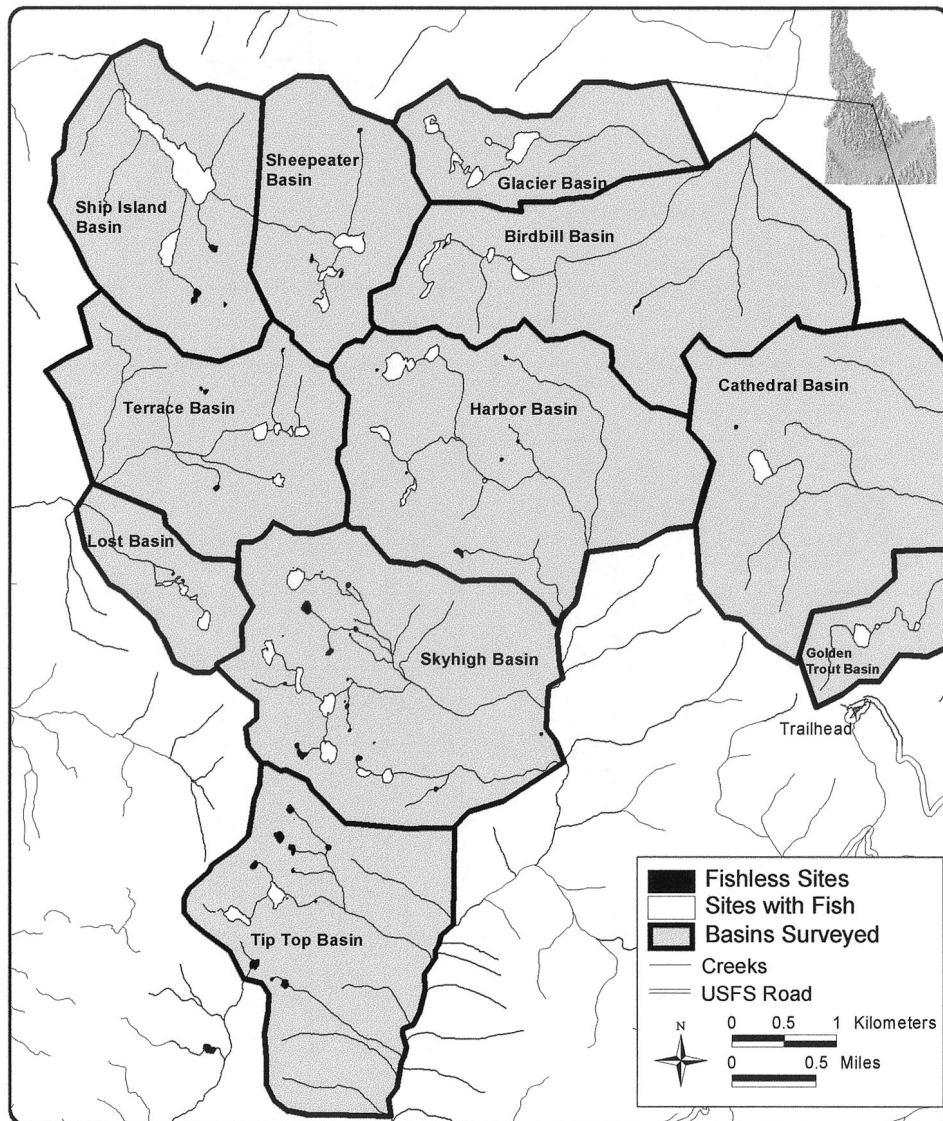
Figure 1. Map of the study area showing the 11 basins studied in the Bighorn Crags, Frank Church–River of No Return Wilderness, Lemhi County, Idaho. Fishless lakes are shown in black; fish-containing sites are white.

lakes. The Environmental Protection Agency and USDA Forest Service report negligible changes in air pollution and water quality in the area since 1985 (Jackson 1996).

Although no biotic surveys were conducted in the study area prior to the initial introduction of fish, steep creek gradients (greater than 17% slope) and falls (more than 3 m) draining each of the basins probably prevented colonizing trout from reaching the headwater lakes (Adams 1999). Therefore, we assumed that all basins were historically fishless (Bahls 1992).

Fish Surveys

We used historical records, hook-and-line angling, gill netting, and visual observations to determine the presence of fish. State stocking ledgers were searched back to 1913, the 1st year for which written records are available. In 1937 and 1938, the Idaho Department of Fish and Game stocked 60,100 cutthroat trout (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) into 12 to 30 previously fishless lakes in the study area to create recreational fisheries (Idaho Department of Fish and Game unpublished). Although a few lakes were again stocked in the 1950s, regular fish stocking did not begin until the mid 1960s, when fish were restocked every 3 to 6 years. In total, more than 300,000 fry or fingerlings have been introduced into 37 lakes. Each of these lakes has been stocked from four to 12 times and at least twice since 1989.

To determine the presence of fish, all small ponds and ephemeral pools less than 1.5 m deep were visually inspected for fish from shore and while

wading ($n = 31$). For water bodies more than 1.5 m deep, we noted the presence of fish during amphibian surveys ($n = 43$). If fish were not observed, we further assessed fish presence/absence using overnight gill net sets (40 $\times$ 1.8 m, seven panels of 10–38-mm mesh) for 12–16 h ($n = 11$) or snorkeling ($n = 8$) and multiple visual surveys in smaller water bodies ($n = 8$).

Amphibian Surveys

The distribution and abundance of amphibians in all lentic habitats in each basin were determined using visual encounter surveys as described by Crump and Scott (1994) and Thoms and others (1997). The earliest surveys were conducted during 1–7 July, approximately 1 week after ice-out on the larger lakes (breeding usually occurred in late June to early July). All sites were surveyed in July and August between 1000 and 1700 h, when air temperatures were above 10°C. Nearly all sites were surveyed each year, and some sites were surveyed two or three times each year between 1994 and 1999 (median, four surveys/site; range, one to 30).

In each of the 11 basins, teams of two trained observers searched the entire perimeter of each lake and pond (2 m of the littoral zone and 2 m of the riparian zone) and flooded areas of meadows. We enumerated each amphibian life stage both from shore and while wading 1 m from the shoreline. In addition, dip nets were used to sweep the substrate and, when present, the aquatic vegetation. We calculated amphibian densities as the maximum number of individuals observed at each site/area searched (m^2). Larval salamanders less than 25 mm snout–vent length (SVL) were considered to be in their 1st year, and larvae more than 26 mm SVL were considered to be 2 or more years old (Anderson 1967). Salamander larvae transformed in July of their 3rd year (at approximately 36–48 mm SVL). Too few adult long-toed salamanders were captured to reliably estimate population size, so we did not analyze adult salamander abundance. Juvenile frogs were defined as postmetamorphic frogs that had overwintered at least once and were less than 46 mm SVL (Turner 1960). We did not include young-of-the-year postmetamorphic frogs in any analyses because relatively few surveys were conducted in late September when recently metamorphosed frogs could be counted.

To evaluate how accurately our visual surveys estimated the abundance of amphibians, we compared visual salamander counts made while wading to counts made using snorkel surveys in 11 lakes and compared visual frog counts with Lincoln-Petersen mark–recapture population estimates in 39 lakes. Salamander counts made using visual surveys were comparable to salamander counts made during snorkel surveys ($n = 11$, Pearson $r^2 = 0.90$, $P < 0.001$); (B. Hoffman and D. S. Pilliod unpublished), and visual survey frog counts were comparable to population estimates ($n = 39$, Pearson $r^2 = 0.96$, $P < 0.001$).

Site Descriptions

We used a combination of field and laboratory measurements to quantify the physical, chemical, and biological characteristics of each lentic wetland. Surface area, perimeter, and elevation were obtained from 1:24,000 topographic maps or a geographic information system (GIS). Maximum depth was measured with a tape measure or hand-held sonar gun. Conductivity and pH were measured at the outlet of each site using Oakton hand-held meters (models T3, pH 2, Forestry Supp. Jackson, MS). Water temperature was recorded at the beginning of each survey (at 5 cm deep and within 1 m from shore) and then averaged within and among years. We estimated the relative amounts of aquatic littoral and terrestrial riparian substrate subclasses along the shoreline or over the area of each site (modified lacustrine and palustrine system classification, National Wetland Inventory) (Cowardin and others 1979). Terrestrial substrate subclasses included forest, shrub, forb-graminoid, rock, and woody debris. Aquatic subclasses included bedrock, cobble-gravel, silt/organic mud, vegetation, and woody debris. We calculated the proportion of shoreline made up of each substrate class by summing the linear distances of each class around a site and dividing by the site perimeter.

Statistical Analyses

To evaluate the local effects of introduced trout on amphibian populations, we first compared amphibian densities in sites with and without fish using a Mann-Whitney U test (Sokal and Rohlf 1995). We did not use parametric models, even with transformed variables, because the data were skewed by the low densities of amphibians in fish-containing sites.

To minimize the potentially confounding influence of habitat differences between sites with and without fish, we used a two-step approach. First, to determine which habitat variables were associated with fish-containing sites, we entered all habitat variables into a backward stepwise logistic regression. We then used the resulting model to select those fishless sites that had similar values for significant habitat variables as sites with fish. This model

identified 10 fishless sites that were very similar in habitat characteristics to fish-containing sites ($n = 43$). This subset of fishless sites was used to evaluate the effects of fish on amphibian densities while minimizing the habitat differences between fish-containing and fishless sites. Amphibian densities in these two types of sites were compared using a Mann-Whitney U test. We used this approach instead of multiple regression because our dependent variables, amphibian densities, were always non-normal due to many sites that lacked any amphibians. These skewed distributions could not be normalized using standard transformations.

To further evaluate whether long-toed salamanders and spotted frogs used deep lakes (at least 2 m) for breeding and to determine whether amphibian reproduction in deep lakes was successful, we compared the densities of 1st-year and 2nd-year amphibian life stages among fishless sites as a function of maximum lake depth (less than 2 m, 2–4 m, 4–6 m, at least 6 m) using chi-square approximations of the Kruskal-Wallis test (Sokal and Rohlf 1995). To determine possible landscape effects of introduced trout on amphibian abundance at the basin scale, we performed simple linear regression analyses on the mean density of amphibians in fishless sites as a function of the percent area of lentic habitat containing trout in a basin. The influence of outliers was assessed with the F approximation of Cook's distance (Ramsey and Schafer 1997).

To differentiate between the effects of fish and the effects of differences in habitat among basins, we first reduced the number of habitat variables using factor analysis with a principal component extraction and varimax rotation. Factor scores were calculated for each site. We then evaluated the significance of differences in the average factor scores among basins using multivariate analysis of variance (MANOVA), with factor scores as our dependent variables and basin as our independent variable. These models met assumptions of normality and homoscedasticity but not equality of covariance matrices. Therefore, we evaluated model significance using Pillai's trace, a conservative and robust multivariate F test (Norusis 1990). To identify which factors were significantly different among basins, we performed multiple univariate analysis of variance (ANOVA), again using factor score as our dependent variable and basin as our independent variable. Finally, to determine which basins were significantly different from each other, we used Tukey's pair-wise comparisons on each of the significant factors. Similarly, to determine whether fishless sites had significantly different habitat among basins, we repeated the above procedure, but only included factor scores from fishless sites.

In regression analyses and MANOVAs, we screened predictor variables for colinearity and excluded redundant variables from analyses. These included area and perimeter, which were correlated with depth, and woody debris and bedrock, due to the redundancy of including all subclasses in percentage estimates. Conductivity was also excluded because there was little variation across sites (mean, 5.5 μS; range, 0–30 μS). We performed all analyses on SPSS software v.10.0 (SPSS Inc Chicago, IL) and used $\alpha = 0.05$ as a significance criterion.

RESULTS

Introduced cutthroat, rainbow, or golden trout and their hybrids were found in all basins, but the percent of sites and area of habitat occupied by trout varied among basins (Table 1 and Figure 1). We found trout in 43% of all lentic sites, accounting for 90% of the available surface area of lentic habitat. Trout occupied the majority of lakes that were one or more ha in surface area and deeper than 4 m, while most sites less than 1 ha in surface area and less than 4 m deep were fishless (Figure 2). As a result, the more lentic habitat that was occupied by trout in a basin, the fewer deep, fishless sites remained (Table 1). Only two basins, Skyhigh and Tip Top, had less than 90% of the surface area of their lentic habitat occupied by trout, and both of these basins contained several deep, fishless lakes that could have supported trout populations. Other basins contained at most one deep, fishless lake (Table 1).

Local-scale Effects of Introduced Trout on Amphibians

The densities of all life stages of long-toed salamanders and spotted frogs were significantly lower in fish-containing sites than in fishless sites (for all life stages; n = 101, U = 647–930, $P \leq 0.018$) (Figure 3). The logistic regression analysis used to identify fishless sites that had similar habitat as fish-containing sites was significant (df = 2, $\chi^2 = 58.50$, $P < 0.001$, $r^2 = 0.59$). Greater maximum depths and rocky substrates characterized lakes with fish. Fishless sites selected using the logistic regression model were also deep, rocky lakes. Comparisons between these 10 fishless sites and the 43 sites where fish occurred indicated that fish-containing sites again had significantly lower densities of all life stages of amphibians than did fishless sites with similar habitat (for all life stages; $n = 53$, U = 48–86, $P \leq 0.002$).

Table 1. Number of Sites and Surface Area of Lentic Habitat Occupied by Fish in 11 Basins in the Bighorn Crags of the Frank Church–River of No Return Wilderness, Idaho

Basin	Total Sites	Fish Present (%)	Total Surface Area Sites (ha)	% Surface Area Fish Present
Birdbill	9	5 (56)	7.17	95.8
Cathedral	2	1 (50)	7.25	99.7
Glacier	7	7 (100)	16.87	100.0
Golden Trout	3	3 (100)	5.29	100.0
Harbor	12	4 (33)	15.38	92.2
Lost	6	4 (67)	5.14	98.1
Sheepeater	5	3 (60)	11.11	95.7
Ship Island	5	2 (40)	43.75	95.7
Skyhigh	29	7 (24)	24.75	81.1
Terrace	7	5 (71)	7.63	95.5
Tip Top	16	2 (13)	14.43	52.5
Totals	101	43 (42.6)	158.8	90.0

Basin-scale Effects of Introduced Trout on Amphibians

Long-toed salamanders and spotted frogs reproduced in lentic sites ranging in depth from 0.2 to 6 or more m and the densities of 1st-year salamander larvae and frog tadpoles were not significantly different among fishless sites across this range of depths (1st-year salamander larvae: df = 3, χ^2 = 3.2, P = 0.36, Figure 4A; spotted frog tadpoles: df = 3, χ^2 = 6.3, P = 0.10, Figure 4B). However, among these fishless sites, densities of amphibian life stages that had overwintered at least once were significantly lower in sites less than 2 m deep than in deeper sites (2nd-year salamander larvae: df = 3, χ^2 = 24.2, P < 0.001, Figure 4A; juvenile frogs: df = 3, χ^2 = 9.3, P = 0.025, Figure 4B).

Among basins, the density of 1st-year amphibian life stages in fishless sites was not related to the percent surface area of lentic sites occupied by trout (Figure 5A and 6A). However, the percent surface area of lentic sites occupied by trout was a highly significant predictor of the density of salamander larvae at least 2 years old in fishless sites (Adj. R^2 = 0.95, $F_{1,7}$ = 167.4, P < 0.001; Figure 5B) and of the density of adult and juvenile frogs in fishless sites (Adj. R^2 = 0.98, $F_{1,7}$ = 330.7, P < 0.001; Figure 6B). Both of these relationships were strongly influenced by the data point for Tip Top Basin (lentic surface area containing fish = 52%), as measured by the F approximation to Cook's distance. When we excluded this data point from the models, no other basins had a disproportionate influence on the regression, and the linear regression was still highly significant for both salamanders

(Figure 5B; Adj. R^2 = 0.64, $F_{1,6}$ = 13.4, P = 0.011) and frogs (Figure 6B; Adj. R^2 = 0.81, $F_{1,6}$ = 31.47, P = 0.001). Therefore, densities of older amphibian life stages in fishless sites decreased with increases in the proportion of lentic habitat occupied by trout.

Habitat characteristics of all sites formed five composite factors, three of which were significantly different among basins (Pillai's trace = 0.83, $F_{50,450}$ = 2.0, P = 0.001). These three significant factors characterized lakes with (a) greater rocky substrate, (b) sparse aquatic vegetation and at higher elevations, and (c) greater maximum depths and forested shorelines. Pair-wise comparisons indicated that Glacier Basin had significantly higher factor scores than Tip Top Basin for the factor that characterized lakes with sparse aquatic vegetation at higher elevations. No other factors were significantly different among individual basins. Habitat characteristics of fishless sites were not significantly different among basins based on composite factor scores (Pillai's trace = 0.69, $F_{35,245}$ = 1.12, P = 0.31). Therefore, the relationships between amphibian density in fishless sites and percent of lentic surface area occupied by trout (Figure 5 and 6) were unlikely to have been confounded by habitat differences among basins.

DISCUSSION

Recent studies have documented the negative local effects of introduced trout on amphibian abundance and occurrence in high-mountain lakes in the western United States (Bradford 1989; Bradford and others 1998; Tyler and others 1998a; Knapp
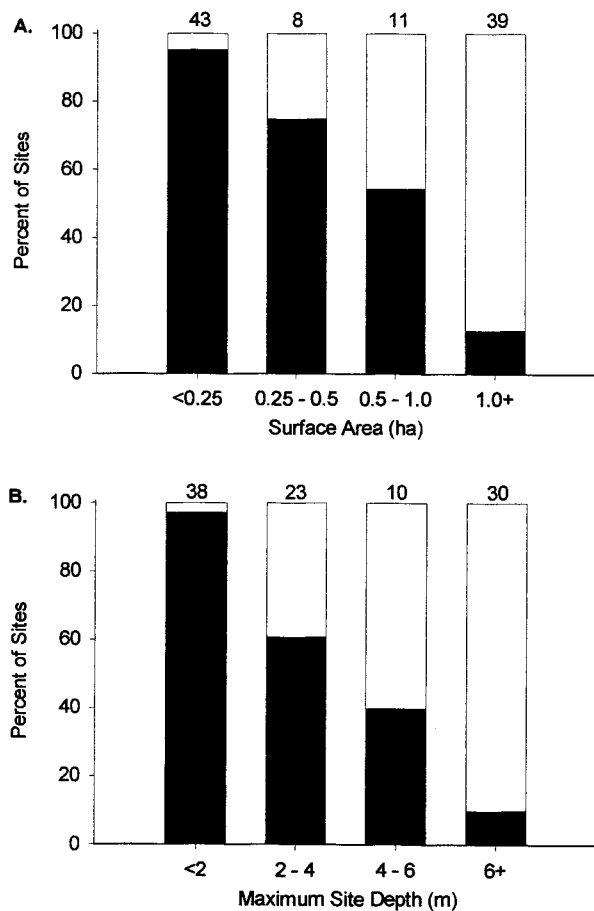
Figure 2. Frequency histograms showing the proportion of fishless (black) and fish-containing (white) lentic sites as a function of surface area (**A**) and maximum lake depth (**B**) in the Bighorn Crags of the Frank Church–River of No Return Wilderness. Numbers above bars indicate the number of sites in each category.

Figure 3. Mean density (number per m^2 searched; + 1 SE) of 1st- and 2nd-year salamander larvae (**A**) and spotted frog tadpoles and juveniles plus adults (**B**) in sites with (black bars) and without (white bars) introduced trout in the Bighorn Crags of the Frank Church–River of No Return Wilderness between 1994 and 1999. Asteriks between pairs of bars indicate that the densities of all life stages of amphibians were significantly lower in lakes with fish compared to fishless sites (*$P < 0.001$).

and Matthews 2000). Our study is unique in that we also examined whether the negative effects in stocked lakes have implications for the distributions of these amphibians across a landscape (that is, whether impacts extend to fishless sites in a basin) and did so by studying two amphibians with very different life histories. This information is needed to explain the reported declines and extirpation of high-mountain amphibians from landscapes (basins, watersheds) where fishless habitats still exist (for example, Fellers and Drost 1993; Bradford and others 1994; Drost and Fellers 1996; Knapp and Matthews 2000).

In congruence with other studies, we found that the abundance of all life stages of long-toed salamanders and spotted frogs was lower in sites with fish than it was in fishless sites (Tyler and others 1998a; Knapp and Matthews 2000). How-
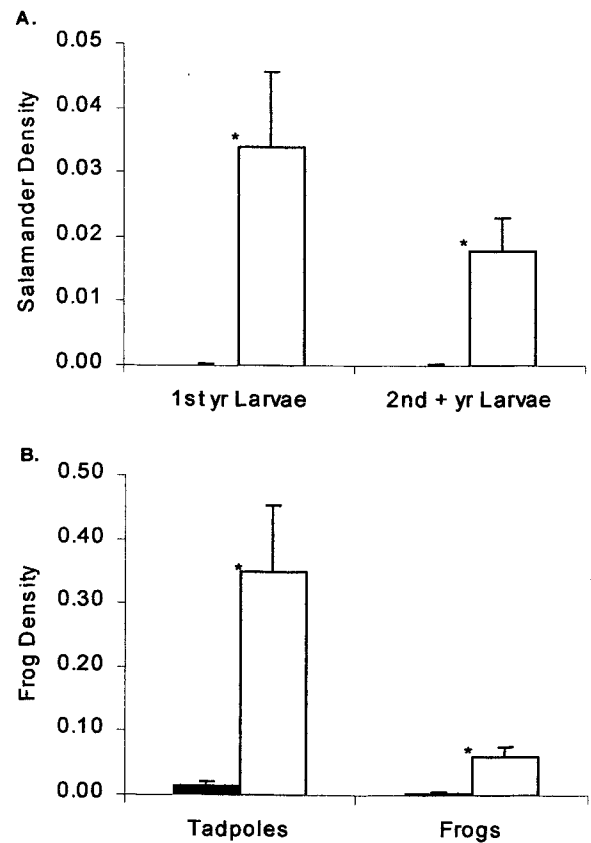
ever, without prestocking records with which to compare current amphibian densities, we cannot be certain whether amphibian populations at fish-containing sites are smaller now than they were before trout were introduced. A common argument is that sites now occupied by trout are, and always were, poor habitat for amphibians because these sites are typically deep, rocky lakes. However, few studies have examined the habitat associations and requirements of high-elevation amphibians; thus, this perception has little scientific basis. We found significantly larger populations of amphibians in fishless than in fish-containing sites, even after accounting for the differences in habitat; this suggests that long-toed salamanders and spotted frogs may historically have had large populations in lakes now occupied by trout. Based on the low abundance and recruitment of amphibians in lakes with fish, we
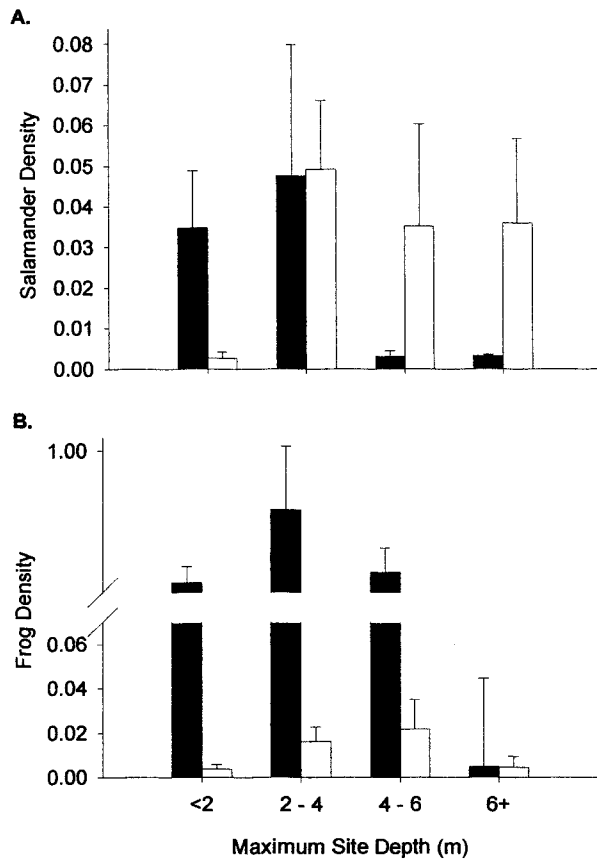
A.

B.

A.

B.

Figure 4. Mean density (number per m^2 searched; + 1 SE) of 1st- (black bars) and 2nd-year (white bars) salamander larvae (**A**) and spotted frog tadpoles (black bars) and juveniles plus adults (white bars) (**B**) in fishless sites as a function of the maximum depth of each site in the Bighorn Crags of the Frank Church–River of No Return Wilderness between 1994 and 1999. First-year larvae and tadpoles were abundant in shallow sites (less than 2 m deep), whereas densities of older life stages were lowest in sites less than 2 m.

Figure 5. Plot of the relationship between the percentage of lentic water surface area containing trout and the mean site density (number per m^2 searched) per basin of 1st-year long-toed salamander larvae (A) and 2nd-year long-toed salamander larvae (B) in fishless sites in the Bighorn Crags of the Frank Church–River of No Return Wilderness. Significant linear regression lines are shown. The Tip Top Basin data point is an outlier in this model, but the relationship remained highly significant when this data point was excluded.

suspect that lakes with fish are sink habitats for amphibians where juvenile recruitment insufficiently compensates for adult mortality (Pulliam 1988; Pulliam and Danielson 1991). Local extinction of amphibian populations at such sites may be prevented by the immigration of juveniles and adults from nearby fishless sites that frequently act as sources.

Despite relatively high levels of reproduction in fishless sites less than 2 m deep (as seen in Figure 4), we rarely found 2nd-year salamander larvae and juvenile frogs in these shallow ponds, suggesting that both species generally require lentic sites at least 2 m deep for surviving through winter. In shallow ponds, long-toed salamanders risk desiccation during summer and freezing or anoxic condi-
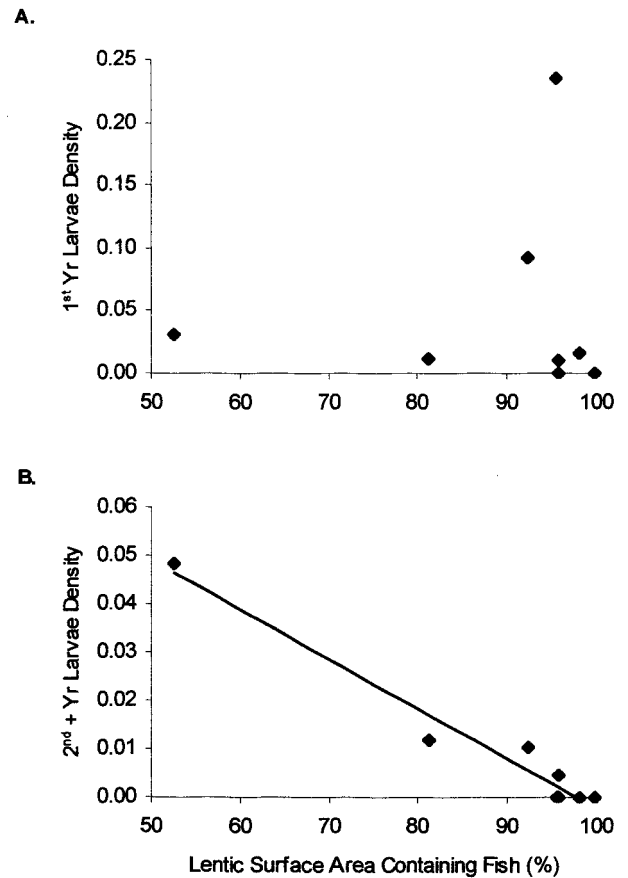
tions during winter (we occasionally found dead larvae in these shallow sites during spring surveys), whereas in deep lakes they risk predation from introduced trout. Because high-elevation populations of long-toed salamanders have a long larval stage (2–3 years) (Anderson 1967), they may be more restricted to deeper water bodies and thus have lost most of their suitable breeding habitat to introduced fish. Mountain yellow-legged frogs, endemic to the Sierra Nevada, also have multiple-year larval stages. Recent research suggests that the loss of deep, fishless breeding sites is threatening the persistence of this species across its range (Knapp and Matthews 2000).

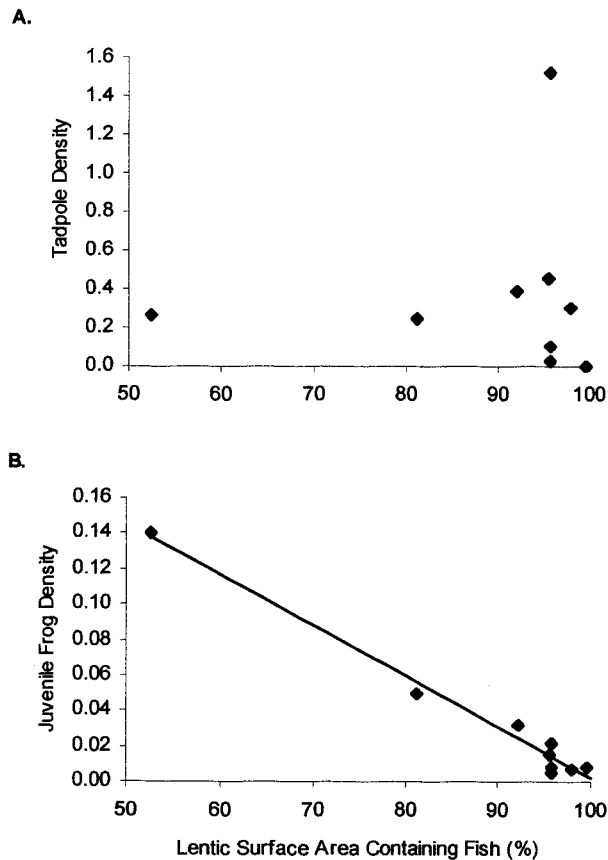In contrast to salamanders, spotted frogs are able

A.

B.

Figure 6. Plot of the relationship between the percentage of lentic water surface area containing trout and the mean site density (number per m² searched) per basin of spotted frog tadpoles (**A**) and juveniles plus adults (**B**) in fishless sites in the Bighorn Crags of the Frank Church–River of No Return Wilderness. Significant linear regression lines are shown.

to breed successfully in shallow, fishless sites, because most of the tadpoles transform into juveniles before the lakes begin to freeze. We did not observe any overwintering tadpoles, a finding consistent with the life history of this species across its range (Reaser and Pilliod forthcoming). In the late summer, recently metamorphosed juveniles migrated with adults and older juveniles to deeper bodies of water to overwinter (D. S. Pilliod unpublished). Based on our observations indicating that the highest overwinter survival of postmetamorphic frogs occurred in deeper, fishless sites, we suggest that predation by trout on juveniles that migrated from shallow fishless sites to deep, fish-containing lakes may effectively eliminate successful reproduction at fishless sites. Because trout now occupy 67% of all lentic sites 2 or more m deep in the study area, the majority of high-quality overwintering habitat for these amphibians has been lost.

The overwintering requirements of long-toed salamander larvae and spotted frogs may provide a mechanism that would explain why the local-scale negative effects of introduced trout can extend to an entire basin. Basins with more lentic habitat occupied by introduced trout had fewer deep, fishless sites and lower densities of late-stage salamander larvae and postmetamorphic frogs (more than 1 year old) in fishless sites. Because 1st-year salamander larvae and frog tadpoles were fairly abundant in fishless sites in all basins, the low density of older life stages of these amphibians in fishless sites in heavily stocked basins was likely due to lower survival in basins that lacked sufficient deep, fishless habitat.

The combined negative effects of introduced trout at local and basin scales demonstrated by this study may have consequences for amphibian persistence within the study basins. Now mostly occupied by trout, deep lentic habitats in the study area likely provided critical breeding and winter habitat for salamanders and frogs and thus may have been important amphibian source populations in many basins prior to fish introductions. We believe that the shallow water bodies that make up the majority of remaining fishless habitat may be sink habitats for amphibians. Although the amphibian populations at these sites may have been maintained by immigration from source populations prior to fish introductions, most of these source populations have been extirpated by the introduced trout. In the absence of immigration, we would expect these populations to eventually disappear.

Based on the negative effects of trout on amphibians in fish and fishless sites, what evidence do we have that this condition may be threatening amphibian persistence? Long-toed salamanders may have already disappeared from three of 11 basins (Cathedral, Ship Island, Sheepeater), including an entire drainage, and they appear to be on the verge of extirpation in several other basins (Glacier, Golden Trout, Lost). We cannot be certain that salamanders historically inhabited the three basins in which they are currently absent, but the wide distribution of this species and characteristics of the habitat in these basins indicate that they most likely once supported salamander populations. Long-toed salamander populations may be particularly vulnerable to extinction following trout introductions because they are generally highly philopatric, have relatively small home ranges (less than 300 m²), and may only disperse up to 100 m away from breeding sites (Sheppard 1977; Beneski and others 1986; Powell and others 1997).

Despite the local- and basin-scale effects of intro-

duced trout on spotted frogs, this species still occurred at almost all sites and in all basins in our study area. Several studies have concluded that local populations of lentic-breeding amphibians may be able to persist in sink habitats due to relatively high immigration and the "rescue effect" associated with some metapopulations (Gill 1978; Sjögren 1991; Gibbs 1993; Sjögren-Gulve 1994; Sinsch 1992, 1997). However, our results also suggest that spotted frogs may be more threatened than their widespread distribution indicates. Tadpole survival, juvenile recruitment, and the abundance of frogs in most of the heavily stocked basins were lower than in basins with less habitat occupied by trout. In addition, the age structure of frogs in fish-dominated basins indicates that the frogs have not reproduced successfully for 6 to 8 years (D. S. Pilliod unpublished). Given the longevity of these animals (12–14 years) (Turner 1960), spotted frogs may soon disappear from the basins where remaining fishless sites do not provide adequate overwintering habitat.

A concluding question that is often asked is, why have fish not eliminated these amphibians sooner? Based on the evidence in this study and others, we believe that the initial local impacts of fish introductions occurred within years (Terrero 1951; Macan 1966; Sexton and Phillips 1986; Aronsson and Stenson 1998; Meyer and others 1998), but that the extirpation of amphibians at broader spatial scales took many decades (Bradford and others 1993; Knapp and Matthews 2000). Frogs and salamanders were probably once widely distributed and were quickly eliminated—or nearly eliminated—from lakes where trout were introduced. The quality of the remaining fishless habitats may have been insufficient to maintain viable populations, and remaining populations are probably continuing to decline slowly. Because the lakes in this study were not regularly stocked until the 1960s, these amphibians have only experienced high trout densities for a relatively short time (40 years, or only about four generations). Factors such as metapopulation dynamics can prolong declines to extinction, especially among long-lived organisms like high-elevation amphibians (Sjögren 1991; Hanski 1997).

Restoration

Conserving natural biodiversity and maintaining functioning ecosystems is a goal of protected area management. The results of this study suggest that wildlife managers need to consider restoring a few deep lakes in each basin to create fishless breeding and overwintering habitat for amphibians (Knapp 1996; Knapp and Matthews 1998; Pilliod and Peter-

son 2000). Given that some amphibian reproduction is occurring, even in heavily stocked basins (see Figures 5A and 6A), we suspect that amphibian populations could recover quickly if a few deep lakes were restored to a fishless state (Brönmark and Edenhamn 1994; Knapp 1996; Funk and Dunlap 1999; Knapp and others 2001). However, because amphibian populations in mountain basins are widely isolated from each other (Howard and Wallace 1981; Call 1997; Tallmon and others 2000), recolonization following the extirpation of amphibians from entire basins could take decades.

REFERENCES

Adams SB. 1999. Mechanisms limiting vertebrate invasion: brook trout in mountain streams of the northwestern USA [dissertation]. Missoula, (MT): Department of Biology, University of Montana.

Anderson JD. 1967. A comparison of the life histories of coastal and montane populations of *Ambystoma macrodactylum* in California. Am Midland Nat 77:323–54.

Aronsson S, Stenson JAE. 1998. Newt–fish interactions in a small forest lake. Amphibia-Reptilia 16:177–84.

Bahls PF. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Sci 66:183–93.

Beneski JT Jr, Zalisko EJ, and Larsen JHJ. 1986. Demography and migratory patterns of the eastern long-toed salamander, *Ambystoma macrodactylum columbianum*. Copeia 1986:398–408.

Bradford DF. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: Implication of the negative effect of fish introductions. Copeia 1989:775–8.

Bradford DF, Cooper SD, Jenkins TM, Kratz K, Sarnelle O, Brown AD. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Can J Fish Aquat Sci 55:2478–91.

Bradford DF, Graber DM, Tabatabai F. 1994. Population declines of the native frog, *Rana muscosa*, in Sequoia and Kings Canyon National Parks, California. Southwestern Nat 39:323–7.

Bradford DF, Tabatabai F, Graber DM. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conserv Biol 7:882–8.

Braña F, Freschilla L, Orizaola G. 1996. Effect of introduced fish on amphibian assemblages in mountain lakes of northern Spain. Herpetol J 6:145–8.

Brönmark C, Edenhamn P. 1994. Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? Conserv Biol 8:841–5.

Call DR. 1997. Microsatellite characteristics and population structure for two anurans (*Rana luteiventris* and *Hyla regilla*). [dissertation]. Pullman (WA): Department of Zoology, Washington State University.

Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. Classifications of wetlands and deepwater habitats of the United States. FWS/OBS-79/31. Washington (DC): USDI Fish and Wildlife Service.

Crump ML, Scott NJJ. 1994. Visual encounter surveys. In: Heyer WR Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Washington (DC): Smithsonian Institute Press. p 84–92.

Drost CA, Fellers GM. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conserv Biol 10:414–25.

Fellers GM, Drost CA. 1993. Disappearance of the Cascades frog *Rana cascadae* at the southern end of its range, California, U.S.A. Biol Conserv 65:177–81.

Finklin AI. 1988. Climate of the Frank Church–River of No Return Wilderness, central Idaho. Ogden (UT): USDA Intermountain Research Station.

Fisher RN, Shaffer HB. 1996. The decline of amphibians in California's Great Central Valley. Conserv Biol 10:1387–97.

Funk WC, Dunlap WW. 1999. Colonization of high-elevation lakes by long-toed salamanders (*Ambystoma macrodactylum*) after the extinction of introduced trout populations. Can J Zool 77:1759–67.

Gamradt SC, Kats LB. 1996. Effect of introduced crayfish and mosquitofish on California newts. Conserv Biol 10:1155–62.

Gibbs JP. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13:25–31.

Gill DE. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecol Monogr 48:145–66.

Goodsell JA, Kats LB. 1999. Effect of introduced mosquitofish on

Pacific treefrogs and the role of alternative prey. Conserv Biol 13:921–4.

Hanski I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. In: Hanski IA, Gilpin ME, editors. Metapopulation biology: ecology, genetics, and evolution. San Diego: Academic Press.

Hayes MP, Jennings MR. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? J Herpetol 20:490–509.

Hecnar SJ, M'Closkey RT. 1997. The effects of predatory fish on amphibian species richness and distribution. Biol Conserv 79:123–31.

Hopey ME, Petranka JW. 1994. Restriction of wood frogs to fish-free habitats: how important is adult choice? Copeia 1994:1023–5.

Howard JH, Wallace RL. 1985. Life history characteristics of populations of the long-toed salamander (*Ambystoma macrodactylum*) from different altitudes. Am Midland Nat 113:361–73.

Howard JH, Wallace RL. 1981. Microecological variation of electrophoretic loci in populations of *Ambystoma macrodactylum columbianum* (Caudata: Ambystomatidae). Copeia 1989:466–71.

Jackson GL. 1996. Air quality impacts: Frank Church–River of No Return Wilderness. Salmon (ID): USDA Salmon and Challis National Forest.

Kats LB, Sih A. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). Copeia 1992:468–73.

Knapp RA. 1996. Non-native trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. In: Sierra Nevada ecosystem project: final report to Congress. Volume III, Assessments, commissioned reports, and background information. Davis (CA): Wildland Resource Center Report. p 363–407.

Knapp RA, Matthews KR. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. Restor Ecol 6:207–13.

Knapp RA, Matthews KR. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv Biol 14:428–38.

Knapp RA, Matthews KR, Sarnelle O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecology. Forthcoming.

Licht LE. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. Can J Zool 53:1254–7.

Macan TT. 1966. The influence of predation on the fauna of a moorland fishpond. Arch Hydrobiol 61:432–52.

Meyer AH, Schmidt BR, Grossenbacher K. 1998. Analysis of three amphibian populations with quarter-century long time-series. Proc R Soc London B 265:523–8.

Norusis MJ. 1990. SPSS advanced statistical users guide. Chicago: SPSS Inc.

Pilliod DS, Fronzuto JA. 2000. Long-toed salamander (*Ambystoma macrodactylum*). In: Lanoo MJ, editor. Status and trends of North American amphibians. Berkeley (CA): University of California Press. Forthcoming.

Pilliod DS, Peterson CR. 2002. Evaluating effects of fish stocking on amphibian populations in wilderness lakes. In: Cole DN, McCool SF, Borrie WT O'Loughlin J, editors. Wilderness science in a time of change conference. Volume 5, Wilderness ecosystems, threats, and management. Proceedings RMRS-P-

15-VOL-5. Ogden (UT): USDA Forest Service, Rocky Mountain Research Station. p 328–35.

Powell GL, Russell AP, James JD, Nelson SJ, Watson SM. 1997. Population biology of the long-toed salamander, *Ambystoma macrodactylum* in the front range of Alberta. In: Green DM, editor. Amphibians in decline: Canadian studies of a global problem. St. Louis: Society for the Studies of Amphibians and Reptiles. p 37–44.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat 132:652–61.

Pulliam HR, Danielson BJ. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am Nat 137:S50–S66.

Ramsey FL, Schafer DW. 1997. The statistical sleuth. Belmont (CA): Duxbury Press.

Reaser JK, Pilliod DS. 2002. Columbia spotted frog (*Rana luteiventris*). In: Lanoo MJ, editor. Status and trends of North American amphibians. Berkeley (CA): University of California Press. Forthcoming.

Resetarits WJ Jr. 1997. Differences in an ensemble of streamside salamanders (Plethodontidae) above and below a barrier to brook trout. Amphibia-Reptilia 18:15–25.

Resetarits WJ Jr, Wilbur HM. 1989. Choice of oviposition sites by *Hyla chrysoscelis*: role of predators and competitors. Ecology 70:220–8.

Sexton OJ, Phillips C. 1986. A qualitative study of fish–amphibian interactions in 3 Missouri ponds. Trans Missouri Acad Sci 20:25–35.

Sheppard RF. 1977. The ecology and home range movements of *Ambystoma macrodactylum krausei* (Amphibia: Urodela) [dissertation]. Calgary: University of Calgary.

Sinsch U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112:42–7.

Sinsch U. 1992. Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). Oecologia 90:489–99.

Sjögren P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biol J Linnean Soc 42:135–47.

Sjögren-Gulve P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75:1357–67.

Sokal RR, Rohlf FJ. 1995. Biometry. 3rd ed. New York: WH. Freeman.

Tallmon DT, Funk WC, Allendorf FW, Dunlap WW. 2000. Genetic differentiation of long-toed salamander (*Ambystoma macrodactylum*) populations. Copeia 2000:27–35.

Terrero D. 1951. Historia local de piscicultura. Montes 39:165–71.

Thoms C, Corkran CC, Olson DH. 1997. Basic amphibian survey for inventory and monitoring in lentic habitats. In: Olson DH, Leonard WP, Bury RB, editors. Sampling amphibians in lentic habitats. Olympia (WA): Society for Northwestern Vertebrate Biology. p 35–46.

Turner FB. 1960. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird and Girard, in Yellowstone Park, Wyoming. Ecol Monogr 30:251–78.

Tyler T, Liss W, Ganio LM, Larson GL, Hoffman R, Deimling E, Lomnicky G. 1998a. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. Conserv Biol 12:94–105.

Tyler TJ, Liss WJ, Hoffman RL, Ganio LM. 1998b. Experimental analysis of trout effects on survival, growth, and habitat use of two species of Ambystomatid salamanders. J Herpetol 32:345–9.