knapp, 2000

Non-Native Fish Introductions and the Decline of the Mountain Yellow-Legged Frog from within Protected Areas

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Abstract: *One of the most puzzling aspects of the worldwide decline of amphibians is their disappearance from within protected areas. Because these areas are ostensibly undisturbed, habitat alterations are generally perceived as unlikely causes. The introduction of non-native fishes into protected areas, however, is a common practice throughout the world and may exert an important influence on amphibian distributions. We quantified the role of introduced fishes (several species of trout) in the decline of the mountain yellow-legged frog (*Rana muscosa*) in California's Sierra Nevada through surveys of >1700 sites in two adjacent and historically fishless protected areas that differed primarily in the distribution of introduced fish. Negative effects of fishes on the distribution of frogs were evident at three spatial scales. At the landscape scale, comparisons between the two protected areas indicated that fish distribution was strongly negatively correlated with the distribution of frogs. At the watershed scale, the percentage of total water-body surface area occupied by fishes was a highly significant predictor of the percentage of total water-body surface area occupied by frogs. At the scale of individual water bodies, frogs were three times more likely to be found and six times more abundant in fishless than in fish-containing waterbodies, after habitat effects were accounted for. The strong effect of introduced fishes on mountain yellow-legged frogs appears to result from the unique life history of this amphibian which frequently restricts larvae to deeper water bodies, the same habitats into which fishes have most frequently been introduced. Because fish populations in at least some Sierra Nevada lakes can be removed with minimal effort, our results suggest that the decline of the mountain yellow-legged frog might be relatively easy to reverse.*

Introducciones de Peces No-nativos y Disminuciones de la Rana de Montaña de Patas Amarillas Dentro de Áreas Protegidas

Resumen: *Uno de los aspectos más enigmáticos de la disminución de anfibios a nivel mundial es su desaparición dentro de zonas protegidas. Debido a que estas áreas aparentemente no son perturbadas, las alteraciones del hábitat, por lo general, no se perciben como causas probables de esta desaparición. Sin embargo, la introducción de peces no-nativos dentro de áreas protegidas es una práctica común alrededor del mundo y puede ejercer una influencia importante en las distribuciones de anfibios. Medimos el efecto de peces introducidos (diversas especies de trucha) sobre la disminución de la rana de montaña de patas amarillas (*Rana muscosa*) en la Sierra Nevada de California mediante muestreos de >1700 sitios en dos áreas adyacentes, protegidas y sin pesca que difieren principalmente en la distribución de peces introducidos. Los efectos negativos de los peces en la distribución de ranas fueron evidentes en tres escalas espaciales. A escala*

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Paper submitted February 18, 1999; revised manuscript accepted August 3, 1999.

Conservation Biology, Pages 428–438
Volume 14, No. 2, April 2000

de paisaje, las comparaciones entre las dos áreas protegidas indican que la distribución de peces estuvo fuertemente correlacionada de manera negativa con la distribución de las ranas. A escala de cuenca, el porcentaje de la superficie del área total de cuerpos de agua ocupado por peces fue un elemento de predicción altamente significativo del porcentaje de la superficie del área total de cuerpos de agua ocupado por ranas. A escala de cuerpos de agua individuales, las ranas fueron tres veces más probables de ser encontradas en cuerpos de agua sin peces que en aquéllos que tenían peces, y seis veces más abundantes en esas áreas después de tomar en cuenta los efectos del hábitat. El efecto fuerte de los peces introducidos en la rana de montaña de patas amarillas parece resultar de la singular historia de vida de este anfibio que frecuentemente restringe a sus larvas a cuerpos de agua más profundos, los mismos hábitats en los que los peces han sido introducidos más frecuentemente. Debido a que las poblaciones de peces en al menos algunos de los lagos de la Sierra Nevada pueden ser removidos con un esfuerzo mínimo, nuestros resultados sugieren que la disminución de la rana de montaña de patas amarillas puede ser revertida de manera relativamente fácil.

Introduction

Increasing evidence indicates that amphibians on several continents are disappearing at an unusually high rate (Richards et al. 1993; Drost & Fellers 1996; Pounds et al. 1997). Although habitat alteration and exotic species introductions have been implicated in the decline of some species (Blaustein & Wake 1995; Fisher & Shaffer 1996), the decline of amphibians in protected areas where habitats are seemingly undisturbed (Bradford et al. 1994; Drost & Fellers 1996; Pounds et al. 1997; Lips 1998) suggests the role of larger-scale effects such as those resulting from UV-B radiation, disease, or environmental contaminants (Blaustein et al. 1994; Blaustein & Wake 1995; Stebbins & Cohen 1995; Berger et al. 1998). Non-native fishes have been widely introduced into naturally fishless habitats, however, including protected areas (Bahls 1992; Cole & Landres 1996; Townsend 1996), and they can have important effects on native amphibian species (Brönmark & Edenhamn 1994; Gamradt & Kats 1996; Bradford et al. 1998; Tyler et al. 1998). Nevertheless, the role of fish introductions in large-scale amphibian declines has been examined only rarely (Fisher & Shaffer 1996; Hecnar & M'Closkey 1997). We used analyses based on surveys conducted over a 100,000-ha landscape to quantify the role of fish introductions in the decline of the mountain yellow-legged frog (*Rana muscosa*).

The mountain yellow-legged frog is endemic to the Sierra Nevada and Transverse Ranges of California and Nevada (U.S.A.) (Zweifel 1955). In the Sierra Nevada, it was historically a common inhabitant of lakes and ponds at elevations of 1400-3700 m (Grinnell & Storer 1924), nearly all of which were naturally fishless (Knapp 1996). Mountain yellow-legged frog larvae require two or more summers to develop through metamorphosis, and adults overwinter underwater (Zweifel 1955; Bradford 1983). These life-history attributes may restrict successful breeding and overwintering to deeper water bodies where the chances of summer drying and winter freezing are reduced (Bradford 1989).

Despite the fact that its habitat has been protected in national parks and wilderness areas for the past 30-80 years, the mountain yellow-legged frog is now extirpated from at least 50% of its historic localities (Bradford et al. 1994; Drost & Fellers 1996; Jennings 1996). The results of previous studies suggest that predation by fishes (Needham & Vestal 1938; Bradford 1989) introduced into the Sierra Nevada's historically fishless lakes may have contributed to this decline (Bradford 1989; Bradford et al. 1998), but because of the relatively small scales at which these studies were conducted, the role of fish introductions in causing the range-wide decline of the mountain yellow-legged frog remains unclear. Other researchers have suggested that larger-scale effects may instead be responsible (Stebbins & Cohen 1995; Drost & Fellers 1996), such as those resulting from increasing UV-B radiation (Blaustein et al. 1994; Anzalone et al. 1998) or environmental contaminants transported from California's agricultural Central Valley (Cory et al. 1970; Zabik & Seiber 1993; Datta et al. 1998).

Our study area encompassed portions of two large, adjacent protected areas that are generally similar except with regard to the distribution of introduced fishes. The John Muir Wilderness (JMW) and Kings Canyon National Park (KCNP) study areas (Fig. 1) encompass a total of approximately 100,000 ha, are managed by the U.S. Forest Service and National Park Service, respectively, and with the exception of introduced fishes, are relatively undisturbed. Current human use of the two areas is limited to nonmechanized recreation. Together, these two areas contain nearly 2000 lakes and ponds (defined below), all of which were historically fishless and fall within the historic range of the mountain yellow-legged frog (Jennings 1996; Knapp 1996). Water bodies in the JMW and KCNP study areas are similar in physical and chemical characteristics because of their common glacial origin and their location in watersheds dominated by intrusive igneous bedrock (California Division of Mines and Geology 1958; Melack et al. 1985).

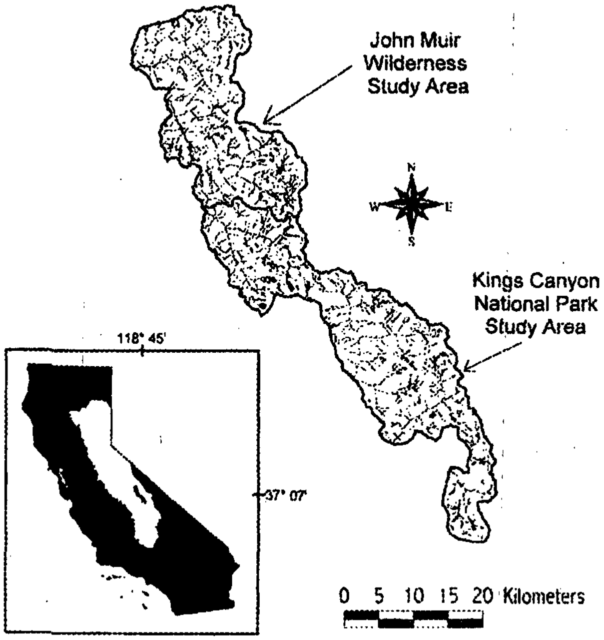

Figure 1. John Muir Wilderness and Kings Canyon National Park study areas. Streams and lakes are shown in black. The inset map is the state of California; the Sierra Nevada is shown in white and the study area is shown as a black area within the Sierra Nevada.

The greater emphasis placed on protection of natural processes by the National Park Service than the U.S. Forest Service has resulted in a lower intensity of historical and current sport-fish introductions in KCNP than in the JMW (California Department of Fish and Game and Kings Canyon National Park, unpublished fish-stocking records). In the JMW study area, 65% of water bodies ≥1 ha are stocked with several species of trout on a regular basis, whereas stocking of lakes in the KCNP study area was terminated in 1977 (California Department of Fish and Game and Kings Canyon National Park, unpublished fish-stocking records). As a result of these differences in historical and current fish-stocking practices, the JMW study area has a larger proportion of lakes containing non-native trout than does the KCNP study area (Bradford et al. 1993; California Department of Fish and Game and Kings Canyon National Park, unpublished fish-stocking records).

We used this difference in fish distribution to determine whether introduced trout influence the present distribution of the mountain yellow-legged frog within the study area. Specifically, if introduced trout are an important factor influencing the distribution of the mountain yellow-legged frog, a smaller proportion of water bodies in the JMW study area should contain frogs than in the KCNP study area. In addition, the distribution of introduced trout and mountain yellow-legged frogs should be negatively correlated at the scale of individual watersheds and water bodies. Because our results indicated a strong negative effect of introduced trout on mountain yellow-legged frogs, we also investigated the mechanism underlying this effect. Based on our understanding of the natural history of the mountain yellow-legged frog, we hypothesized that the strong effect of introduced trout on mountain yellow-legged frogs is due to the similar habitat requirements of these two taxa. Specifically, we predicted that both mountain yellow-legged frogs and introduced trout would have a higher probability of occurrence in deep than in shallow water bodies and that the size of mountain yellow-legged frog populations would be larger in deep than in shallow water bodies.

Methods

Between 1995 and 1997, we visited all 1728 lentic water bodies within the JMW and KCNP study areas (Fig. 1). Water bodies were identified from U.S. Geological Survey (USGS) 1:24,000 topographic maps and included 669 and 1059 water bodies in the JMW and KCNP study areas, respectively. Surveys were conducted during the warm summer months when water bodies were ice-free and fish and frogs were active. Water bodies in the JMW study area were surveyed during 23 August–15 September 1995 and 22 July–13 September 1996. Surveys in the KCNP study area were conducted during 29 June–15 September 1997. Most of the precipitation in the study area falls as snow, and snowfall in 1995, 1996, and 1997 was 168%, 108%, and 100% of the average, respectively (California Department of Water Resources 1998).

Frog and Fish Surveys

The number of mountain yellow-legged frogs at each water body was determined by visual encounter surveys (Crump & Scott 1994) of the entire shoreline. During the summer, adults and larvae occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes by shoreline searches (Bradford 1989). If they were present, we counted the number of adult (i.e., post-metamorphic) frogs and larvae and used these counts as a measure of relative abundance. As part of a separate study, counts of mountain yellow-legged frogs were made at 62 water bodies in the KCNP study area in 1996. To evaluate count repeatability, we used these data in combination with counts from the same 62 water bodies made in 1997 as part of the survey effort for the current study. Counts in 1996 and 1997 were highly correlated for adults ($r = 0.91$; $p = 0.0001$) and larvae ($r = 0.70$; $p = 0.0001$). Therefore, counts of mountain yellow-legged frog adults and larvae at individual water bodies were highly repeatable between years.

The presence or absence of trout was determined at each water body by visual encounter surveys or gillnets. In shallow water bodies (<3 m deep) in which the entire bottom could be seen, we determined trout presence or absence by visual encounter surveys conducted while we walked the entire shoreline and the first 100 m of each inlet and outlet stream. In deeper water bodies, we determined fish presence or absence and species composition using a single monofilament gill-net set for 8–12 hours. Repeated gill-net sets in six lakes indicated that single 8- to 12-hour gill-net sets were 100% accurate in determining fish presence or absence, even in lakes with low fish densities (R.A.K., unpublished data).

Habitat Description

To characterize the physical attributes of each water body, we used information on water-body elevation, perimeter, surface area, maximum depth, littoral-zone (i.e., near-shore) substrate composition, solar radiation input, stream connectivity, and isolation from other waterbodies or frog populations. Water-body elevation, perimeter, and surface area were obtained from USGS 1:24,000 topographic maps. We determined maximum lake depth by sounding with a weighted line. We determined littoral-zone substrate composition by visually estimating the dominant substrate along approximately 50 3-m-long transects evenly spaced around the water-body perimeter and placed perpendicular to shore. Substrates were categorized as silt (<0.5 mm), sand (0.5–2 mm), gravel (>2–75 mm), cobble (>75–300 mm), boulder (>300 mm), or bedrock. We determined the percentage of the littoral zone occupied by aquatic vegetation by noting its presence or absence at each transect.

Two measures of stream connectivity, the number of inlet streams and the width of the outlet stream, were recorded during shoreline surveys. Only those streams wider than 10 cm were included. Two measures of water-body isolation and one measure of frog population isolation were calculated with a geographic information system. These were the number of lakes (water bodies with surface area ≥0.5 ha) within 1 km of the shoreline of each water body, the number of ponds (water bodies with surface area of <0.5 ha) within 250 m of the shoreline of each water body, and the number of mountain yellow-legged frog larvae within 1 km of the shoreline of each water body, respectively. To calculate these isolation measures for the 1728 surveyed water bodies, only those water bodies or frog populations within the same drainage as the target water body were considered.

Average daily solar radiation, used as a surrogate for water temperature and the duration of the ice-free period, was calculated for each water body with the program SOLARFLUX (Dubayah & Rich 1995). SOLARFLUX calculates direct-beam radiation across a digital elevation model according to slope and aspect. We first divided the JMW and KCNP study areas into 10 m × 10 m cells by inputting 50-m contour intervals from U.S. Geological Survey digital line graphs into the TOPOGRID algorithm in Arc/Info, version 7.1. Next, we estimated the daily radiation received by a particular water body by calculating radiation loads for each cell whose center lay within the water body. Radiation loads were calculated for all daylight hours with a 1-hour time step and then averaged across time steps and across all cells associated with that water body. Daily radiation was calculated on the longest and shortest days of the year and on the days halfway between the longest and shortest days of the year. Radiation levels for these four dates were highly correlated and were averaged to produce a single measure of mean daily solar radiation.

Data Analysis

We conducted analyses at three spatial scales: landscape, watershed, and water body. Analyses at the landscape scale involved comparisons of the distributions of introduced trout and mountain yellow-legged frogs between the KCNP and JMW study areas. We made these comparisons based on both the overall percentage of water bodies occupied by trout or frogs and the percentage of the total water-body surface area occupied by trout or frogs. We included comparisons made on the basis of the percentage of the total water-body surface area to provide a truer depiction of fish and frog distributions. Comparisons based on the percentage of water bodies occupied were weighted toward the smallest water bodies, those that constituted the majority of surveyed habitats but in which both trout and frogs were uncommon. The statistical significance of differences between the KCNP and JMW study areas in the percentage of lakes that contained fishes or frogs was determined with Pearson's chi-square tests. No statistical analyses of the comparisons based on water-body surface area were necessary because the data represented the entire population of rather than a sample of water bodies.

For analyses at the watershed scale, we divided the entire study area into 14 watersheds based on natural drainage patterns (Table 1). We then used linear regression to describe the relationship between the percentage of the total water-body surface area in each watershed that contained trout and the percentage that contained frogs. Prior to analysis, percentage data were arcsine-transformed (Sokal & Rohlf 1981).

At the scale of individual water bodies, we quantified the relationship between trout presence and mountain yellow-legged frog presence and abundance. The simplest analyses of these data would compare the percentage of fishless versus fish-containing water bodies occupied by frogs or the number of frogs in fishless versus

Table 1. Characteristics of the 14 watersheds in the John Muir Wilderness (JMW) and Kings Canyon National Park (KCNP) study areas.

Watershed name	*Jurisdiction*	*Area (ha)*	*Number of water bodies*	*Water body surface area (ha)*
Mono Creek	JMW	15,508	97	216
Bear Creek	JMW	9,466	185	203
French Canyon	JMW	4,399	77	258
Lower Piute Creek	JMW	3,799	108	65
Humphreys Basin	JMW	6,045	199	302
Evolution Valley	KCNP	9,288	158	381
Goddard Canyon	KCNP	7,375	83	188
Upper MF Kings River	KCNP	8,044	151	176
Lower MF Kings River	KCNP	3,434	52	39
Palisade Creek	KCNP	6,881	122	183
Cartridge Creek	KCNP	5,205	120	113
South Fork Kings River	KCNP	11,585	159	213
North Fork Woods Creek	KCNP	2,887	89	104
South Fork Woods Creek	KCNP	5,806	128	197

fish-containing water bodies. Such comparisons, however, could be badly confounded if water bodies with and without fishes differed in their physical characteristics and therefore in their suitability for frogs. To remove any such confounding factors, we used generalized additive models (nonparametric logistic regression, nonparametric Gaussian regression) to make these comparisons after first accounting for habitat effects. Generalized additive models (GAMs) are analogous to generalized linear models in that both relax the assumption that the dependent variable is distributed homoscedastically, thereby allowing the analysis of dependent variables characterized by other distributions (e.g., binomial). Unlike generalized linear models, however, GAMs also relax the assumption that the relationships between the dependent and independent variables are linear. Relaxation of this assumption is accomplished with a nonparametric smoothing function (e.g., loess) to determine the fitted model that best fits the independent variables (Cleveland & Devlin 1988; Hastie & Tibshirani 1991). Therefore, instead of assuming that the dependent variable is a linear function of the significant independent variables, one assumes only that it is a sum of the smooth functions for each of these variables.

To quantify the effect of trout presence or absence on the probability of mountain yellow-legged frog presence or absence without potentially confounding habitat and isolation effects, we used nonparametric logistic regression. Because the effects of trout on mountain yellow-legged frogs at the landscape and watershed scales were similar for adults and larvae (see Results), we restricted our analyses to larvae. Independent variables included in this analysis were fish presence or absence, water-body elevation, surface area, maximum depth, percent silt, number of inlets, width of outlets, solar radiation, number of lakes within 1 km, number of ponds within 250 m, and number of mountain yellow-legged frog larvae within 1 km. This subset of variables was selected to minimize collinearity. Water-body surface area was used instead of perimeter because the two variables were highly collinear and surface area provided a better fit to the data in preliminary analyses. After accounting for the effects of all significant habitat and isolation variables, we used the odds ratio (Hastie & Tibshirani 1991) to determine the difference in the odds of finding mountain yellow-legged frog larvae in the presence versus absence of trout.

To evaluate the effect of trout presence or absence on the number of mountain yellow-legged frog larvae without potentially confounding habitat and isolation effects, we used nonparametric Gaussian regression. In this analysis, we included only those water bodies containing ≥1 mountain yellow-legged frog larva. Independent variables were fish presence or absence, water-body perimeter, maximum depth, percent silt, and number of mountain yellow-legged frog larvae within 1 km. The smaller number of independent variables used in this analysis than in the nonparametric logistic regression analysis was necessitated by the smaller sample size of water bodies included (i.e., only those containing ≥1 larva) and was restricted to those showing significant effects in the analysis of frog presence or absence. Water-body perimeter was used instead of surface area because the two variables were highly collinear and water-body perimeter provided a better fit to the data in preliminary analyses. After accounting for the effects of all significant habitat and isolation variables, we calculated the number of mountain yellow-legged frog larvae expected in the presence versus absence of trout.

In both models, the form of each smooth function was estimated with loess. The best combination of independent variables was determined by evaluating the change in deviance resulting from dropping each variable in the presence of all other variables. The statistical significance of each model was tested by analysis of deviance and likelihood-ratio tests. All regression-related calculations were made with S-Plus (version 4.5; S-Plus 1997). A description of the habitat effects on frog presence or absence and abundance is beyond the scope of this paper and will be presented elsewhere (R.A.K. & K.R.M., unpublished data). We present only the significance of the overall model and the effect of trout.

To determine whether water bodies ≥2 m deep were more likely to contain fishes or frogs than those <2 m deep, we used Pearson's chi-square tests. For fishes we included all water bodies in the JMW and KCNP study areas. For frogs we included only fishless water bodies to ensure that the relationship between frog occurrence and water-body depth was not influenced by the presence of fish. To determine whether water bodies ≥2 m deep contained larger numbers of frog larvae than those <2 m deep, we used a *t* test for unequal variances. We included only those water bodies that were fishless and contained ≥1 mountain yellow-legged frog larva.

Results

Study lakes in the KCNP and JMW study areas were generally similar, differing by <25% for 11 of the 15 measured habitat characteristics (Table 2). Only percent sand, percent silt, width of outlets, and the number of ponds within 250 m differed by more than 25%. Introduced trout (***Oncorhynchus mykiss* × *O. m. aguabonita*** hybrids, ***Salvelinus fontinalis***, and ***Salmo trutta***) were the only fish species present in the study area, and trout species composition was similar between the KCNP and JMW study areas (percentage of lakes inhabited by each species: KCNP, ***Oncorhynchus*** hybrids = 82%, ***S. fontinalis*** = 27%, ***S. trutta*** = 2%; JMW; ***Oncorhynchus*** hybrids = 86%, ***S. fontinalis*** = 25%, ***S. trutta*** = 0%; percentages do not add to 100% because some lakes contained more than one species). In the JMW study area, 29% of all water bodies contained trout versus 20% of all water bodies in the KCNP study area ($\chi^2 = 19.9, p < 0.0001$). The majority of the total water-body surface area in both study areas contained trout, and the percentage of that area occupied by trout was nearly twice as high in the JMW study area than in the KCNP study area (Fig. 2).

In support of our hypothesis that introduced trout exert an important influence on the current distribution of mountain yellow-legged frogs, a negative correlation between trout and frogs was evident at the landscape scale in comparisons between the JMW and KCNP study areas. In the JMW study area, only 4% of all water bodies contained frog adults versus 31% in the KCNP study area ($\chi^2 = 181.6, p < 0.0001$). Similarly, the percentage of water bodies containing frog larvae in the JMW versus KNCP study areas was 3% and 20%, respectively ($\chi^2 = 106.9, p < 0.0001$). The percentage of the total water-body surface area containing mountain yellow-legged frog adults was 6.4 times higher in the KCNP study area than in the JMW study area (Fig. 2). Similarly, the percentage of the total water-body surface area containing mountain yellow-legged frog larvae was 5.7 times higher in the KCNP study area than in the JMW study area (Fig. 2).

For the 14 watersheds delineated for the two study areas, the percentage of total water-body surface area occupied by trout was a highly significant predictor of the percentage of that area occupied by mountain yellow-legged frog adults (Fig. 3; adjusted $r^2 = 0.58, p < 0.001$) and larvae (Fig. 3; adjusted $r^2 = 0.67, p < 0.0005$). At

Table 2. Comparison of physical characteristics of water bodies in the John Muir Wilderness (JMW) and Kings Canyon National Park (KCNP) study areas.

Parameter	*$\bar{x}$ JMW (n = 669)*	*$\bar{x}$ KCNP (n = 1059)*	*Percent difference*[a]
Lake area (ha)	1.56	1.51	3.3
Elevation (m)	3397	3402	0
Lake depth (m)	3.4	4.2	21.1
Bedrock (%)	4.0	4.0	0.0
Boulder (%)	43.6	38.4	12.7
Cobble (%)	14.4	16.6	14.2
Gravel (%)	10.4	11.1	6.5
Sand (%)	11.4	4.3	90.4
Silt (%)	16.0	25.6	46.2
Aquatic vegetation (%)	6.3	7.4	15.5
Number of inlets	0.9	0.8	11.8
Width of outlets (cm)	180	109	49.1
Solar radiation (MJ $m^{-2}day^{-1}$)	7.8	7.8	0.0
Number of lakes within 1 km[b]	4.2	4.4	4.7
Number of ponds within 250 m[c]	3.6	2.5	36.1

[a] *Percent difference calculated as* $((|X_{JMW} - X_{KCNP}|)/(X_{JMW} + X_{KCNP}/2)) \times 100$.
[b] *Bodies of water with surface area ≥0.5 ha.*
[c] *Bodies of water with surface area <0.5 ha.*

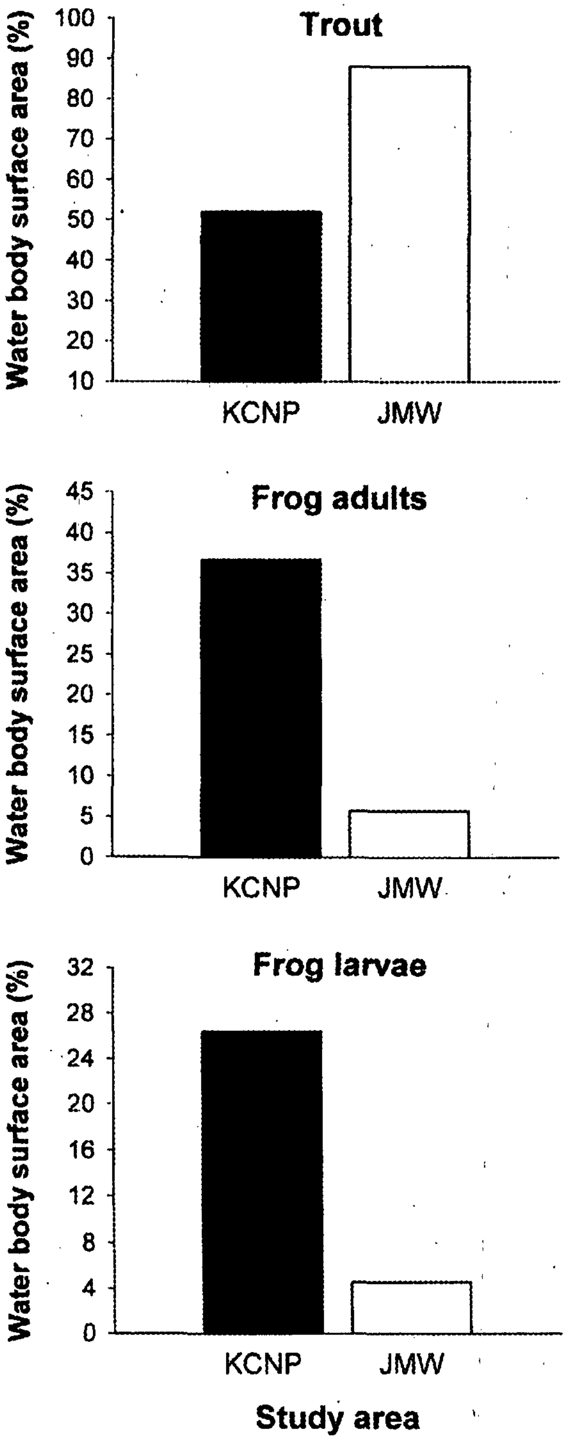

Figure 2. The percentage of total water-body surface area in the Kings Canyon National Park (KCNP) and John Muir Wilderness (JMW) study areas containing trout, mountain yellow-legged frog adults, and mountain yellow-legged frog larvae. Sample sizes for all comparisons are 1059 and 669 for the KCNP and JMW study areas, respectively.

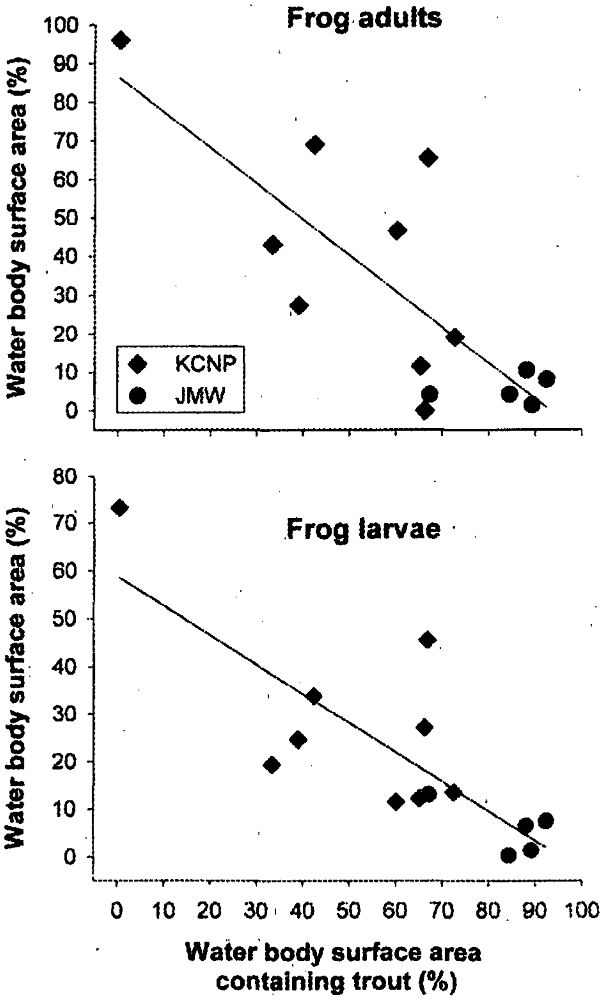

Figure 3. For all 14 watersheds in the Kings Canyon National Park (KCNP) and John Muir Wilderness (JMW) study areas, the relationship between the percentage of water-body surface area containing trout and the percentage of water-body surface area containing mountain yellow-legged frog adults or larvae. Both relationships are highly significant, and linear regression lines are shown.

the watershed scale, therefore, introduced trout alone accounted for approximately 60% of the variance in frog distribution.

At the scale of individual water bodies, the overall nonparametric logistic regression model of larval presence or absence was highly significant ($n = 1728$; $p < 0.0001$), as was the individual effect of trout presence or absence ($p < 0.0001$). After the effects of all significant habitat and isolation variables were accounted for (4 of 10), the probability of finding mountain yellow-legged frog larvae in water bodies with no trout was 3.5 times greater than in waterbodies with trout (approximate

95% confidence limits: 2.3–5.3). The overall nonparametric Gaussian regression model of larval abundance was also highly significant ($n = 238$; $p < 0.0001$), as was the individual effect of trout presence or absence ($p < 0.0001$). After the effects of all significant habitat variables were accounted for (2 of 4), the expected number of frog larvae in water bodies without trout was 6.8 times greater than in water bodies with trout (approximate 95% confidence limits: 3.3–14.0).

Over the entire study area, the percentage of fishless water bodies ($n = 1328$) inhabited by mountain yellow-legged frog larvae increased with water depth (Fig. 4). Water bodies ≥2 m deep were significantly more likely to contain frog larvae than were water bodies <2 m deep ($\chi^2 = 66.0, p < 0.0001$). For fishless water bodies inhabited by mountain yellow-legged frog larvae ($n = 198$), those ≥2 m deep contained significantly more larvae than did water bodies <2 m deep (Fig. 4; $\bar{x}_{\geq 2\mathrm{m}} = 366$, $\bar{x}_{<2\mathrm{m}} = 105$, $t = 3.8$, $\mathrm{df} = 149$, $p < 0.0002$). Across all water bodies used in this study ($n = 1728$), the percentage containing trout showed a pattern similar to that observed for frog larvae (Fig. 4). Those water bodies ≥2 m deep were significantly more likely to contain trout than were water bodies <2 m deep ($\chi^2 = 115.7, p < 0.0001$).

Discussion

Our results indicate a strong negative correlation between introduced trout and mountain yellow-legged frogs at the scales of the landscape, watershed, and individual water body. These results are in agreement with the results of previous research that also indicated a negative effect of introduced trout on the mountain yellow-legged frog (Bradford 1989; Bradford et al. 1998). The results of our study substantially extend these previous findings to a much larger geographic scale, thereby allowing us to make comparisons of frog distributions at several different spatial scales, including among large landscapes under different fish-stocking management, among watersheds differing in the distribution of introduced trout, and at the scale of individual water bodies (after habitat and isolation effects were accounted for). Such analyses have not been possible in past studies because these studies were based on a much smaller number of sites (e.g., 67 sites, Bradford 1989; 104 sites, Bradford et al. 1998).

Our results also support the hypothesis that the strong negative effect of introduced trout on mountain yellow-legged frogs is due in part to the similar habitat requirements of these two taxa. Although amphibian species typically utilize shallow water bodies and have larvae that complete metamorphosis during several weeks to months, in the high-elevation habitats of the Sierra Nevada, mountain yellow-legged frog larvae require 2–4 years to complete metamorphosis (Zweifel 1955; Knapp & Matthews, personal observation). Therefore, the survival to metamorphosis of mountain yellow-legged frog larvae is possible only in bodies of water deep enough to protect them from complete summer drying. Mortality of adults due to oxygen depletion during periods of winter ice cover may also be higher in shallow- than deep-water bodies (Bradford 1983), although recent observations indicate that adults can overwinter successfully in

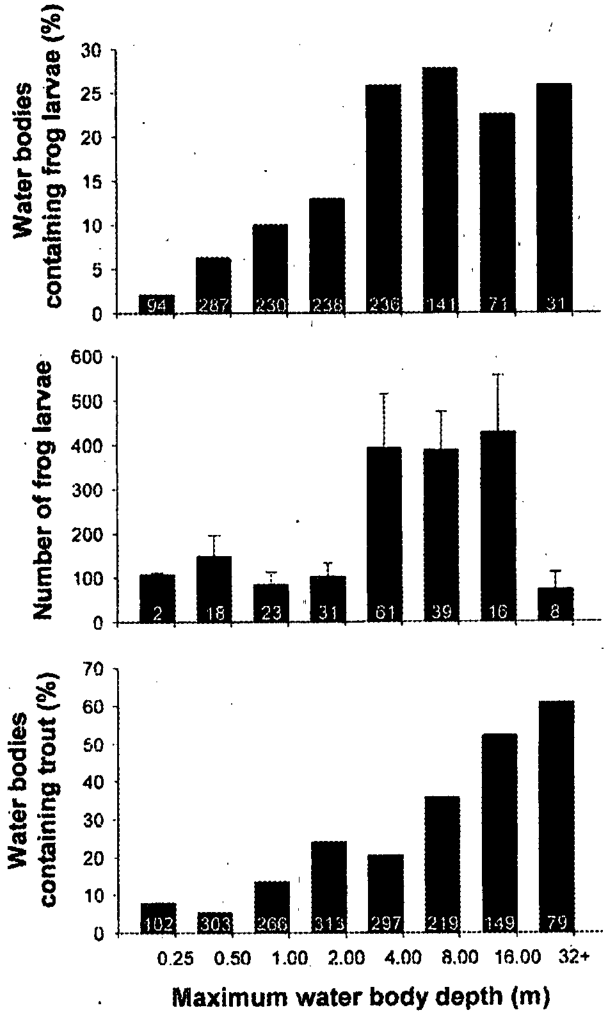

Figure 4. The relationship between maximum water-body depth and the percentage of fishless water bodies (n = 1328) containing mountain yellow-legged frog larvae, the average number (+1 SE) of frog larvae in those fishless water bodies that contained frog larvae (n = 198), and the percentage of all water bodies (n = 1728) containing trout. The number of water bodies in each depth category is given at the base of the corresponding bar.

some ponds that freeze to the bottom (Pope 1999). The requirement by the mountain yellow-legged frog for permanent water bodies likely explains why in fishless water bodies the probability of occurrence for larvae and the number of larvae both increased with water body depth and both showed a marked increase in water bodies deeper than 2 m. As with the mountain yellow-legged frog, trout population persistence is also possible only in bodies of water that are deep enough to protect them from complete summer drying and winter freezing. In combination with historical fish-stocking practices in which larger, deeper lakes were targeted, these habitat requirements have resulted in the percentage of water bodies containing fish also increasing with water depth. Therefore, the habitats in which mountain yellow-legged frog larvae were historically most common and abundant are now generally occupied by predatory trout and as a result are no longer suitable.

In contrast to our focus on introduced fishes, much of the attention surrounding the causes of amphibian declines has instead been focused on the role of UV-B radiation and environmental contaminants (Blaustein et al. 1994; Blaustein & Wake 1995; Datta et al. 1998). Although the role of these potential stressors in causing the decline of the mountain yellow-legged frog have not yet been examined, our study design provides an opportunity to evaluate the extent to which these factors might be influencing the current distribution of the mountain yellow-legged frog in our study area. Although direct measurements of UV-B radiation across our study area are not available, UV-B radiation is generally similar across large geographic areas of similar latitude (Scotto et al. 1988) and is therefore likely to be similar across the approximately 80 × 12 km area used in our study. Measurements of airborne contaminants have been made at scattered locations throughout the Sierra Nevada and indicate a decrease with increasing latitude (Cahill et al. 1996). Although the available data are sparse, they suggest that across our 80-km-long study area the gradient in contaminant concentrations is likely to be small. Therefore, if UV-B radiation or environmental contaminants were exerting a strong influence on the distribution of mountain yellow-legged frogs within our study area, we would expect the frog distribution in the KCNP and JMW study areas to be similar. Instead, our data indicate that mountain yellow-legged frogs were much more widely distributed in the more southern KCNP study area than in the more northern JMW study area. We conclude that the current distribution of the mountain yellow-legged frog in our study area appears to be much more closely associated with the distribution of introduced trout. Because fish-stocking practices have resulted in trout being introduced into most larger lakes throughout the Sierra Nevada (Bahls 1992; Knapp 1996), the important influence of trout on mountain yellow-legged frogs evident in our study area is likely to apply to much of the Sierra Nevada.

Although our results provide strong support for the hypothesis that introduced trout are an important and perhaps primary anthropogenic influence on the distribution of the mountain yellow-legged frog in the Sierra Nevada, others have suggested several reasons why introduced trout may not be the main cause of the declines. First, mountain yellow-legged frogs and fishes coexist at some sites; second, mountain yellow-legged frogs have disappeared from some sites that have never been stocked with trout; third, trout introductions took place several decades before the decline of the mountain yellow-legged frog began in the 1970s (Stebbins & Cohen 1995; Drost & Fellers 1996). It is important to evaluate each of these reasons in light of existing theory and empirical data.

First, the results of our study indicate that mountain yellow-legged frogs and trout do co-occur at some sites, but our data also clearly show that the odds of finding larvae at a given site are greatly decreased by the presence of trout and that, when fish and larvae co-occur, larval abundance is much lower than when trout are absent. Based on these data and on the fact that anuran populations, including those of the mountain yellow-legged frog, are frequently structured as metapopulations (Sjögren 1991; Bradford et al. 1993), we suggest that those mountain yellow-legged frog populations co-occurring with trout generally represent "sink" populations in which the population growth rate is negative in the absence of immigration (Hanski & Simberloff 1997). As such, the co-occurrence of frogs and trout is insufficient evidence that trout are having relatively minor effects on frogs, because the persistence of these populations is likely dependent on immigration from source populations (e.g., large, fishless water bodies).

Second, existing data on mountain yellow-legged frogs does indicate that this species has disappeared from sites lacking trout (Bradford 1991). Although these extinctions may suggest the importance of factors other than trout, they could also result from the fragmentation of frog populations by intensive fish stocking. In the John Muir Wilderness study area, for example, where non-native trout now occupy >90% of the total water-body surface area, remaining mountain yellow-legged frog populations are generally restricted to marginal habitats, are extremely isolated, and likely represent nonequilibrium metapopulations (i.e., extinction rates exceed colonization rates; Bradford et al. 1993; Hanski & Simberloff 1997). Under these conditions, extinctions would be expected regardless of the presence or absence of trout.

Third, several researchers documented the extinction of numerous mountain yellow-legged populations during the 1970s (Bradford 1991; Bradford et al. 1994; L. Cory, personal communication, as cited in Stebbins and Cohen 1995), but the observations of Grinnell and Storer (1924; 663) suggest a much earlier start to the de-

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cline. During faunal surveys conducted in the Sierra Nevada in 1915-1919, they reported that mountain yellow-legged frogs, particularly larvae, did not occur in lakes containing introduced trout, and they surmised that this was due to predation by trout on the larvae. Based on these observations, we suggest that the decline of the mountain yellow-legged frog in the Sierra Nevada started soon after fish introductions began in the 1850s (Knapp 1996). A century later, when non-native trout were present in most larger water bodies, frogs were frequently restricted to marginal and isolated (albeit fishless) habitats, and it is from these habitats that they are now slowly going extinct. Under this scenario, the recent population extinctions observed by Cory and Bradford were more likely the end of a century-long decline, not the start of a decline. Such time lags between habitat modification and population extinction are predicted by metapopulation theory (Hanski 1997). In sum, we suggest that the available data are all consistent with introduced trout being the primary cause of the decline of the mountain yellow-legged frog in the Sierra Nevada. Additional research will be necessary, however, to determine whether other anthropogenic factors also play important roles.

Our results do provide at least one hopeful note regarding the decline of the mountain yellow-legged frog. Although many of the proposed causes of amphibian declines, such as disease, environmental contaminants, and increasing UV-B radiation (Blaustein et al. 1994; Stebbins & Cohen 1995; Berger et al. 1998), would be relatively difficult to ameliorate, the linkage provided by our study between introduced trout and the decline of the mountain yellow-legged frog suggests that returning at least some habitats to their historic fishless condition could be a relatively simple means to reverse this decline. A recent study (Knapp & Matthews 1998) reported that, of the thousands of historically fishless lakes in the Sierra Nevada that now contain introduced trout populations, up to 20% could be returned to a fishless condition relatively simply by means of intensive gill netting. Preliminary results from a recent trout-eradication project conducted in a lake containing mountain yellow-legged frogs indicate a rapid increase in the frog population following fish removal (R.A.K., unpublished data). Based on the initial success of this project, we suggest that reversing the decline of the mountain yellow-legged frog could be accomplished if similar projects were undertaken promptly throughout the historic range of this species.

Protected areas are increasingly important in the global preservation of biodiversity (Soulé & Sanjayan 1998), and although it is widely recognized that species diversity within reserves can be reduced by external factors (Janzen 1986), the importance of internal anthropogenic effects is often overlooked (Cole & Landres 1996). The results of our study emphasize that even protected areas can be substantially modified by management practices occurring within their boundaries and that these disturbances can severely compromise the ability of protected areas to serve as reservoirs of biodiversity. Because the introduction of trout into aquatic ecosystems where they did not naturally occur is a common practice throughout the world (Nilsson 1972; Dawidowicz & Gliwicz 1983; Donald 1987; Bahls 1992; Townsend 1996), effects similar to those we describe are likely to be widespread.

Acknowledgments

We thank 23 field assistants for their help with the 1995-1997 surveys, H. Preisler for assisting with statistical analyses, R. Jellison for setting up the geographic information system (GIS), D. Court for GIS and SOLARFLUX support, D. Dawson for logistical support at the Sierra Nevada Aquatic Research Laboratory, O. Sarnelle, E. Armbrust, and two anonymous reviewers for helpful comments on an earlier version of the manuscript, and L. Decker, who was instrumental in obtaining funding for this project from the U.S. Forest Service. R.A.K. was supported during this research by Challenge Cost-Share Agreement PSW-95-001-CCS and Cooperative Agreement PSW-96-0007CA between the Pacific Southwest Research Station and the Marine Science Institute of the University of California, Santa Barbara.

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