



Effects of Nonnative Trout on Pacific Treefrogs (*Hyla regilla*) in the Sierra Nevada

Author(s): Kathleen R. Matthews, Karen L. Pope, Haiganoush K. Preisler and Roland A. Knapp

Source: *Copeia*, Dec. 20, 2001, Vol. 2001, No. 4 (Dec. 20, 2001), pp. 1130-1137

Published by: American Society of Ichthyologists and Herpetologists (ASIH)

Stable URL: <https://www.jstor.org/stable/1448405>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

American Society of Ichthyologists and Herpetologists (ASIH) is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*

Effects of Nonnative Trout on Pacific Treefrogs (*Hyla regilla*) in the Sierra Nevada

KATHLEEN R. MATTHEWS, KAREN L. POPE, HAIGANOUSH K. PREISLER, AND
ROLAND A. KNAPP

We used analyses based on surveys of > 1700 water bodies in a 100,000-ha area in the John Muir Wilderness (JMW) and Kings Canyon National Park (KCNP) to determine the influence of nonnative trout on the distribution and abundance of *Hyla regilla* in the High Sierra Nevada. At the landscape scale (JMW compared to KCNP), a negative relationship between trout and frogs in lakes was evident. In the JMW study area where trout are more abundant, only 7.2% of all water bodies contained *H. regilla* versus 26.6% in the KCNP study area. Also, the percentage of the total water body surface area containing *H. regilla* was 19.4 times higher in the KCNP study area than in the JMW study area. *Hyla regilla* were most abundant in portions of KCNP where the probability of finding lakes with trout is lowest and least abundant in the northern part of the JMW where the probability of finding lakes with trout is highest. At the water body scale, after accounting for the effects of all significant habitat and isolation variables, the odds of finding *H. regilla* in water bodies with no trout was 2.4 times greater than in water bodies with trout, and the expected number of *H. regilla* in water bodies with *H. regilla* and without trout was 3.7 times greater than in water bodies with both *H. regilla* and trout. *Hyla regilla* were significantly more likely to be found at the lower elevations (3000–3400 m) compared to higher elevations (3400–3800 m) and in shallow water bodies with high percentages of silt in near-shore habitats. Our study demonstrates a negative relationship between fish presence and *H. regilla* distribution and abundance in lakes and suggests that *H. regilla* has declined in portions of the High Sierra with high numbers of trout-containing lakes. It adds an additional native species to the mounting evidence of landscape-scale declines of native species resulting from the introduction of predatory fish.

SEVERAL species of amphibians have declined in the Sierra Nevada of California (Drost and Fellers, 1996; Matthews and Knapp, 1999; Knapp and Matthews, 2000) even though the majority of the land is within national parks and U.S. Forest Service wilderness areas. Amphibians were the most ubiquitous vertebrate within the historically fishless aquatic habitats of the High Sierra Nevada (e.g., Grinnell and Storer, 1924). However, within the past century, trout have been introduced to the majority of the large water bodies of the High Sierra and are at least partially responsible for the dramatic declines reported in some amphibian populations (Knapp and Matthews, 2000). For example, recent studies (Bradford et al., 1994; Knapp and Matthews, 2000) have documented that the once common mountain yellow-legged frog, *Rana muscosa*, has declined in the Sierra Nevada in large part because of the introduction of nonnative trout. Knapp and Matthews (2000) found *R. muscosa* were more abundant in Kings Canyon National Park (KCNP) where introduced fish are less common because of historically lower levels of fish stocking and where the

National Park Service terminated fish stocking to reduce impacts to native species. In contrast, the adjacent John Muir Wilderness (JMW) is managed by the U.S. Forest Service, and introduced fish are currently more abundant because of higher historical levels of stocking and continued fish stocking.

Introduced fish have exerted a strong effect on the distribution and abundance of *R. muscosa*, apparently because of its unique life history where the larvae are frequently found in water bodies deeper than 2 m, the same habitats into which fish have most frequently been introduced (Bradford et al., 1994; Knapp and Matthews, 2000). Moreover, *R. muscosa* larvae overwinter 2–3 yr and are therefore exposed to predation pressure for an extended period.

The Pacific treefrog, *Hyla regilla*, is commonly found in sympatry with mountain yellow-legged frogs in the high-elevation lakes, ponds, and streams of the Sierra Nevada. The Pacific treefrog is the most abundant amphibian in western North America (Brattstrom and Warren, 1955), occurs from sea level to 3540 m (Stebbins, 1985), and can be found in a variety of aquatic

habitats including high-elevation lakes and ponds throughout the Sierra Nevada (Storer and Usinger, 1963). Several studies have concluded that *H. regilla* populations, in contrast to many other amphibians in the western United States, do not show evidence of decline (Fisher and Shaffer, 1996) or possibly declining but only at higher elevations (Drost and Fellers, 1996). Indeed, it is difficult to determine whether populations of *H. regilla* are declining because they are so ubiquitous, populations fluctuate naturally, and there have not been any published studies of long-term population trends. However, if distribution and abundance patterns of *H. regilla* are shown to be restricted or reduced in areas with a specific known threat (i.e., introduced trout) across a landscape, we may conclude that the threat is affecting at least local population levels.

Compared to *R. muscosa*, *H. regilla* may not be as vulnerable to introduced fish, because *H. regilla* can breed successfully in shallow ephemeral ponds, adults are more terrestrial, and larvae metamorphose within one season (Schaub and Larsen, 1978). Even so, in aquatic ecosystems of the High Sierra Nevada, predation by introduced trout on the egg and larval stages of *H. regilla* may be strong enough to influence the current distribution and abundance of *H. regilla* on both a local and landscape scale.

We used analyses based on surveys of > 1700 water bodies in a 100,000-ha area in the JMW and KCNP to determine whether the distribution of trout affects the distribution and abundance of *H. regilla*. In the JMW study area, 65% of water bodies ≥ 1 ha are stocked with trout (*Oncorhynchus* sp.) on a regular basis, whereas stocking of lakes in the KCNP study area was phased out starting in 1977 (California Dept. of Fish and Game and Kings Canyon National Park, unpubl. fish stocking records). All water bodies in the study area were historically fishless. To analyze effects occurring on a landscape scale, we used the difference in fish distribution in the JMW and KCNP to determine whether introduced trout influence the present distribution of *H. regilla* within the study area. In the JMW study area, 29% of all water bodies contained trout, whereas only 20% of all water bodies in KCNP contained trout (Knapp and Matthews, 2000). In addition, the percentage of the total water body surface area occupied by trout was nearly twice as high in the JMW (88%) study area than in the KCNP (52%) study area (Knapp and Matthews, 2000). If introduced trout influence the distribution of *H. regilla*, a smaller proportion of water bodies in the JMW study area should contain treefrogs than in the

KCNP study area. At the water body scale, we predicted that there would be a higher probability of finding *H. regilla* in water bodies without trout than in water bodies with trout. In addition, we assessed whether the abundance of *H. regilla* is lower in habitats where they overlap with fish compared to similar areas without fish. To account for possible confounding habitat, isolation, temporal, and spatial effects, we used generalized additive regression models (Hastie and Tibshirani, 1990) for the analyses.

MATERIALS AND METHODS

Between 1995 and 1997, we visited 1728 lentic water bodies within the JMW and KCNP study areas. More detailed habitat descriptions, methods, and a map of the study area are found in Knapp and Matthews (2000). 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. In the field, all unmapped water bodies encountered (with the exception of ice-bound water bodies) were surveyed and were later added to the GIS lake coverage. Using this sampling approach, essentially all ponded water within the JMW and KCNP study areas was included in our surveys. Surveys were conducted during the warm summer months when most water bodies were ice-free, and fish and frogs were active. Water bodies in the JMW study area were surveyed during 23 August to 15 September 1995 and 22 July to 13 September 1996. Surveys in the KCNP study area were conducted from 29 June to 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, unpubl.).

Frog and fish surveys.—The number of *H. regilla* at each water body was determined using visual encounter surveys (Crump and Scott, 1994) of the entire shoreline. During warm summer days, larvae occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes using shoreline searches. However, subadults (recent metamorphs) and adults may only be in lakes or ponds for a short period during breeding or just after metamorphosis. As a result, the chance of encountering subadults and adults is reduced when sampling ponds and lakes. Thus, for analyses, we combined all life-history stages of treefrogs. If present, we counted the number of adult and subadult (i.e., postmetamorphic) frogs and larvae

and used these counts as a measure of abundance. The presence or absence of trout was determined at each water body using visual encounter surveys in shallow water bodies or gill-nets in deep lakes.

Habitat description.—To characterize the physical attributes of each water body, we used information on water body elevation, surface area, maximum depth, littoral zone (i.e., near-shore) substrate composition, stream connectivity, and isolation from other water bodies. Water body elevation and surface area were obtained from USGS 1:24,000 topographic maps. Maximum lake depth was determined by sounding with a weighted line. We determined near-shore substrate composition by visually estimating the dominant substrate along approximately 50 3-m long transects evenly spaced and perpendicular to the water body shoreline. 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. The percentage of the littoral zone occupied by aquatic vegetation was determined by noting its presence or absence at each transect.

Stream connectivity was represented by the presence/absence of inlet streams, which was recorded during shoreline surveys. Only those streams wider than 10 cm were included. The spatial location (UTMs) of the water bodies and two measures of water body isolation were calculated using a geographic information system. The water body isolation variables were the number of lakes (water bodies with surface area ≥ 0.5 ha) within 1 km of the shoreline of each water body, and the number of ponds (water bodies with surface area < 0.5 ha) within 250 m of the shoreline of each water body. To calculate these isolation measures for the 1728 surveyed water bodies, only those water bodies within the same drainage as the target water body were considered.

Data analysis.—We conducted analyses at two spatial scales: the landscape scale and water body scale. Analyses at the landscape scale involved comparisons of the estimated percentage of water bodies occupied by introduced trout and *H. regilla* in the JMW and KCNP study areas. Also at a landscape scale, we used nonparametric logistic regression to study the spatial pattern of presence/absence of *H. regilla* and trout across the landscape. Specifically, we modeled the probability of the binary response Y_i (presence/absence of *H. regilla* or trout at lake i) with east and north UTM coordinates (UTM_e , UTM_n), by the formula

$$\Pr(Y_i = 1) = \frac{e^{\theta_i}}{1 + e^{\theta_i}} \quad (1)$$

We estimated the linear predictor θ , as a function of UTM coordinates using the nonparametric smoother loess (lo) within the framework of generalized additive models (Hastie and Tibshirani, 1990). We used the likelihood ratio statistic to test whether *H. regilla* or trout are distributed homogeneously throughout the landscape.

At the scale of individual water bodies, we used semiparametric logistic regression to quantify the effect of trout presence/absence on the probability of finding *H. regilla* in a water body with particular habitat and isolation characteristics. This was done by fitting the model in equation (1) with a linear predictor θ , given by

$$\theta = \text{fish} + \text{inlets} + \text{year} + \text{lo}(\text{UTMs}) \\ + \text{lo}(X_1) + \dots + \text{lo}(X_7), \quad (2)$$

where *fish*, *inlets*, and *year* are categorical variables indicating presence/absence of fish and inlets and specific year of survey, and *lo*(.) is a nonparametric smooth function of the covariates. The covariates X_1, \dots, X_7 were water body elevation, square root of surface area, maximum depth, percent silt, day of sample (day number starting from 1 January), number of lakes within 1 km, and the number of ponds within 250 m. Only one shoreline substrate category was used (percent silt) to minimize collinearity. The spatial surface, represented by $\text{lo}(UTM_e, UTM_n)$, can be viewed as a surrogate for any habitat characteristics at locations with coordinates (UTM_e, UTM_n) that were not measured but that might have an effect on the probability of *H. regilla* presence (Hobert et al., 1997). Year of survey was included in the model to account for the possible effects of differences in *H. regilla* recruitment from year to year and to eliminate the possible effects of interannual differences in surveyor bias or experience. We used the likelihood ratio statistic and the Akaike information criteria (AIC; Linhart and Zucchini, 1986) to determine the significance and relative importance of each covariate in equation (1) in the presence of all other covariates.

We used the estimated fish effect from equation (1) to estimate the change in the odds of finding *H. regilla* in the presence versus absence of trout after having controlled for the effects of all significant habitat/isolation variables (Hastie and Tibshirani, 1990).

We used the logistic regression results to develop a tree-based regression model (Clark and Pregibon, 1993) to further explore the effect of

various habitat conditions on the presence or absence of *H. regilla* in lakes. Tree-based regression models are fitted by partitioning the data set into increasingly homogeneous subsets. The partitions are based on the deviance function where the split that maximizes the change in deviance is the one chosen at a given partition step (likelihood ratio test). Variables used in the model included elevation, maximum depth, percent silt, day of survey before 1 September, number of lakes within 1 km, number of ponds within 250 m, and presence or absence of fish. For this model, we only used the water bodies occurring below 3400 m and that were surveyed before 1 September because we wanted to focus on specific habitat features that affected the probability of occurrence in regions and during times when occurrence was most likely. The model provides the proportion of study lakes with specific habitat characteristics (e.g., percent silt > 23 and no fish) that were found to support *H. regilla*.

We used Poisson regression to evaluate the effect of trout presence/absence on the number of *H. regilla* in lakes with *H. regilla* present. In this analysis, the dependent variable was the number of *H. regilla* observed during the surveys in lakes containing at least one *H. regilla* (either larvae, subadult, or adult). The independent variables were fish presence/absence, year of survey, water body area, elevation, date of sample, maximum depth, number of lakes within 1 km, number of ponds within 250 m, and percent silt. For this analysis, we only used lakes where *H. regilla* were found ($n = 330$), and the lower sample size precluded the use of the spatial variable. The estimation technique uses a robust procedure and the Poisson distribution within generalized additive models (Hastie, 1993). A robust procedure was used because we did not want one lake in the dataset that had a very large number of *H. regilla* (estimated at > 10,000) to have a disproportionate effect on the results. After accounting for the effects of all significant habitat and isolation variables using the Poisson regression model, we calculated the change in the expected number of *H. regilla* in the presence versus absence of trout. All regression-related calculations were made using S-Plus 2000.

RESULTS

The first indication that introduced trout might be exerting an influence on the current distribution of *H. regilla* at the landscape scale was the observed difference in the percentage of lakes containing *H. regilla* in the JMW and

KCNP study areas. In the JMW study area, only 7.2% of all water bodies contained *H. regilla* versus 26.6% in the KCNP study area ($X^2 = 12.8$, $P < 0.001$). The percentage of the total water body surface area containing *H. regilla* was 19.4 times higher in the KCNP study area than in the JMW study area.

The spatial patterns of introduced trout and of *H. regilla* in the study area did not appear to be homogeneous (likelihood ratio test statistic $X^2 = 92.9$, $df = 7.15$, $P < 10^{-7}$ and $X^2 = 138$, $df = 7.06$, $P < 10^{-7}$, respectively; Fig. 1A–B). The lowest proportion of fish-containing lakes are in the southern part of the JMW and the northern and central portions of the KCNP study area. The section of the study area with highest proportion of lakes with trout is in the northern part of the JMW. *Hyla regilla*, on the other hand, appears to be most abundant in the middle and southern part of KCNP and least abundant in the northern part of the JMW where the probability of finding lakes with trout is highest (Fig. 1B). Thus, our landscape scale analyses suggested that fish presence influenced the distribution of *H. regilla*. This was further explored taking habitat variables into consideration.

The negative influence of fish on the presence of *H. regilla* was significant at the scale of individual water bodies after the habitat and temporal characteristics were taken into account (Table 1). The overall semiparametric logistic regression model of *H. regilla* presence/absence was highly significant ($n = 1728$; $P < 10^{-11}$) as was the individual effect of trout presence/absence ($P = 2.1 \times 10^{-4}$; Table 1, Fig. 2). Based on the AIC, the relative order of importance of the independent variables was elevation, percent silt, presence/absence of inlets, spatial location, number of lakes within 1 km, lake area, maximum depth, fish presence/absence, year of survey, number of ponds within 250 m, and day of survey (Table 1). The most highly significant continuous variables (elevation, percent silt, number of lakes within 1 km, lake area, and lake maximum depth) had significant nonlinear effects on the probability of finding *H. regilla* in a lake (Fig. 2). After accounting for the effects of all significant habitat and isolation variables, the odds of finding *H. regilla* in water bodies with no trout was 2.4 times greater than in water bodies with trout (odds ratio, approximate 95% confidence limits: 1.5–3.7).

The tree regression (Fig. 3) further illustrates the roles of fish and habitat features that influence the probability of finding *H. regilla* in a water body. For example, in lakes at elevations

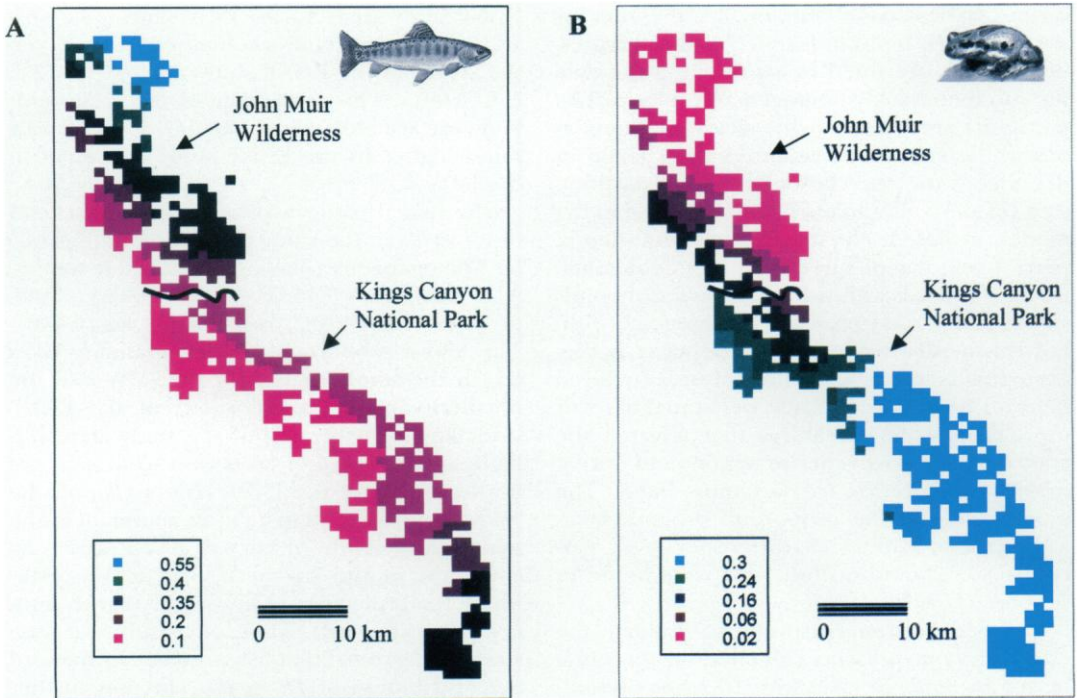


Fig. 1. Estimated proportion of water bodies with (A) introduced trout and (B) *Hyla regilla* within the John Muir Wilderness and Kings Canyon National Park study areas (black line indicates boundary between the JMW and KCNP).

less than 3400 m surveyed before 1 September ($n = 502$), the probability of finding *H. regilla* increases (from 18–52%) with more silt (the tree separates lakes with less than 23% silt and lakes with more than 23% silt). In the lakes with more than 23% silt, the probability of finding

H. regilla increases from 25% in lakes with fish to 61% in lakes without fish (Fig. 3).

The overall nonparametric Poisson regression of *H. regilla* abundance was also highly significant ($n = 330$; $P < 10^{-7}$), as was the individual effect of trout presence/absence ($P = 1.9 \times$

TABLE 1. TEST STATISTIC, STATISTICAL SIGNIFICANCE (P VALUE), AIC-VALUES, AND DIRECTION OF EFFECT OF THE VARIABLES IN THE LOGISTIC REGRESSION MODEL ASSESSING THE PROBABILITY OF FINDING *Hyla regilla* AT A LAKE. Variables ordered by relative significance determined by AIC-value.

Variable	Test statistic ^a	df	Pvalue	AIC ^b	Direction of effect
Elevation	114.0	3.9	$<10^{-10}$	1320.0	–
Percent silt	114.0	3.7	$<10^{-10}$	1260.1	+
Presence/absence of inlets	27.6	1.0	1.5×10^{-7}	1239.5	–
Spatial distribution (UTMs)	38.6	7.4	3.5×10^{-6}	1237.6	NA ^c
Number of lakes within 1 km	31.0	3.7	2.1×10^{-6}	1237.5	+
Lake area	26.6	5.3	8.8×10^{-5}	1229.9	+
Maximum depth	20.3	3.9	3.9×10^{-4}	1226.4	–
Fish presence/absence	13.8	1.0	2.1×10^{-4}	1225.6	–
Year of survey	11.8	2.0	0.003	1221.5	+
Number of ponds within 250 m	9.6	3.6	0.036	1216.2	+
Day of survey	6.5	3.4	0.116	1213.5	NA

^a Test statistic = log likelihood ratio statistic.

^b AIC = Akaike information criteria = -2 (max. \leq g likelihood) + 2 (number of parameters).

^c NA = Not applicable.

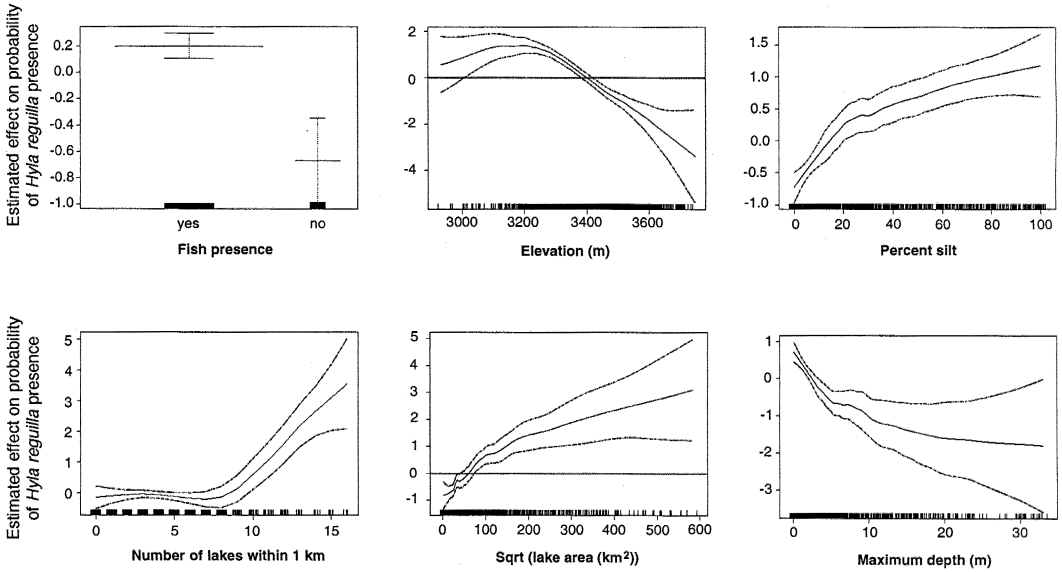


Fig. 2. Estimated effects of fish and significant nonlinear covariates on the probability of *Hyla regilla* presence in a water body. Dotted lines represent approximate 95% confidence intervals, and horizontal line indicates the average effect level, whereas 95% bounds completely above or below the line indicate significance. Hatch marks at the bottom of each graph represent datapoints.

10⁻⁴; Table 2). Based on the AIC, the relative order of importance of the significant independent variables was silt, fish presence/absence, number of ponds within 250 m, number of lakes within 1 km, elevation, and lake area (Table 2). After accounting for the effects of all significant habitat variables, the expected number of *H. regilla* in water bodies with *H. regilla* and without trout was 3.7 times greater than in

water bodies with both *H. regilla* and trout (approximate 95% confidence limits: 1.5–9.3).

DISCUSSION

To our knowledge, this is the first study showing that nonnative fish exert a negative influence on the distribution and abundance of *H. regilla*. Other studies of the influence of fish on treefrogs are equivocal. European treefrogs were largely absent from waters containing fish (Brönmark and Edenhamn, 1994), but other *H. regilla* studies in California either show no effect of introduced trout (Bradford et al., 1994) or a trend (although not significant) of trout excluding *H. regilla* (Bradford, 1989). Our study demonstrates that the presence of fish seems to negatively affect the presence and abundance of *H. regilla* at both the landscape and water body scale.

Although not surprising that nonnative trout impact *R. muscosa* since they both occur predominantly in very similar habitats in the Sierra Nevada (i.e., lakes deeper than 2 m; Knapp and Matthews, 2000), *H. regilla* are often reported to be associated with shallow ponds where fish do not occur and they spend considerably less time in lakes and ponds compared to *R. muscosa*. Thus, it might not be expected that fish would have such an effect on *H. regilla*. Evidently, because of the extensive fish stocking that has oc-

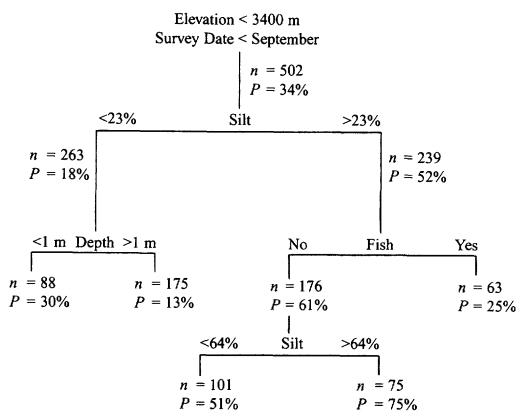


Fig. 3. Tree regression diagram showing the relationship of significant variables in estimating the probability of finding *Hyla regilla* in a given lake where *n* = number of lakes with specified lake characteristics and *P* = probability of finding *H. regilla* based on the given the preceding characteristics.

TABLE 2. TEST STATISTIC (*F*-VALUE), STATISTICAL SIGNIFICANCE (*P*-VALUE) AND AIC-VALUES OF THE VARIABLES IN THE ROBUST POISSON REGRESSION MODEL THAT HAD A SIGNIFICANT EFFECT ON NUMBER OF *Hyla regilla* IN A LAKE. Variables ordered by relative significance determined by AIC-value.

Variable	<i>F</i> -value	df ₁	df ₂	<i>P</i> -value	AIC ^a
Percent silt	9.6	304.1	2.4	2.6×10^{-5}	304.3
Fish presence/absence	14.2	304.1	1.0	1.9×10^{-4}	298.2
Number of ponds with 250 m	6.7	304.1	2.7	3.8×10^{-4}	298.1
Number of lakes within 1 km	5.8	304.1	2.7	0.001	296.4
Elevation	2.9	304.1	3.1	0.035	288.7
Lake area	2.7	304.1	3.8	0.032	288.7

^a AIC = Akaike information criteria = -2 (max. log likelihood) + 2 (number of parameters).

curred in High Sierra lakes managed by the Forest Service, even a species that is noted for its use of a wide variety of habitat types (Stebbins, 1962) as well as being somewhat resilient to environmental changes (Blaustein et al., 1994) can be impacted by fish introductions. Despite the shorter period of time that fish and treefrogs overlap (as a result of the 2–3 month time to *H. regilla* metamorphosis), nonnative trout are still having significant effects on *H. regilla* distribution and abundance.

Although *H. regilla* do appear to prefer shallow water bodies, we found that the probability of finding *H. regilla* in a water body was more strongly influenced by percent silt in near-shore habitats. In lentic habitats in the Sierra Nevada, silt is usually found in shallow, low-gradient areas in a water body. These areas generally have warmer daytime water temperatures, temperatures that are favored by *H. regilla* larvae (Cunningham and Mullally, 1956). Water bodies in KCNP had over 25% more silt than those in the JMW (Knapp and Matthews, 2000). This habitat difference likely accounts for some of the difference in the percentage of lakes in KCNP and the JMW that support *H. regilla*. However, when the difference in silt habitats was taken into account, fish presence/absence was still highly significant in influencing the probability of *H. regilla* occurrence.

The probability of finding *H. regilla* was also strongly influenced by water body elevation, number of lakes within 1 km, lake area, and presence/absence of inlets. Knowledge of how these environmental factors influence the distribution of *H. regilla* may be used to predict habitats in the Sierra Nevada where frogs should or should not occur. *Hyla regilla* were significantly more likely to be found at the lower elevations (3000–3400 m) compared to higher elevations (3400–3800 m). The number of lakes within 1 km, number of ponds within 250 m, and the presence/absence of inlets are measures of habitat isolation. Hence, metapopula-

tion factors (Hanski and Gilpin, 1997) may be influencing the observed distribution pattern.

Based on this study and results of previous research, fish have caused significant reductions in the two historically most common amphibians (e.g., Grinnell and Storer, 1924) in the High Sierra (*R. muscosa* and *H. regilla*). The negative relationship between fish presence and *H. regilla* distribution and abundance suggests that *H. regilla* has declined in portions of the High Sierra with high numbers of stocked lakes. Unlike *R. muscosa*, which is currently at risk of extirpation in many parts of the High Sierra, we expect that *H. regilla* will persist even with continued high levels of fish stocking, although will not be as common and abundant as it once was. Although the threat of fish introductions may not be as severe for *H. regilla* as for *R. muscosa*, it is important that the landscape-scale consequences of widespread introductions of predatory fish to native species be documented. This study adds an additional native species to the mounting evidence of landscape-scale declines of native prey species resulting from the introduction of predatory fish (amphibians: Fisher and Shaffer, 1996; Hecnar and M'Closkey, 1997; Knapp and Matthews, 2000; zooplankton: Stoddard, 1987; Bradford et al., 1998; Knapp et al. 2001; benthic invertebrates: Bradford et al., 1998; Carlisle and Hawkins, 1998; Knapp et al. 2001). The consequences of these declines likely extend beyond the boundary of water bodies and impact native predators of amphibians (e.g., garter snakes, Jennings et al., 1992; Matthews et al., in press) and other species in the High Sierra food web. Nevertheless, with some simple management changes and stocking reductions, fish populations could be reduced and even removed in at least some Sierra Nevada lakes (Knapp and Matthews, 1998) thereby possibly reversing the decline of native amphibians.

ACKNOWLEDGMENTS

We thank 23 field assistants for their help with data collection, D. Court for data input, and L.

Decker who was instrumental in obtaining funding for this project from the U.S. Forest Service's Region 5 Ecosystem Conservation Group. The research was also supported by the USFS Pacific Southwest Research Station. Research and animal handling were conducted under the conditions of the National Park Service Scientific Research and Collecting Permit SEKI-1997-RHK and KRM, and U.S. Forest Service Special Use Permit (KRM).

LITERATURE CITED

- BLAUSTEIN, A. R., P. D. HOFFMAN, G. D. HOKIT, J. M. KIESECKER, S. C. WALLS AND J. B. HAYS. 1994. UV repair and resistance to solar UV-B in amphibian eggs: link to population declines? *Proc. Nat. Acad. Sci.* 91:1791–1795.
- . 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* 1989:775–778.
- BRADFORD, D. F., D. M. GRABER, AND F. TABATABAI. 1994. Population declines of the native frog, *Rana muscosa*, in Sequoia and Kings Canyon National Parks, California. *Southwest. Nat.* 39:323–327.
- , S. D. COOPER, T. M. JENKINS, K. KRATZ, O. SARNELLE, AND A. D. BROWN. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. *Can. J. Fish. Aquat. Sci.* 55:2478–2491.
- BRATTSTROM, B. H., AND J. W. WARREN. 1955. Observations on the ecology and behavior of the Pacific treefrog, *Hyla regilla*. *Copeia* 1955:181–191.
- BRÖNMARK, C., AND P. EDENHAMN. 1994. Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? *Conserv. Biol.* 8 :841–845.
- CARLISLE, D. M. AND C. P. HAWKINS. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. *J. N. Am. Benthol. Soc.* 17:286–300.
- CLARK, L. A. AND D. PREGIBON. 1993. Tree-based models, p. 377–419. *In: Statistical models in S. J. M. Chambers and T. J. Hastie (eds.)*. Chapman and Hall, Yonkers, NY.
- CRUMP, M. L. AND N. J. SCOTT. 1994. Visual encounter surveys, p. 84–91. *In: Measuring and monitoring biological diversity: standard methods for amphibians*. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.). Smithsonian Press, Washington, DC.
- CUNNINGHAM, J. D., AND D. P. MULLALLY. 1956. Thermal factors in the ecology of the Pacific treefrog. *Herpetologica* 12:68–79.
- DROST, C. M., AND G. M. FELLERS. 1996. Collapse of a regional frog fauna in the Yosemite area of the California. *Conserv. Biol.* 10:414–425.
- FISHER, R. N., AND H. B. SHAFFER. 1996. The decline of amphibians in California's Great Central Valley. *Ibid.* 10:1387–1397.
- GRINNELL, J., AND T. I. STORER. 1924. Animal life in the Yosemite. Univ. of California Press, Berkeley.
- HANSKI, I. A., AND M. E. GILPIN. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.
- HASTIE, T. J. 1993. Generalized additive models, p. 249–304. *In: Statistical models in S. J. M. Chambers and T. J. Hastie (eds.)*. Chapman and Hall, Yonkers, NY.
- HASTIE, T. J., AND R. TIBSHIRANI. 1990. Generalized additive models. Chapman and Hall, London.
- HECNAR, S. J., AND R. T. M'CLOSKEY. 1997. Regional dynamics and the status of amphibians. *Ecology* 77: 2091–2097.
- HOBERT, J. P., N. S. ALTMAN, AND C. I. SCHOFIELD. 1997. Analysis of fish species richness with spatial covariate. *J. Am. Stat. Assoc.* 92:846–854.
- JENNINGS, W. B., D. F. BRADFORD, AND D. F. JOHNSON. 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. *J. Herpetol.* 26:505–508.
- KNAPP, R. A., AND K. R. MATTHEWS. 1998. Eradication of nonnative fish by gill-netting from a small mountain lake in California. *Restor. Ecol.* 6:207–213.
- , AND ———. 2000. Nonnative fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conserv. Biol.* 14:428–438.
- , ———, O. SARNELLE. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecolog. Monogr.* 71:401–421.
- LINHART, H., AND W. ZUCCHINI. 1986. Model selection. John Wiley and Sons, New York.
- MATTHEWS, K. R., AND R. A. KNAPP. 1999. A study of high mountain lake fish stocking effects in the U.S. Sierra Nevada Wilderness. *Int. J. Wilderness* 5:24–26.
- , ———, AND K. L. POPE. In Press. Garter snake distribution in high elevation ecosystems: is there a link with declining amphibians and nonnative trout introductions? *J. Herpetol.*
- SCHAUB, D. L., AND J. H. LARSEN JR. 1978. The reproductive ecology of the Pacific treefrog (*Hyla regilla*). *Herpetologica* 34:409–416.
- STEBBINS, R. C. 1962. Amphibians of western North America. Univ. of California Press, Berkeley.
- . 1985. Western reptiles and amphibians. Houghton Mifflin Co., New York.
- STODDARD, J. L. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, Calif. *J. Plankton Res.* 9:631–650.
- STORER, T. I., AND R. L. USINGER. 1963. Sierra Nevada natural history. Univ. of California Press, Berkeley.
- (KRM, KLP, HKP) U.S.D.A. PACIFIC SOUTHWEST RESEARCH STATION BOX 245, BERKELEY, CALIFORNIA 94701; AND (RAK) SIERRA NEVADA AQUATIC RESEARCH LABORATORY, UNIVERSITY OF CALIFORNIA STAR ROUTE 1, BOX 198, MAMMOTH LAKES, CALIFORNIA 93546. E-mail: (KRM) kmatthews@fs.fed.us. Send reprint requests to KRM. Submitted: 2 May 2000. Accepted: 2 May 2001. Section editor: W. L. Montgomery.