

DEVELOPING PROBABILISTIC MODELS TO PREDICT AMPHIBIAN SITE OCCUPANCY IN A PATCHY LANDSCAPE

ROLAND A. KNAPP,^{1,3} KATHLEEN R. MATTHEWS,² HAIGANOUSH K. PREISLER,² AND ROBERT JELLISON¹

¹Sierra Nevada Aquatic Research Laboratory, University of California, HCR 79, Box 198, Crowley Lake, California 93546 USA

²U. S. Department of Agriculture, Pacific Southwest Research Station, Box 245, Berkeley, California 94701 USA

Abstract. Human-caused fragmentation of habitats is threatening an increasing number of animal and plant species, making an understanding of the factors influencing patch occupancy ever more important. The overall goal of the current study was to develop probabilistic models of patch occupancy for the mountain yellow-legged frog (*Rana muscosa*). This once-common species has declined dramatically, at least in part as a result of habitat fragmentation resulting from the introduction of predatory fish. We first describe a model of frog patch occupancy developed using semiparametric logistic regression that is based on habitat characteristics, fish presence/absence, and a spatial location term (the latter to account for spatial autocorrelation in the data). This model had several limitations including being constrained in its use to only the study area. We therefore developed a more general model that incorporated spatial autocorrelation through the use of an autocovariate term that describes the degree of isolation from neighboring frog populations (autologistic model). After accounting for spatial autocorrelation in patch occupancy, both models indicated that the probability of frog presence was strongly influenced by lake depth, elevation, fish presence/absence, substrate characteristics, and the degree of lake isolation. Based on cross-validation procedures, both models provided good fits to the data, but the autologistic model was more useful in predicting patch occupancy by frogs. We conclude by describing a possible application of this model in assessing the likelihood of persistence by frog populations.

Key words: alpine lakes; amphibians; exotic species; fish; habitat fragmentation; habitat models; metapopulation; patch occupancy; *Rana muscosa*; Sierra Nevada; spatial autocorrelation.

INTRODUCTION

Human-caused fragmentation of natural habitats is a primary cause of species endangerment worldwide (Wilcove et al. 1986, Turner 1996). The pace of habitat fragmentation has resulted in considerable interest in the spatial structure of populations, with the metapopulation concept as a central focus. A metapopulation can be loosely defined as a set of populations connected to varying degrees by dispersal (Hanski and Simberloff 1997). By subdividing continuous habitat into patches or by reducing the number of habitat patches, habitat fragmentation reduces the total area of suitable habitat and increases the degree of isolation experienced by organisms inhabiting each patch. Both effects can greatly reduce the likelihood of patch occupancy (Hanski 1989, 1998). In addition to patch size and isolation, patch occupancy can also be affected by patch quality (Sjögren Gulve 1994, Sarre et al. 1995, Dennis and Eales 1999) and by characteristics of habitat surrounding patches (i.e., matrix habitat; Vos and Stumpel 1996, Pope et al. 2000, Joly et al. 2001). Ensuring the persistence of animal and plant populations in fragmented landscapes will require a thorough species-spe-

cific understanding of the relative importance of such factors in influencing patch occupancy.

Describing the relative importance of those factors controlling animal and plant distributions is complicated by the fact that distributional data is frequently spatially autocorrelated, such that sites in close proximity are more similar than sites separated by greater distances (Thomson et al. 1996, Koenig 1999, Trenham et al. 2001). Spatial autocorrelation may arise from numerous sources, including unrecorded habitat variables, dispersal, conspecific attraction, or synchronous population fluctuations (Augustin et al. 1998). Spatial autocorrelation presents a problem for statistical testing because most relevant statistical models (e.g., ordinary or generalized linear regression) assume independence of error terms. As a result, use of classical statistical tests is not appropriate when analyzing spatially autocorrelated data (Legendre 1993). When developing habitat models, ignoring spatial autocorrelation could result in some variables appearing to influence patterns of patch occupancy when in fact the relationships are not statistically significant (Legendre 1993, Carroll and Pearson 2000). Few examples of habitat models exist, however, in which spatial autocorrelation has been incorporated into the estimation process (for notable examples, see Hinch et al. 1994, Wu and Huffer 1997, Carroll et al. 1999).

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³ E-mail: knapp@lifesci.ucsb.edu



FIG. 1. Typical lake in the Sierra Nevada study area. The lake shown here is 1.4 ha in surface area, 3.5 m deep, and is situated at an elevation of 3440 m in the John Muir Wilderness (Sierra National Forest, California). The lake is surrounded by granitic rock, patches of meadow vegetation, and scattered whitebark pine (*Pinus albicaulis*) and lodgepole pine (*Pinus contorta*).

The overall goal of our study was to develop a probabilistic model of patch occupancy for the mountain yellow-legged frog (*Rana muscosa*). In a recent paper, Knapp and Matthews (2000) evaluated the role of nonnative fish in influencing the distribution of *R. muscosa*. In the current study, we extend the findings of Knapp and Matthews (2000) considerably by (1) quantifying the effects of a wide variety of biotic and abiotic variables (including fish presence/absence) on frog distribution after accounting for spatial autocorrelation, and (2) developing predictive patch occupancy models based on the significant independent variables identified in (1). We conclude by describing a possible application of these models to assess the likelihood of persistence of frog populations.

Natural history of the mountain yellow-legged frog

Mountain yellow-legged frogs are endemic to the Sierra Nevada of California and Nevada (USA) and to the Transverse Ranges of southern California (USA) (Zweifel 1955). *R. muscosa* in the Sierra Nevada are genetically distinct from frogs in southern California (Macey et al. 2001) and occupy very different habitats (lakes, ponds, and occasionally streams vs. exclusively streams, respectively). This paper focuses solely on *R. muscosa* in the Sierra Nevada, where historically this species was a common inhabitant of lakes and ponds at elevations of 1400–3600 m (Grinnell and Storer 1924, Zweifel 1955). *R. muscosa* is highly aquatic, with adults overwintering underwater and rarely found more than a few meters from water during the summer active season (Bradford 1989, Matthews and Pope 1999). In addition, the aquatic larvae require two or more summers to develop through metamorphosis. *R. muscosa* larvae and adults are therefore restricted primarily to distinct habitat patches (lakes and ponds) (Bradford et al. 1993).

In the Sierra Nevada, the majority of *R. muscosa* habitat lies within designated national park and national forest wilderness areas. Despite this high level of protection, *R. muscosa* is now extirpated from at least 50% of historic localities (Bradford et al. 1994, Drost and Fellers 1996, Jennings 1996) and is currently being considered for listing under the U.S. Endangered Species Act. Numerous studies indicate that predation by nonnative fish and associated fragmentation of habitats is likely a primary cause of this decline (Bradford 1989, Bradford et al. 1993, 1998, Knapp and Matthews 2000). Nearly all lakes in the Sierra Nevada were naturally fishless, but at least 70% of larger lakes now contain trout introduced during the past 150 years to create recreational fisheries (Knapp 1996). Additional possible causes of decline include airborne agricultural contaminants (Sparling et al. 2001, Davidson et al. 2002) and disease (Fellers et al. 2001).

METHODS

Study area description

The study area is located in the Sierra Nevada of California, and encompasses portions of the John Muir Wilderness (Sierra National Forest) and Kings Canyon National Park (see Knapp and Matthews [2000] for a map of the study area). The 1400-km² study area contains over 1700 lakes and ponds (“water bodies”), nearly all of which are located in the subalpine and alpine zones (above ~3000 m). Water bodies throughout the study area are generally small (<10 ha), oligotrophic, and species poor, and are ice-free for only four to five months per year (Fig. 1; Melack et al. 1985). Watersheds in the study area are dominated by intrusive igneous bedrock (California Division of Mines and Geology 1958). The entire study area was naturally fishless as a result of numerous barriers to upstream move-

ment by fishes (Knapp 1996, Knapp and Matthews 2000). Between 1900 and 1960, the majority of these fishless lakes were stocked with one or more species of trout (golden trout, *Oncorhynchus mykiss aguabonita*; rainbow trout, *O. mykiss*; and brook trout, *Salvelinus fontinalis*; Knapp and Matthews 2000).

Amphibian, fish, and habitat surveys

Data to describe the faunal and habitat characteristics of all 1718 lakes and ponds in the study area were collected during single site visits from 26 July to 14 September 1995, 22 July to 13 September 1996, or 29 June to 14 September 1997. Most of the precipitation in the study area falls as snow, and snowfall in 1995, 1996, and 1997 was 175%, 103%, and 98% of the average, respectively (California Department of Water Resources, online reports DLYSWEQ.19950331, DLYSWEQ.19960331, DLYSWEQ.19970331; accessed on October 24, 2001).⁴

The number of mountain yellow-legged frogs at each water body was determined using visual encounter surveys (Crump and 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 using shoreline searches (Bradford 1989). As a result, single surveys at sites allow accurate assessment of frog presence/absence (Knapp and Matthews 2000). The presence or absence of trout was determined at each water body using visual encounter surveys or gillnets. In shallow water bodies (<3 m deep) in which the entire bottom could be seen, trout presence or absence was determined using visual encounter surveys conducted while walking the entire shoreline and the first 100 m of each inlet and outlet stream. In deeper water bodies, we determined fish presence or absence using both visual surveys and a single monofilament gill net set for 8–12 h. Repeated gill net sets in six lakes indicated that single 8–12 h gill net sets were 100% accurate in determining fish presence or absence, even in lakes with very low fish densities (<5 fish/ha; R. A. Knapp, unpublished data).

We characterized the physical attributes of each water body using elevation, maximum depth, littoral zone (i.e., near-shore) substrate composition, stream connectivity, and isolation from other water bodies. Water body elevation was obtained from USGS 1:24 000 topographic maps. Maximum lake depth was determined by sounding with a weighted line. We characterized 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. No measures of terrestrial

habitat were made because mountain yellow-legged frogs are only rarely found away from water (Matthews and Pope 1999).

Two measures of stream connectivity, the number of inlet streams and the width of outlet streams, were recorded during shoreline surveys. Only those streams wider than 10 cm were included. Based on habitat associations described for *R. muscosa* in previous studies (Bradford 1989, Knapp and Matthews 2000), we used a geographic information system to calculate two variables that both quantified the degree of isolation between a target water body and surrounding water bodies. These were (1) the number of “high-quality” lakes (>3 m deep, ≥ 0.5 ha in area, <3500 m in elevation, and fishless) within 1 km, and (2) the proportion of lakes in a drainage that were “high quality.” For both variables, we counted only those lakes that are located in the same drainage as the target water body because the steep ridges that separate drainages likely preclude any frog movement between drainages (Matthews and Pope 1999, Pope and Matthews 2001). Although these two isolation variables are similar, the first uses a measure of habitat quality in the immediate vicinity of each water body while the second uses a measure of relative habitat quality in the entire drainage.

Statistical analysis

Model development.—Because we expected our frog occurrence data to be spatially autocorrelated, we used two modeling approaches that are designed specifically to allow spatially autocorrelated data to be analyzed using regression. In these different approaches, we used a generalized additive model and incorporated spatial autocorrelation either by the inclusion of a locational covariate (e.g., easting and northing) or an autologistic term (“autocovariate”; Augustin et al. 1998). An autocovariate describes the response at a given site as a function of the responses at neighboring sites. Generalized additive models (GAMs) are analogous to generalized linear models (GLMs), but unlike GLMs, GAMs relax the assumption that the relationships between the dependent variable (when transformed to a logit scale) and independent variables are linear. Relaxation of this assumption is accomplished by estimating a nonparametric smooth function to describe the relationships between the dependent and independent variables (Cleveland and Devlin 1988, Hastie and Tibshirani 1991).

The dependent variable in our analyses was the presence or absence of frog larvae. We chose to use larvae instead of adults as the dependent variable for two reasons. First, adults frequently move between habitats during the course of the summer (Matthews and Pope 1999, Pope and Matthews 2001) while larvae typically remain in their natal water body through metamorphosis. Second, the presence of larvae indicates a reproducing population while the presence of adults may not

⁴ URL: (<http://cdec.water.ca.gov/cgi-progs/lisodir>)

(e.g., adult frogs may persist at a lake for many years without breeding successfully).

In multiple regression, collinearity between predictor variables may confound their independent effects. Therefore, prior to regression analysis we calculated Pearson correlation coefficients for all pairwise combinations of independent variables (Hair et al. 1998). Correlation coefficients (r) ranged between -0.58 and 0.50 . These values are well below the suggested cutoff of $|r| \geq 0.85$ that would indicate collinearity for our sample size (Berry and Felman 1985), and all independent variables were therefore included in the regression.

Preliminary regression analyses indicated that a model could not be fit when all substrate variables were included. Based on correlation analysis and principal components analysis (PCA), we determined that the percent of transects dominated by silt was correlated with other substrate categories and with an overall measure of substrate composition (PCA Axis 1). Therefore, in subsequent analyses substrate characteristics were described solely by the percent of transects dominated by silt.

In our first model, p_i is the probability of finding *R. muscosa* larvae at location i , and is defined as

$$p_i = \frac{e^{\theta_i}}{1 + e^{\theta_i}}$$

where the linear predictor (i.e., logit line) θ_i is a function of the independent variables. The specific relationship we used for θ_i was

$$\begin{aligned} \theta_i = & \mu + \alpha_i(\delta_{\text{FISH}=1}) + g_1(\text{ELEV}_i) + g_2(\text{DEPTH}_i) \\ & + g_3(\text{SILT}_i) + g_4(\text{INLET}_i) + g_5(\text{OUTLET}_i) \\ & + g_6(\text{HQLAKES}_i) + g_7(\text{PHQLAKES}_i) \\ & + g_8(\text{UTME}, \text{UTMN}) \end{aligned} \quad (1)$$

where μ is the overall mean, δ is an indicator function that equals one when the condition is true (when fish are present, $\text{FISH} = 1$) and equals zero otherwise, α_i describes the increase or decrease in μ due to fish presence, and $g_1(\cdot), \dots, g_7(\cdot)$ are nonparametric smooth functions that characterize the effect of each continuous independent variable on the probability of response. Variable names are defined in Table 1. We incorporated spatial autocorrelation into this model by including a locational term ($g_8(\text{UTME}, \text{UTMN})$) that was a smooth surface of UTM easting and northing (Hobert et al. 1997, Augustin et al. 1998). Because this model contains nonparametric terms and a parametric term (FISH), Eq. 1 represents a "semiparametric" regression model. We refer to this model as the "exploratory spatial model" because we used it to evaluate the relative importance of the independent variables and to describe the shapes of the response curves for each of the significant independent variables.

The nonparametric functions within the generalized additive model were estimated simultaneously using a loess smoother (Cleveland and Devlin 1988). The best combination of independent variables was determined by evaluating the change in deviance resulting from dropping each variable from the model in the presence of all other variables. Analysis of deviance and likelihood ratio tests (based on the binomial distribution) were used to test the significance of each of the independent variables on the probability of frog presence (McCullagh and Nelder 1989). The relative importance of significant variables was determined by calculating the Akaike Information Criteria (AIC; Linhart and Zucchini 1986). Larger AIC values indicate a greater relative importance.

After identifying the independent variables that had highly significant ($P < 0.01$) effects on frog occurrence, we used these variables to develop a simplified model that could be used to predict the probability of frog occurrence for all water bodies in the study area. We refer to this model as the "predictive spatial model." We based the predictive spatial model solely on the highly significant independent variables to ensure that only those independent variables with substantial explanatory power were included in the model. Nonparametric regression terms are useful for evaluating the relative importance of independent variables and for describing the shape of response curves, but parametric terms are preferable when developing a predictive model due to their ease of use (Yee and Mitchell 1991). For example, in the current study parametric terms can be incorporated into an equation that allows for easy calculation of p_i while calculation of p_i based on nonparametric terms would require using a statistical package and loess smoothers. Therefore, based on the shapes of the response curves, we developed parametric functions (e.g., linear, polynomial, logarithmic) for as many of the nonparametric terms as possible. Slope and intercept for each parametric function were estimated using GLM. To assess whether the parametric functional forms we used in the predictive spatial model accurately represented the response curves of the exploratory spatial model, the total deviances of the two models were compared. Since the fits of the two models were similar, we then used the predictive spatial model to calculate, for each waterbody, the probability of occurrence of *R. muscosa* larvae.

The predictive spatial model provided a good fit to the data (see *Results*), but had three shortcomings. First, because it contained a locational covariate term (UTM easting and northing) it is constrained to being used only within the study area. Second, the response surface that describes the effect of location on the probability of frog occupancy was complex and could not be approximated with a parametric function. Third, the reason for the significant effect of the locational covariate on frog presence/absence is difficult to interpret. We sought to overcome these limitations by replacing

TABLE 1. Description of variables used in the logistic regression models.

Variable name	Code	Description
Fish presence/absence	FISH	Presence or absence of nonnative trout as determined using visual and/or gill net surveys
Water body elevation (m)	ELEV	Elevation of water body as determined from USGS 7.5' topographic maps
Water body depth (m)	DEPTH	Maximum depth of water body as determined by sounding with a weighted line
Littoral zone silt (%)	SILT	Percentage of the littoral zone dominated by silt (particles <1 mm in diameter)
Number of inlets	INLET	Number of streams (>10 cm in width) flowing into water body as determined during habitat survey
Width of outlets (m)	OUTLET	Combined width of all streams (>10 cm in width) flowing out of water body as measured during habitat survey
Number of high-quality lakes within 1 km	HQLAKES	Number of water bodies located within 1 km of the water body shoreline that are fishless, >3 m deep, ≥ 0.5 ha in area, and <3500 m in elevation
Percentage of high-quality lakes in drainage	PHQLAKES	Percentage of water bodies in a drainage that are fishless, >3 m deep, ≥ 0.5 ha in area, and <3,500 m in elevation
Water body location	UTME, UTMN	Smooth function of UTM easting and northing
Weighted-distance autocovariate	WTDIST	Distance-weighted number of frog-containing water bodies within 2 km of the target water body

the locational covariate term with an autocovariate term (Augustin et al. 1998). In the resulting model, the probability of frog occupancy (p_i) is conditional on whether or not frog larvae are present in surrounding water bodies, and the model is called an "autologistic" model (Besag 1972).

The autocovariate term represents the distance-weighted number of larvae-containing water bodies in the vicinity of the target water body. This term was calculated as

$$\sum_{j \neq i} w_{ij} y_j$$

where w_{ij} is the weighted distance between the target water body i and neighboring water body j , and $y_j = 1$ when larvae are present in water body j and $y_j = 0$ when larvae are absent. Weighted distance was calculated as

$$\frac{d_{ij}^{-1/2}}{\sum_{j \neq i} d_{ij}^{-1/2}}$$

where d_{ij} is the distance (in meters) between the target water body i and neighboring water body j . The weighted distance is calculated only when the neighboring water body j is within 2 km of the target water body i and is in the same drainage. The 2-km cutoff was chosen because frogs rarely move between water bodies separated by greater than 1 km (Matthews and Pope 1999, Pope and Matthews 2001). All "neighboring" water bodies were surveyed for amphibians (as well as fish and habitat characteristics) as part of the overall survey effort to create the data set used in the current study ($n = 1718$).

Standard logistic regression programs can be used to estimate the parameters of an autologistic model, but standard errors calculated by these programs for the estimated parameters are not appropriate. Instead, we

estimated standard errors using a grouped jackknife method (Efron and Tibshirani 1993:149) in which subsets of observations are removed from the data set and parameters are estimated from the remaining observations. The standard errors of the parameter estimates are then determined by calculating the standard deviation of the pseudo-values $\hat{\theta}_k = k\hat{\theta} - (k-1)\hat{\theta}_{(k)}$ where $\hat{\theta}$ is an estimate of the parameter using all the data and $\hat{\theta}_{(k)}$ is an estimate with the k th subset removed (Efron and Tibshirani 1993:145). The jackknife method is an appropriate technique for estimating standard errors for our autologistic model because the data consist of natural groupings that are independent (i.e., 28 drainages; Efron and Tibshirani 1993). All regression-related calculations were conducted using S-Plus (S-Plus 1999).

Model cross-validation.—Cross-validation allows an assessment of how well a model fits data not used in model development, and is typically conducted using one of two methods. One method entails splitting the data set into two groups, developing a model based on one group, and then testing model accuracy using the other group. In the second method, a model is first developed using the entire data set. Next, the data set is split into several groups (often more than 10) and the parameters in the model developed from the full data set are reestimated using data from all groups but one ("dropped group"). This model is then used to estimate the probabilities of occurrence at all sites in the dropped group. After these calculations are made, the dropped group is returned to the data set, and the process is repeated until all groups have been dropped and replaced (Neter et al. 1996). We used this second method of cross-validation because it allowed us to estimate model parameters using the entire data set.

We used separate cross-validation procedures to quantify how well the predictive spatial model and the autologistic model fit data from water bodies not used

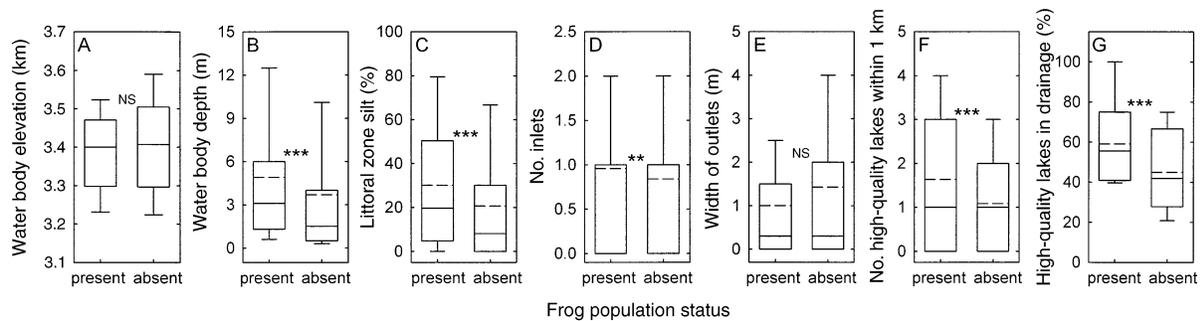


FIG. 2. Box plots showing differences in habitat characteristics between water bodies with and without mountain yellow-legged frog (*Rana muscosa*) larvae. Variables include (A) elevation, (B) depth, (C) percentage of the littoral zone dominated by silt, (D) number of inlets, (E) width of outlets, (F) number of high-quality lakes within 1 km, and (G) percentage of high-quality lakes in the drainage. The solid line within each box marks the median, the dashed line marks the mean, the bottom and top of each box indicate the 25th and 75th percentiles, and the whiskers below and above each box indicate the 10th and 90th percentiles. Sample sizes are 237 and 1481 for water bodies with and without frog larvae, respectively. Asterisks between each pair of bars provide the results of Wilcoxon rank-sum tests: *** $P < 0.001$; ** $P \leq 0.01$; NS (not significant), $P > 0.05$.

in model development. Both cross-validations were conducted by first dropping one of the 28 drainages from the data set and reestimating model parameters using the remaining 27 drainages. We then used the reparameterized model to calculate the predicted probability of occurrence by frog larvae (\hat{p}) for all water bodies in the dropped drainage. This procedure was repeated 27 times, each time dropping a different drainage from the model. Once complete, we grouped all water bodies into 29 categories based on their \hat{p} values. We chose to use 29 categories in order to have as many groups as possible while ensuring that each category contained at least 10 data points. For each category, we then averaged the \hat{p} values across all water bodies and compared this predicted probability of occurrence to the actual proportion of occupied water bodies in the category. If the models provide a good fit to data not used in model development, the mean predicted probability of occurrence for each category should closely match the proportion of water bodies in the category that were actually occupied by frogs. The similarity between the average observed and predicted probabilities of frog occurrence for each of the 29 categories was determined by calculating the Pearson chi-square statistic, which was then compared to a chi-square distribution (Hosmer and Lemeshow 1989). The degrees of freedom for the chi-square tests were calculated as (number of groups) – (number of parameters estimated in model). The number of groups for both models was 29. The number of parameters estimated was 14.3 for the predictive spatial model (1 intercept + 6 variables + 7.3 parameters needed for the locational covariate) and 7 for the autologistic model (1 intercept + 6 variables), respectively. A P value < 0.05 indicates that the model does not provide a good fit to the data.

Visualization of model fit.—To visualize model fit, we compared the water body-specific predicted prob-

abilities of frog occurrence with the locations actually occupied by frogs in one of the 29 study drainages. The results of our cross-validation analyses indicated that the predictive accuracy of the autologistic model was insensitive to what drainages were used in model development (see *Results*). Therefore, we calculated the predicted probabilities of frog occurrence for all water bodies in the selected drainage using the autologistic model developed based on the entire data set. To maximize the range of model predictions, we selected a drainage that included water bodies characterized by a wide range of parameter values for each of the variables included in the autologistic model. The objective of this graphical analysis was to visualize (not test) model fit, and a single drainage was sufficient to meet this objective.

RESULTS

R. muscosa larvae were found in 238 (14%) of the 1718 water bodies surveyed. Water bodies with and without larvae were significantly different for all habitat characteristics except water body elevation and width of outlet streams (Fig. 2). Water bodies occupied by larvae were deeper (Fig. 2B), had a greater percentage of the littoral zone dominated by silt (Fig. 2C), had more inlet streams (Fig. 2D), had more high-quality (i.e., large, deep, fishless) lakes within 1 km (Fig. 2F), and had a higher percentage of lakes in the drainage that were high quality (Fig. 2G). In addition, fishless water bodies were more likely to contain frog larvae than were fish-containing water bodies (14% vs. 24%, respectively; chi-square test: $\chi^2 = 10.6$, $df = 1$, $P = 0.001$).

Exploratory spatial model

The semiparametric exploratory spatial model (Eq. 1) was highly significant ($P < 1 \times 10^{-10}$). Six of the nine independent variables (water body location, depth,

TABLE 2. Analysis of deviance table showing the statistical significance (*P* value) and Akaike Information Criteria (AIC) of the independent variables in the exploratory spatial model.

Model	Model		Test		<i>P</i> value	AIC§
	Deviance	df	Deviance†	df‡		
Null model	1379	1717				
Full model	968	1680				
Full model less:						
Water body location	1099	1687	131	7	$<1 \times 10^{-10}$	1160.4
Water body depth	1036	1684	68	4	$<1 \times 10^{-10}$	1103.5
Water body elevation	1003	1684	35	4	2.7×10^{-7}	1071.2
Fish presence/absence	991	1681	23	1	9.5×10^{-7}	1064.8
Littoral zone silt	984	1684	16	4	2.2×10^{-3}	1052.0
No. high-quality lakes within 1 km	982	1684	15	4	5.5×10^{-3}	1049.9
Number of inlets	978	1684	11	4	0.033	1045.7
Percentage of high-quality lakes in drainage	977	1684	9	4	0.073	1043.7
Width of outlets	976	1685	8	5	0.15	1041.5

† Test deviance = (deviance of full model less one covariate) – (deviance of full model).

‡ Test df = (df of full model less one covariate) – (df of full model).

§ AIC = (deviance of full model less one covariate) + 2(1718 – df of full model less one covariate).

elevation, fish presence/absence, littoral zone silt, number of high-quality lakes within 1 km) had highly significant effects on the occurrence of frog larvae, while two independent variables (number of inlets, percentage of high-quality lakes in drainage) had marginally significant effects (Table 2). Width of outlet streams did not have a significant effect on frog occurrence (Table 2). Varying the loess “smoothness” parameter (i.e., span) from the default value of 0.5 to values between 0.35 and 0.70 had very minor effects on the relative importance of the independent variables, changing the order only of the four variables with the smallest AIC values (Table 2).

After accounting for the effects of all other significant variables, the probability of frog occurrence (p_i) was higher in the absence of fish than in the presence of fish (Fig. 3A). For the continuous variables, the relationships between the probability of frog occurrence (on a logit scale) and water body depth and elevation

were significantly nonlinear ($P < 1 \times 10^{-5}$; Fig. 3B, 3C) while the nonlinearity associated with the effect of the number of high-quality lakes within 1 km was marginally nonsignificant ($P = 0.09$; Fig. 3E). The effect of littoral zone silt was not significantly different from linear ($P > 0.2$; Fig. 3D). The response curve for water body depth indicated that p_i increased steeply between 0 and 4 m, beyond which depth had little influence on frog occurrence (Fig. 3B). The response curve for elevation indicated that p_i changed little between elevations of 2900 and 3500 m, but decreased sharply above 3500 m (Fig. 3C). The exact shape of the relationship between p_i and the number of high-quality lakes within 1 km was difficult to determine because of the wide confidence interval resulting from a relatively low number of water bodies that had greater than five high-quality lakes nearby. However, for water bodies with fewer than five neighboring high-quality lakes, the probability of frog occurrence increased with

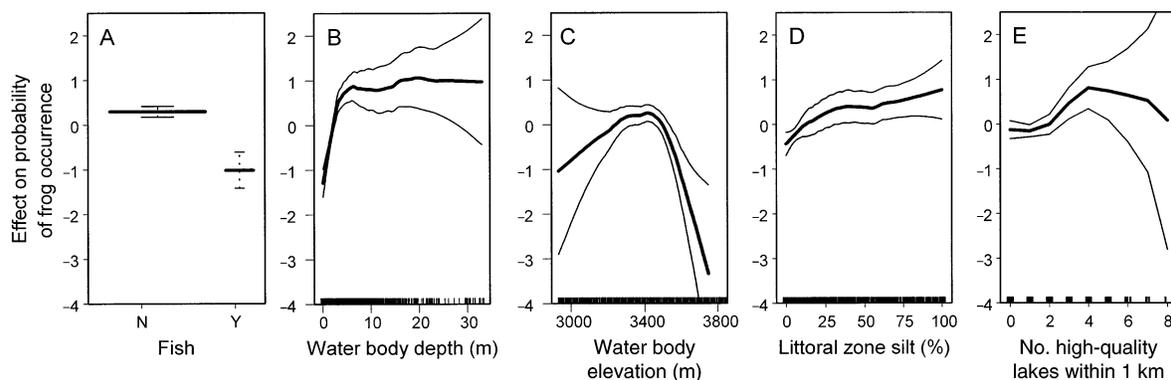


FIG. 3. Effect of each of the highly significant independent variables (including approximate pointwise 95% confidence intervals) on the probability of occurrence by *R. muscosa* larvae, as determined from the exploratory spatial model (span = 0.5). Variables are (A) fish presence/absence, (B) water body depth, (C) water body elevation, (D) littoral zone silt, and (E) number of high-quality lakes within 1 km. Fish presence/absence is a categorical variable, and all other variables are continuous. Continuous variables are displayed in order of decreasing importance. Hatch marks above the *x*-axes in panels (B), (C), (D), and (E) indicate the observed values for each independent variable.

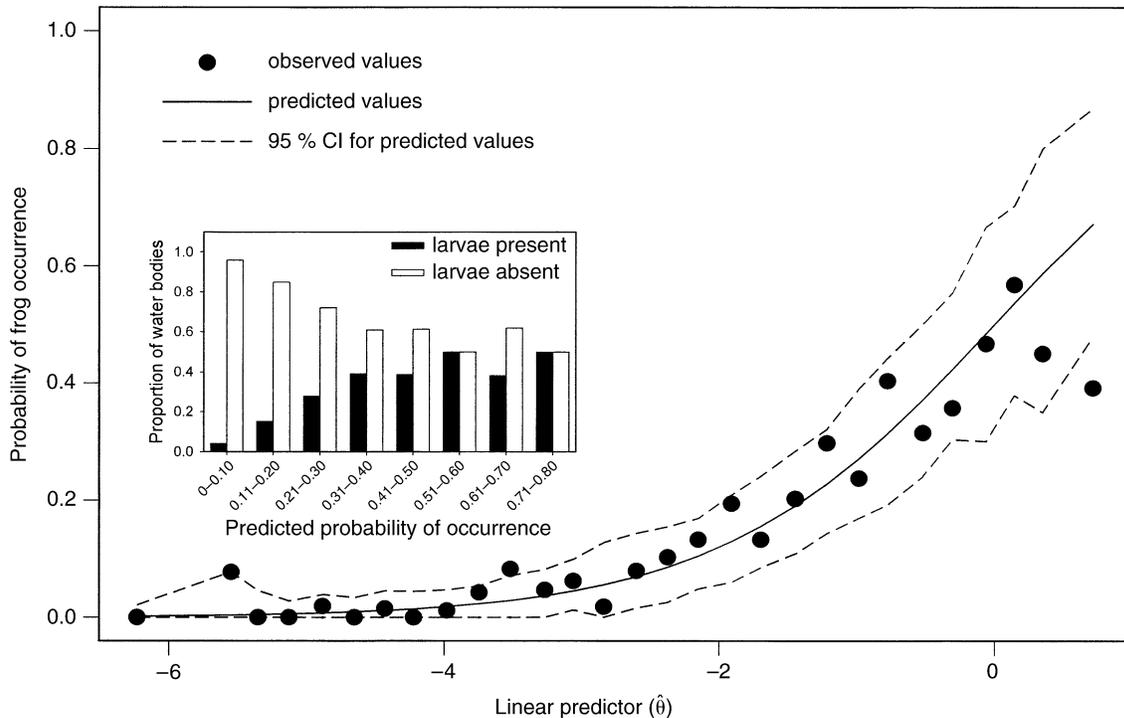


FIG. 4. Results of the cross-validation procedure for the predictive spatial model showing the observed and predicted probability of *R. muscosa* occurrence ($\pm 95\%$ confidence limits) for 29 categories of the linear predictor ($\hat{\theta}$). Values for three of the categories lie outside the 95% confidence interval. The inset figure shows the same data but as a histogram of the proportion of lakes in which larvae are present versus absent as a function of the predicted probability of occurrence (\hat{p}).

increasing numbers of high-quality lakes within 1 km (Fig. 3E).

Predictive spatial model

To develop the predictive spatial model, we approximated the littoral zone silt response curve with a straight line, the water body depth and number of high-quality lakes within 1 km response curves with two lines, and the water body elevation response curve with a second degree polynomial (Fig. 3). This led to the model

$$\begin{aligned} \theta_i = & \mu + \alpha_i(\delta_{\text{FISH}=1}) + \beta_{\text{ELEV1}}(\text{ELEV}_i) + \beta_{\text{ELEV2}}(\text{ELEV}_i)^2 \\ & + \beta_{\text{DEPTH}}(\text{DEPTH}_i - 3.5)\delta_{\text{DEPTH}_i \geq 3.5} + \beta_{\text{SILT}}(\text{SILT}_i) \\ & + \beta_{\text{HQLAKES}}(\text{HQLAKES}_i - 4)\delta_{\text{HQLAKES}_i \geq 4} \\ & + g(\text{UTME}, \text{UTMN}) \end{aligned} \quad (2)$$

where μ , α_p , δ , and g are defined as in Eq. 1. The difference in deviance between the exploratory spatial model and the predictive spatial model was not significant ($\chi^2 = 13.0$, $df = 10$, $P = 0.24$), indicating that our choice of functional forms provided a good approximation of the actual shapes of the response curves. The cross-validation procedure indicated that the predicted p_i values calculated using Eq. 2 matched the observed p_i values relatively closely (Fig. 4). However, three of the 29 groups fell outside of the 95%

confidence interval (Fig. 4), resulting in a large overall chi-square value and associated small P value ($\chi^2 = 53.8$, $df = 14.7$, $P = 2.3 \times 10^{-6}$). Therefore, while the predictive spatial model generally provided a good fit to the data from drainages not used in model parameterization, the three groups falling outside the 95% confidence interval were sufficient to create an overall lack of fit. A histogram of the proportion of water bodies in which larvae were present versus absent as a function of the predicted probability of occurrence (Fig. 4) indicates that the proportion of lakes actually occupied by frogs increases in step with the predicted probability of occurrence below $\hat{p} = 0.4$, but instead of continuing to increase as \hat{p} values increase from 0.41 to 0.80 the proportion of occupied lakes reaches a plateau of $\sim 50\%$ occupancy. These results suggest that the predictive spatial model overestimated the probability of occurrence of frog larvae.

Autologistic model

Results from the grouped jackknife procedure indicated that replacing the locational covariate in the predictive spatial model with the weighted distance autocovariate (WTDIST) had little effect on the relative importance of the independent variables. The effect of the autocovariate on the probability of site occupancy was highly significant (Table 3). In addition, water body depth, fish presence/absence, littoral zone silt, and

TABLE 3. Coefficients, standard errors, and P values estimated for the autologistic model using the grouped jackknife method.

Variable name	Coefficient (β)	1 SE	P value
Intercept	-232.8853		
Weighted-distance autocovariate	7.1141	0.5622	$<1 \times 10^{-10}$
Water body depth	0.8095	0.1242	8.3×10^{-7}
Fish presence/absence	-1.3017	0.2006	9.8×10^{-7}
Littoral zone silt	0.0152	3.0107×10^{-3}	3.1×10^{-5}
(Water body elevation) ²	-2.0305×10^{-5}	5.9116×10^{-6}	2.9×10^{-3}
Water body elevation	0.1369	3.9976×10^{-2}	3.1×10^{-3}
No. high-quality lakes within 1 km	-5.8802×10^{-3}	0.1232	0.89

water body elevation remained highly significant while the effect of the number of high-quality lakes within 1 km was no longer significant (Table 3). The final model produced when only the highly significant independent variables were included in the autologistic model was

$$\begin{aligned} \theta_i = & -232.2 - 1.299\delta_{\text{FISH}=1} + 0.136(\text{ELEV}_i) \\ & - 0.00002(\text{ELEV}_i)^2 \\ & + 0.809(\text{DEPTH}_i - 3.5)\delta_{\text{DEPTH}_i=3.5} \\ & + 0.015(\text{SILT}_i) + 7.107(\text{WTDIST}_i) \end{aligned} \quad (3)$$

where μ , α_p , and δ are defined as in Eq. 1. Dropping the nonsignificant variable, HQLAKES, changed the regression coefficients only slightly (compare coefficients in Table 3 vs. Eq. 3). The cross-validation procedure indicated a close association between the observed and predicted probabilities of frog occurrence (Fig. 5), and the results of the goodness-of-fit test ($\chi^2 = 28.7$, $df = 22$, $P = 0.15$) suggested that the autologistic model provided a close fit to the data from drainages not used in model parameterization. Therefore, this model may more accurately predict the occurrence of mountain yellow-legged frog larvae than the exploratory spatial model. A histogram of the proportion of lakes in which larvae are present vs. absent as a function of the predicted probability of occurrence (Fig. 5) also indicates a closer correspondence between the predicted and observed probabilities than was the case for the predictive spatial model (Fig. 4). Results from the autologistic model suggest that the proportion of lakes occupied by frogs increases in step with the predicted probability of occurrence across the entire range of predicted values (Fig. 5).

Visualization of the predictive ability of the autologistic model using one drainage in the study area (Palisade Creek, Kings Canyon National Park) demonstrates the high degree of correspondence between the predicted probabilities of frog occurrence (\hat{p}) and the actual presence/absence of frogs at those water bodies (Fig. 6). For water bodies with $\hat{p} < 0.5$, only 18 of 92 (19.6%) actually contained frog larvae. This actual probability of occurrence (0.196) was very similar to the predicted probability of occurrence of 0.174 (calculated as the mean \hat{p} of water bodies with $\hat{p} < 0.5$).

For water bodies with $\hat{p} \geq 0.5$, 21 of 31 (67.7%) actually contained frog larvae. Again, this actual probability of occurrence (0.677) was very similar to the predicted probability of occurrence of 0.671 (calculated as the mean \hat{p} for water bodies with $\hat{p} \geq 0.5$).

DISCUSSION

Effects of habitat variables and fish on patch occupancy

The models developed in this study provide the first comprehensive analysis of the factors influencing the probability of patch occupancy by *R. muscosa*, and suggested important effects of several variables. Our regression results indicated that the occurrence of larvae appeared to be strongly influenced by water body depth. Unlike other anurans (i.e., frogs and toads) in the Sierra Nevada whose larvae inhabit shallow ponds (typically <1 m deep: Matthews et al. 2001), *R. muscosa* larvae were most likely to be found in water bodies deeper than 3 m. Earlier studies also suggested the importance of water body depth in influencing patch occupancy by *R. muscosa* (Bradford 1989, Knapp and Matthews 2000), but our results describe the actual shape of the relationship between water body depth and the probability of frog occurrence after accounting for the effects of all other significant independent variables. The dependence of *R. muscosa* on deep water bodies for successful breeding is a consequence of the inability of larvae to complete metamorphosis in a single summer. As a result, larvae overwinter one or more times before reaching metamorphosis. At high elevations in the Sierra Nevada, shallow ponds often dry by late summer or freeze solid in winter, and as a result successful breeding is more likely in deeper, more permanent water bodies (R. A. Knapp and K. R. Matthews, *personal observation*).

Water body elevation also appeared to have a significant effect on patch occupancy, with the probability of occurrence by *R. muscosa* larvae being relatively high and constant from 2900 m to 3500 m but dropping sharply in occurrence above 3500 m. This result supports earlier observations that mountain yellow-legged frogs do not occur above 3650 m (Stebbins 1985). The unusual ability of this species to breed successfully at elevations exceeding 3000 m where the growing season

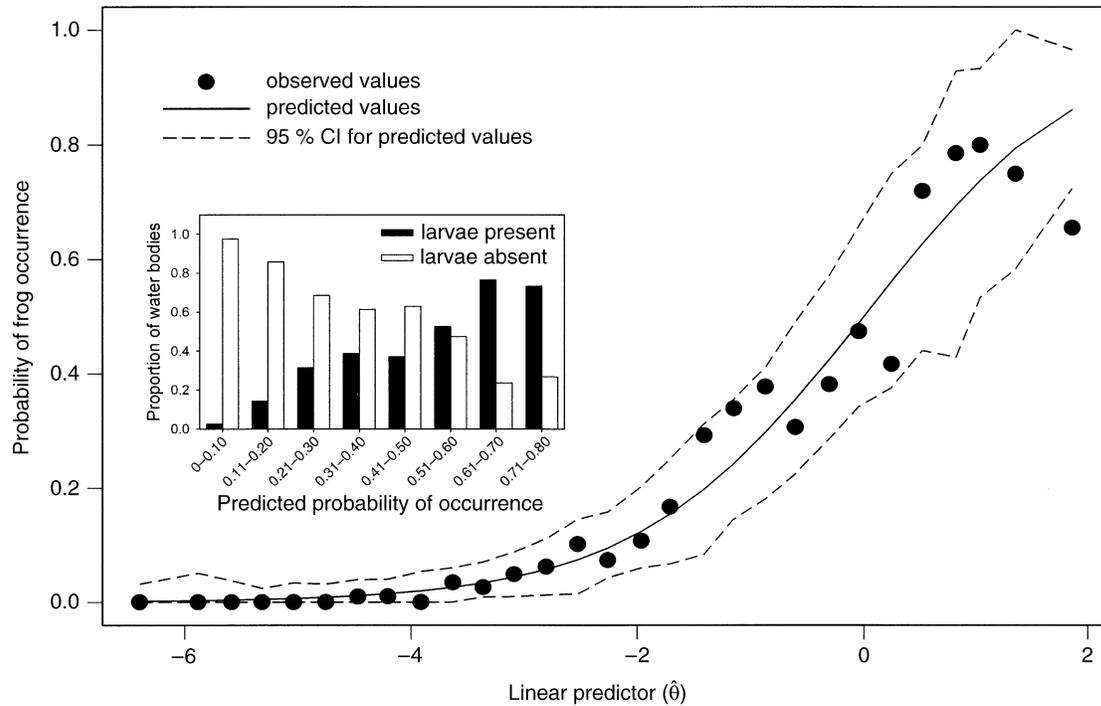


FIG. 5. Results of the cross-validation procedure for the autologistic model showing the observed and predicted probability of *R. muscosa* occurrence ($\pm 95\%$ confidence limits) for 29 categories of the linear predictor ($\hat{\theta}$). The value for one of the categories lies outside the 95% confidence interval. The inset figure shows the same data but as a histogram of the proportion of lakes in which larvae are present versus absent as a function of the predicted probability of occurrence (\hat{p}).

for larvae is probably less than four months long (late June to early September; Bradford 1983) appears due to the ability by larvae to overwinter.

The regression models also indicated a highly significant negative effect of nonnative trout presence/absence on the probability of larval occurrence. This is likely the result of predation by fish on frog larvae and adults (observations of predation described in Needham and Vestal 1938). This result lends support to previous studies that also suggested an important role for introduced trout in the decline of *R. muscosa* (Bradford 1989, Bradford et al. 1998, Knapp and Matthews 2000). Studies conducted on other amphibian species in the Sierra Nevada and elsewhere in North America and in Europe have also indicated that the introduction of fish into naturally fishless mountain lakes can limit amphibian distributions (Braña et al. 1996, Matthews et al. 2001, Pilliod and Peterson 2001).

Patch occupancy was also significantly influenced by the percentage of the littoral zone dominated by silt. The importance of substrate characteristics to *R. muscosa* was not recognized previously, and silt may be important for at least two reasons. First, diets of *R. muscosa* larvae are dominated by benthic algae and detritus, and silt substrates of Sierra Nevada alpine lakes are characterized by a much higher algal biomass than is characteristic of hard substrates (R. A. Knapp, unpublished data). Second, higher amounts of littoral

zone silt are indicative of warmer lakes with higher productivity, habitats that may be more likely to sustain frog populations than boulder-dominated low productivity lakes (Matthews et al. 2001).

Finally, the regression results indicated that the probability of patch occupancy by larvae was an increasing function of the number of nearby fishless lakes or the weighted distance to nearby frog populations. The isolation effects represented by these variables have at least two important implications for understanding both the historic and current distribution of *R. muscosa*. First, drainages containing only a few water bodies may never have supported frog populations despite the presence of otherwise suitable habitat. A possible example is the drainage in Fig. 6A indicated with a white arrow. This drainage contains only two water bodies with suitable *R. muscosa* habitat (>3 m deep, <3500 m in elevation). Despite the fact that the drainage has never been stocked with trout, there are no records of historic or current presence by *R. muscosa*. Second, given that the presence of trout generally results in the exclusion of *R. muscosa* (Bradford 1989, Knapp and Matthews 2000), the introduction of trout into the majority of Sierra Nevada lakes appears to have dramatically increased the degree of isolation between remaining frog populations (Bradford et al. 1993). Based on our results indicating the important influence of water body isolation on patch occupancy, we concur with Bradford

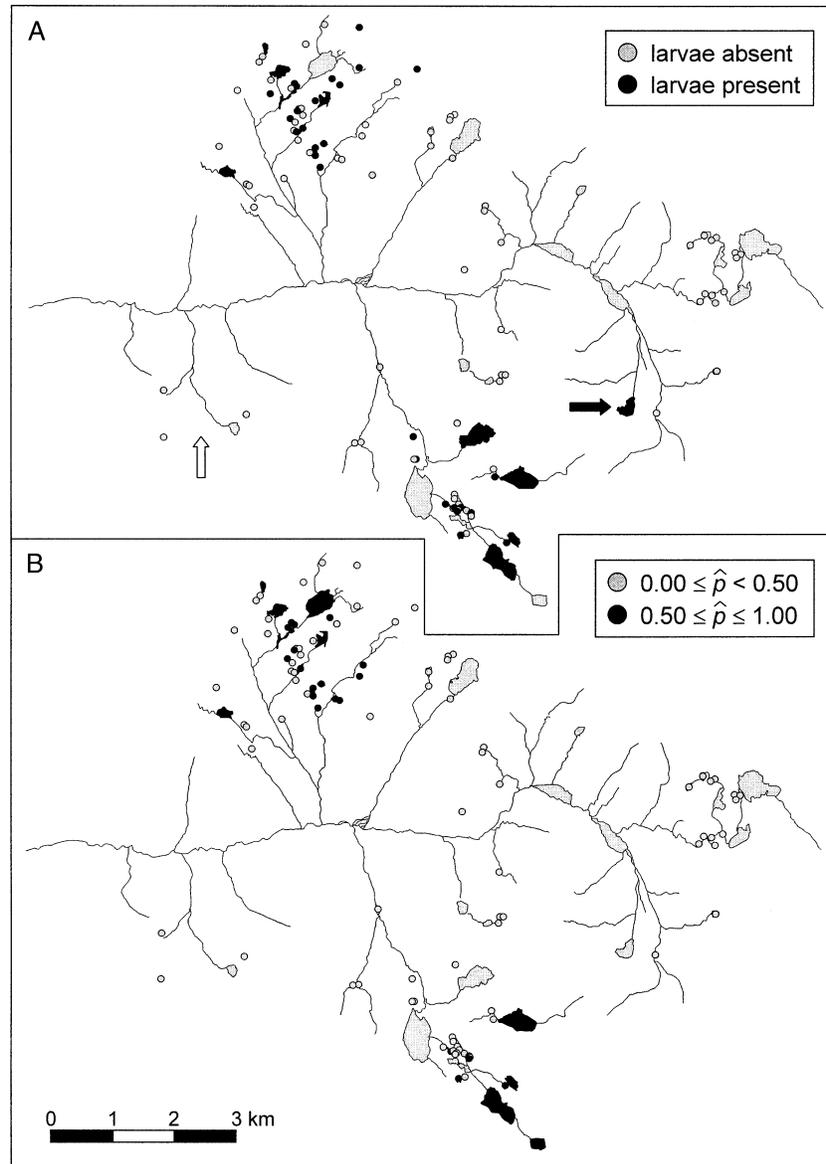


FIG. 6. Map of the Palisade Creek drainage within the study area, showing (A) the locations of water bodies with and without *R. muscosa* larvae, and (B) the predicted probabilities of occurrence by *R. muscosa* larvae (\hat{p}) calculated using the autologistic model (Eq. 3). To enhance readability, all water bodies <1 ha in area were replaced with a dot with area = 1.1 ha. The main stream in the drainage flows from right to left. The arrows refer to lakes mentioned in the *Discussion*.

et al. (1993) that the documented disappearance of *R. muscosa* even from fishless water bodies (Bradford 1991, Bradford et al. 1994) may be a consequence of this reduced connectivity. Lower connectivity is the result of several inter-related factors, including (1) the elimination of many frog populations by fish predation, and (2) reduced rates of successful frog dispersal because of greater distances between frog populations and the presence of predatory fish along dispersal corridors (lakes and streams). As a result, *R. muscosa* may be much less likely to recolonize sites following natural extinction events than was the case prior to fish intro-

ductions. Based on these observations, long-term persistence of particularly isolated *R. muscosa* populations will be unlikely unless population connectivity is restored. This could be accomplished by removing fish (Knapp and Matthews 1998) from water bodies near the isolated populations and reestablishing *R. muscosa*. The feasibility of this approach is supported by three recent studies. Knapp et al. (2001) showed that *R. muscosa* was able to recolonize the majority of lakes in which the termination of trout stocking resulted in disappearance of fish populations. In addition, recent experiments in which the entire trout population was re-

moved from several lakes showed that fish removals allowed rapid recolonization by *R. muscosa* (Vredenburg 2002, R. A. Knapp, unpublished data).

Spatial autocorrelation

Of the six independent variables included in the predictive spatial model, the locational covariate was the most important predictor of patch occupancy by *R. muscosa* larvae (based on AIC values). When the locational covariate was replaced with a weighted distance autocovariate in the autologistic model, the autocovariate was the most important predictor of patch occupancy. Therefore, patch occupancy data were characterized by strong spatial autocorrelation even after accounting for several significant habitat effects.

Several authors have warned that failure to account for spatial autocorrelation may invalidate results from classical statistical tests (Legendre 1993, Carroll and Pearson 2000). Indeed, removal of the locational covariate or autocovariate terms from our models inappropriately inflated the statistical importance of some variables. For example, removal of the locational covariate term from the exploratory spatial model (Eq. 1) increased the *P* value associated with the PHQLAKES variable from 0.073 (Table 2) to 3.3×10^{-9} . This example supports the argument that the development of useful predictive models of animal or plant distributions will often require that spatial autocorrelation be incorporated into modeling efforts (Augustin et al. 1998).

Spatial autocorrelation in the distribution of occupied patches may result from several factors. Dispersal and synchronous population fluctuations are likely contributors to the high degree of spatial autocorrelation we observed in the distribution of *R. muscosa* larvae. Although movement by *R. muscosa* larvae among sites appears to be relatively uncommon, inter-patch movements by adults are frequently observed (Matthews and Pope 1999, Pope and Matthews 2001). Adult dispersal may create spatial autocorrelation in the distribution of larvae if, for example, the presence of a breeding population of frogs in a high-quality lake increases the chances that some adults will move to and breed in adjacent lower-quality sites (e.g., source-sink dynamics; Dias 1996). Dispersal could also cause spatial autocorrelation if *R. muscosa* populations are subject to extinction-recolonization dynamics. If *R. muscosa* populations frequently go extinct, the probability of site occupancy may decrease with increasing isolation from other *R. muscosa* populations, as a lack of nearby occupied sites may preclude recolonization. In addition to dispersal, synchronous population fluctuations could also contribute to the observed spatial autocorrelation in the distribution of *R. muscosa*. Populations in close proximity will often experience more similar environments (e.g., weather patterns) than will populations separated by greater distances, and this may result in a positive correlation in population dynamics (Moran

effect; Ranta et al. 1997, Koenig 2002). For example, Bradford (1983) reported a concurrent die-off of nearly all *R. muscosa* adults in 21 lakes within a single drainage, apparently as a result of an unusually long winter that resulted in oxygen depletion. Similar correlated fluctuations in *R. muscosa* populations as a result of disease outbreaks have also been observed (Bradford 1991; R. A. Knapp, unpublished data). Together, these observations suggest that population dynamics in *R. muscosa* may frequently be synchronous across entire drainages, resulting in spatial autocorrelation of occupied sites.

Relevance to conservation planning

An intriguing application of our predictive spatial model and autologistic model is to identify *R. muscosa* populations that are vulnerable to extinction. While habitat models are frequently used to identify sites likely to harbor a particular animal or plant species (Scott et al. 2002) some authors have argued that because habitat is the ultimate determinant of population viability, habitat models could be used to predict population persistence (Roloff and Haufler 2002). For example, the lake in Fig. 6A indicated by a black arrow contains frogs, but the predicted probability of occurrence calculated using Eq. 3 is relatively low ($\hat{p} = 0.21$). If the variables in Eq. 3 affect the viability of frog populations, then p_i may be directly proportional to the likelihood of population persistence. Under this scenario, this site may have a relatively low probability of retaining *R. muscosa* over the long-term. Although this application of our models remains speculative, results from resurveys of frog populations within our study area provide preliminary support. In 2001, one of us (R. A. Knapp) resurveyed frog populations in 33 of the 238 study lakes that contained *R. muscosa* larvae when initially surveyed in 1995–1997 (initial surveys conducted as part of the current study). During the 4–6-yr period between surveys, three of the 33 lakes lost their frog populations. These three sites had significantly lower p_i values (calculated using Eq. 3) than the 30 sites in which frog populations persisted ($\bar{X}_{\text{extinct}} = 0.04$, $\bar{X}_{\text{extant}} = 0.36$; two-sample *t* test [one-sided]: $t = -2.3$, $P = 0.01$). If these preliminary results are supported by the more extensive resurveys currently underway, our predictive model could provide a useful tool for evaluating population viability that requires far less species-specific life history information and makes fewer assumptions than more traditional population viability analyses that use stochastic simulation models (Boyce 1992).

In conclusion, although ecological data are often characterized by spatial autocorrelation, a feature that can invalidate results obtained from classical regression models, the techniques we used in the current study allowed us to explicitly incorporate spatial autocorrelation into the modeling process. Although still rarely used by ecologists, these modeling techniques

have wide applicability to efforts aimed at understanding the factors that influence patch occupancy and at predicting animal and plant distributions.

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