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BIODIVERSITY RESEARCH

Sub-alpine amphibian distributions related to species palatability to non-native salmonids in the Klamath mountains of northern California

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ABSTRACT

The goal of this study was to examine how introduced trout influence the distributions and abundances of a sub-alpine amphibian assemblage whose members display a variety of different life-history and defence strategies. Our study was conducted in the sub-alpine lentic habitats of three wilderness areas that form the core of the Klamath-Siskiyou Bioregion of northern California, a biodiversity 'hotspot' that supports the highest diversity of sub-alpine, lentic-breeding amphibians in the western USA. These wilderness areas contain no native fishes, but all have been populated with non-native trout for recreational fishing. Five of the eight amphibian species that occur in this region were sufficiently common to use in our study; these included one that breeds in both temporary and permanent waters and is palatable to fish (Pacific treefrog, *Pseudacris regilla*), two that breed primarily in permanent waters and are unpalatable to fish (western toad, *Bufo boreas*, and rough-skinned newt, *Taricha granulosa*), and two that breed primarily in permanent waters and are palatable to fish (Cascades frog, *Rana cascadae*, and long-toed salamander, *Ambystoma macrodactylum*). Based on life histories and predator defence strategies (i.e. palatable or not), we predicted that the three palatable species would likely be negatively correlated with introduced trout, but with *P. regilla* less impacted because of its use of both temporary and permanent waters. We predicted that *B. boreas* and *T. granulosa* would not be significantly correlated with introduced trout due to the lack of any predator/prey interactions between them. We surveyed 728 pond, lake, or wet meadow sites during the summers of 1999–2002, using timed gill-net sets to measure trout occurrence and relative density, and visual encounter surveys to determine amphibian presence and abundance. We used semiparametric logistic regression models to quantify the effect of trout presence/absence and density on the probability of finding amphibian species in a water body while accounting for variation within and among the various lentic habitats sampled. The distributions of *P. regilla*, *A. macrodactylum* and *R. cascadae* were strongly negatively correlated with trout presence across all three wilderness areas. *Ambystoma macrodactylum* was 44 times more likely to be found in lakes without fish than in lakes with fish. *Rana cascadae* and *P. regilla* were 3.7 and 3.0 times more likely, respectively, to be found in fishless than fish-containing waters. In contrast, the two unpalatable species were either uncorrelated (*T. granulosa*) or positively correlated (*B. boreas*) with fish presence. We found that the relative density of fish (catch per unit effort) was negatively correlated with the combined abundances of the three palatable amphibians, and also with both the length and the condition of the fish themselves. Our results are consistent with a compelling body of evidence that introduced fishes greatly alter the aquatic community structure of mountain lakes, ponds, and wet meadows.

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INTRODUCTION

In high-elevation environments of the western USA there is now extensive evidence that non-native fish negatively impact native amphibians and other lentic-associated biota (e.g. Bradford, 1989; Tyler *et al.*, 1998a; Knapp *et al.*, 2001; Matthews *et al.*, 2001; Pilliod & Peterson, 2001; Hoffman *et al.*, 2003; Vredenburg, 2004; Knapp, 2005) (see Kats & Ferrer (2003) for a general review of the impacts of alien predators on amphibians). The majority of these studies focused on alpine lake habitats where there is low native amphibian diversity, little habitat complexity, and the amphibian species have minimal defences from fish predation (but see Knapp, 2005). Amphibians use multiple strategies as antipredator mechanisms against fish and other predators, including chemical repellents (Daly, 1995; Toledo & Jared, 1995), cryptic colouration (Wassersug, 1971), detection of chemical cues to indicate a predatory threat (Kats *et al.*, 1988), and rapid larval development so breeding can occur in temporary waters where predation risk is lower than in permanent waters (Woodward, 1983). When comparing the habitat type and palatability of amphibian larvae from a variety of regions, Kats *et al.* (1988) found that larvae generally conformed to one of three groups: (1) those that live in ephemeral pools without fish, (2) those that live in permanent habitats and are unpalatable to fish, and (3) those that live in permanent waters and are palatable to fish. Species in the third group usually show strong avoidance behaviours in the presence of fish, such as increased refuge use (Kats *et al.*, 1988).

Many western North American native amphibians, especially ranid frogs, occupying sub-alpine and alpine habitats are members of the third group. This is likely because (1) there was no strong evolutionary pressure to develop costly chemical defences since there were no native fish predators, and (2) larval development takes longer at higher elevations due to the cold temperatures so amphibians at high elevations must breed in more permanent waters to avoid die-offs due to desiccation or freezing (Knapp & Matthews, 2000; Pilliod & Peterson, 2001). It therefore is likely that these high-elevation amphibians are strongly adversely affected by predation from introduced fish. In sub-alpine regions where environmental conditions are not as extreme, non-native fish may not have as strong an effect, especially if the amphibians are members of the first or second of Kats *et al.*'s (1988) groupings. In sub-alpine habitats, there is often greater amphibian diversity and more habitat complexity compared to alpine habitats. The amphibians found in these regions often overlap in at least a portion of their range with some native fishes and therefore may have experienced more recent evolutionary pressure to develop defences to fish predation.

The primary goal of this study was to evaluate how introduced salmonids (trout and char, hereafter 'trout') affect the distribution of native sub-alpine amphibians with a range of life-history and defence strategies. We focused on the sub-alpine lentic habitats of three wilderness areas in the Klamath Mountains of northern California, a region with (1) high levels of biotic diversity and endemism (Coleman & Kruckeberg, 1999; DellaSala *et al.*, 1999); (2) a relatively high diversity of amphibian species (Bury & Pearl, 1999); and (3) no native fishes. The five common amphibian species of this region include one that breeds in both temporary and permanent ponds (Pacific treefrog, *Pseudacris regilla*) (Stebbins & Cohen, 1995), two that breed primarily in permanent lentic and lotic waters and are unpalatable to fish during the majority of their lifecycle (western toad, *Bufo boreas*, and rough-skinned newt, *Taricha granulosa*) (Brodie, 1968; Kruse & Stone, 1984; Kiesecker *et al.*, 1996), and two that breed primarily in permanent lentic waters at high elevations and are palatable to fish (Cascades frog, *Rana cascadae*, and long-toed salamander, *Ambystoma macrodactylum*) (Leonard *et al.*, 1996; Peterson & Blaustein, 1992; Tyler *et al.*, 1998b). Chemical defences are common in amphibians (Daly, 1995), and two of the most effective poisons, the water-soluble alkaloid tetrodotoxin and cardiac glycosides called bufadienolides (Flier *et al.*, 1980; Toledo & Jared, 1995), are found in adult *T. granulosa* and *B. boreas* skin, respectively. Tetrodotoxin has been found in the eggs and adults of *T. granulosa* but has not been isolated from the larvae (Furman, 1967). Therefore, the larval stage may be susceptible to predation by fish. *Rana cascadae* spends its entire life in or close to water (O'Hara, 1981), while *A. macrodactylum* migrates away from water following metamorphosis, returning only to breed (Pilliod & Fonzuto, 2005). In the sub-alpine of the Klamath Mountains, *R. cascadae* larvae usually metamorphose in one season; whereas, we have found that *A. macrodactylum* frequently must overwinter as larvae and metamorphose after two summers of development. We predicted that the highly aquatic nature of *R. cascadae* and the long aquatic development stage of *A. macrodactylum* would make these species most susceptible to trout predation. We also predicted that *P. regilla* would be susceptible to trout predation due to its palatability and the past research results that have found a negative correlation between trout and treefrogs (Matthews *et al.*, 2001); however, we postulated that the effects would be less so than on *A. macrodactylum* and *R. cascadae* due to their use of both permanent and temporary lentic habitats for breeding. We did not anticipate that the distribution or abundance of *B. boreas* or *T. granulosa* would be significantly affected by introduced trout because there is no evidence of predator–prey interactions between them.

The final goal of the study was to assess whether the density of trout in a water body negatively influences the abundance of palatable amphibians, and the size and condition of the trout themselves. We hypothesized that trout are density-dependent in these systems and therefore can strongly influence prey numbers. Moreover, the release of trout in these lakes by stocking large numbers of fingerlings on an annual or bi-yearly basis may create an unbalanced system where trout numbers exceed the carrying capacity of the habitat. The high intraspecific competition for a limited food supply in lakes with high densities of trout would likely result in small size and poor condition of trout, similar to findings in the Sierra Nevada (Schindler *et al.*, 2001; Armstrong & Knapp, 2004). This assessment is intended to provide information useful for the management of montane lentic systems that could promote the coexistence of introduced trout and native amphibians while simultaneously improving the recreational fishery.

The specific objectives of this study were to census all lentic habitats (lakes, ponds, and wet meadow complexes) within the

Trinity Alps, Russian, and Marble Mountain wilderness areas and: (1) quantify the current distributions and relative abundances of the native lentic-breeding amphibians and introduced trout across these landscapes; (2) assess the effects of non-native trout on the distribution and abundance of the amphibians; (3) examine habitat, isolation, and geographical relationships that might influence the interaction between fish and amphibians; and (4) evaluate whether the density of trout in a lake is correlated with their average size and condition.

METHODS

Study area

The three federally designated wilderness areas, Trinity Alps (TA), Marble Mountains (MM), and Russian Wildernesses (RW), are located in the Klamath Mountains of northern California within the Klamath, Shasta-Trinity, and Six Rivers National Forests (Fig. 1). These areas are lightly managed, primarily for their wilderness values, and thus are relatively pristine with trails for hiking and pack animal use, but no roads, no logging, and no off-road vehicle use, and with minimal grazing. In these wilderness areas, steep canyon gradients created during Pleistocene glaciations prevented colonization by fish into lakes higher than 1500 m in elevation. Water bodies we surveyed were between 1525 m and 2290 m in elevation, mostly within sub-alpine habitats. Beginning in the late 1800s, various salmonids (primarily *Oncorhynchus*, *Salmo*, and *Salvelinus* spp.) were introduced to large lakes for recreational purposes. Aerial and pack stocking in the Klamath-Siskiyou Bioregion persists today. Prior to 2002, over 90% of lakes greater than 1 ha in TA, MM, and RW were stocked on an annual or bi-yearly basis. Since 2002, the California Department of Fish and Game (CDFG) suspended stocking in approximately half of the lakes in order to assess both the impacts and the sustainability of introduced trout.

Field methods

Surveys were conducted during the warm summer months when water bodies were ice-free and fish and amphibians were active. We attempted to survey all water bodies in the area. Water bodies in TA were surveyed from 9 July to 19 August 1999, 6 June to 18 September 2000, 6 June to 21 August 2001, and 5 June to 8 September 2002. Surveys were conducted in RW from 15 August to 19 September 2001 and 28 June to 13 August 2002, and in MM from 23 June to 17 September 2001 and 10 July to 23 August 2002.

Because of the high number of water bodies and the difficulty in reaching remote sites, most were visited only once and a shoreline visual encounter survey (Crump & Scott, 1994), as opposed to trapping, was used to determine presence and relative abundance of the five targeted amphibian species. When amphibians were found, we documented which species were present and counted the number of post-metamorphic frogs (i.e. adult and sub-adult) and larvae. During the summer, *R. cascadae*, *P. regilla*, and *B. boreas* larvae occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes using shoreline searches. *Taricha granulosa* and *A. macrodactylum* larvae, however, are quite cryptic and often lie still in the silt along the littoral zone. We therefore also agitated the near-shore substrates during surveys to search for these larvae. Sub-adults and adults of *R. cascadae* are highly aquatic and are almost always found near water. *Taricha granulosa* is reported as the most aquatic of the western newts (Stebbins & Cohen, 1995) and we found all life stages in the water during all time periods of the study. Sub-adult and adults of *P. regilla*, *B. boreas*, and *A. macrodactylum*, however, may only be in lakes or ponds for a short period during breeding or just after metamorphosis. As a result, the chance of encountering sub-adults and adults of these three species is reduced when sampling ponds and lakes.

The presence or absence of trout was determined at each water body using visual encounter surveys in shallow water bodies

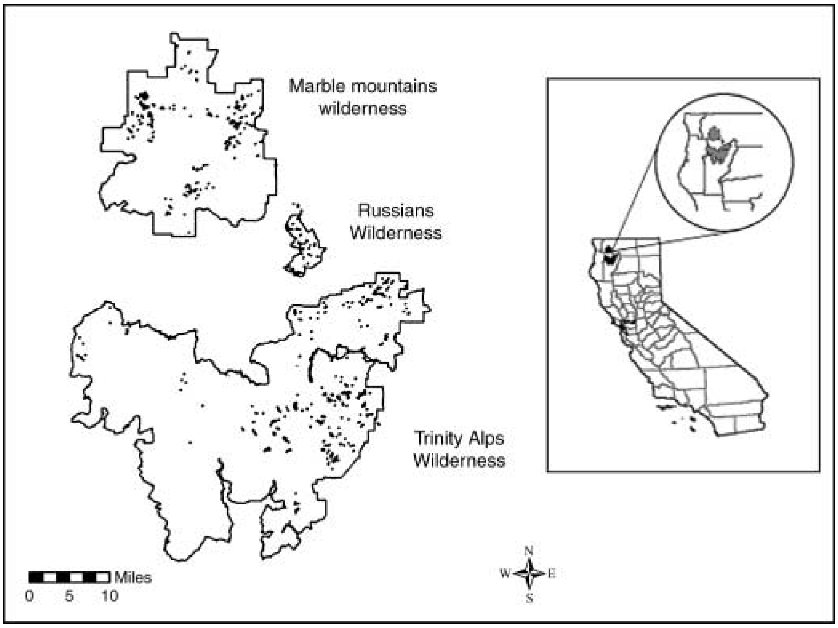

Figure 1 Map of the three northern California wilderness study areas. Dots represent survey locations.

when the entire bottom could be seen, or with gill nets. In the Sierra Nevada, repeated gill-net sets indicated that single net sets were close to 100% accurate in determining fish presence or absence (Knapp & Matthews, 2000). A single 36-m-long, variable mesh, monofilament gill net was set perpendicular to the shoreline for 4–10 h in each lake. In gill-netted lakes, fish densities were also estimated as catch per unit effort (CPUE: number of fish captured per hour of net set). When the nets were retrieved, we recorded species and weight and length of each fish. To establish that CPUE was an accurate measure of density similar to findings in the Sierra Nevada (Schindler *et al*., 2001), we compared our CPUE findings in four lakes in TA to actual fish densities in those lakes determined by removing the entire population of trout using repeated gill net sets (K. Pope & S. Lawler, unpublished data).

Describing lentic habitats

To characterize the physical attributes of each water body, we used information on elevation, perimeter, surface area, maximum depth, littoral zone (i.e. near-shore) substrate composition, and distance (= isolation) from adjacent water bodies. Elevation, perimeter, and surface area were obtained from GIS topographical coverage for mapped sites. All unmapped sites were mapped using GPS, with areas and perimeters estimated in the field. Maximum lake depth was determined by sonar. Near-shore substrates and amounts of aquatic vegetation were estimated by walking the perimeter of each site and collecting information at approximately 50 equidistant points of the littoral zone. The relative amount of silt or emergent vegetation was estimated by calculating the proportion of total points that were recorded for the substrate class or with vegetation present. We focused on the substrate class ‘silt’ (i.e. percentage of silt) because previous researchers found it to be the most highly correlated substrate type with presence of amphibians (Knapp & Matthews, 2000). A measure of water body isolation, the number of lentic sites within 1 km of the shoreline of each water body, was calculated using a GIS. For this measure we considered only those water bodies within the same drainage (as defined by the California State Department of Water Resources — CalWaters GIS coverage).

Methods of analysis

Proportion of sites occupied by amphibians and fishes

We included 407 lentic sites in TA, 69 sites in RW, and 252 sites in MM in the analyses for a total of 728 unique aquatic sites. We did not include five sites that were frozen or lacked a complete survey for fish, amphibians, and habitat. To assess the patterns of distribution of amphibians and trout for each wilderness area, we calculated the overall percentage of water bodies where fish and amphibians were found, stratified by maximum lake depth.

Patterns of amphibian occurrence in relation to fish

We used semiparametric logistic regression models to quantify the effect of trout presence/absence on the probability of finding amphibian species in a water body, while accounting for both habitat and isolation differences of the water bodies. We found that none of the amphibian species were highly correlated (Pearson correlation coefficient < 0.4) with each other, and therefore we ran independent models for each species. We ran initial regression analyses on each wilderness area separately to ensure that patterns relating to fish and amphibians held across wilderness areas. We then combined the data from all three wildernesses into one data set to increase analytical power. ‘Wilderness area’ was still included as a categorical variable in all analyses since there appear to be distributional differences among these areas for some amphibians. For example, *T. granulosa* was most common in MM in the northern part of the region, moderately common in RW, and least common in TA in the southern part of the region.

We used generalized additive models (GAMs) for these analyses because they allow the relationships between the dependent and independent variables to be nonlinear. Six different models were run for detection/non-detection of (1) *R. cascadae* eggs or larvae, (2) *R. cascadae* adults or sub-adults, (3) *A. macrodactylum*, (4) *P. regilla*, (5) *B. boreas*, and (6) *T. granulosa*. For all species except *R. cascadae*, we combined detections of all life-history stages for analysis. We believe this is appropriate for all but *R. cascadae* because finding adults and/or eggs in the spring, larvae during mid-summer or post-metamorphic animals in the fall all suggest breeding occurs in the particular water body. In contrast, *R. cascadae* adults and sub-adults are similar to *R. muscosa* of the Sierra Nevada in that they disperse widely from breeding lakes and ponds to other aquatic habitats during the summer (Pope & Matthews, 2001; J. Garwood, unpublished data). Therefore, only eggs and larvae were used for the analysis of reproduction at sites, and adult and sub-adults frogs were analysed separately.

We modelled the probability of the binary response Y_i (detection/non-detection of amphibians at site i) by the formula

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

The linear predictor θ is given by θ = fish + *T. granulosa* presence + month + year + wilderness area +

$$lo(X_1) + \dots + lo(X_6) \tag{2}$$

where fish, *T. granulosa* presence, month, year, and wilderness area are categorical variables indicating presence/non-presence of fish and *T. granulosa*, specific month and year the site was surveyed, and the wilderness area where the site is located. $Lo(\cdot)$ is a nonparametric smoothing function of the continuous covariates percentage of near-shore silt, maximum water depth, elevation, water body perimeter, UTMs, and number of water bodies within 1 km. Including a spatial variable incorporates spatial autocorrelation into the model, so that a highly significant spatial variable suggests that sites close to each other are not ‘independent’, and thus are likely amphibian ‘hotspots’ or ‘coldspots’. Number of water bodies within 1 km was also included as a relative habitat isolation variable to estimate the number of other potentially suitable habitats nearby. Sites with other water bodies nearby may be more likely to have migration of amphibians and therefore may have a higher likelihood of being inhabited than isolated sites. Month and year were included as variables to account for seasonal and yearly variation in occurrence.

To determine the independent variables for the a priori models, we first reviewed the existing literature for variables that have been found to influence the distribution of related amphibian species (Knapp & Matthews, 2000; Matthews *et al*., 2001; Pilliod & Peterson, 2001; Knapp, 2005). We then calculated Pearson correlation coefficients for all pairwise combinations of covariates to prevent including collinear predictor variables. Although fish and water depth had a fairly high correlation value ($r = 0.69$), we decided to include both variables due to their potential biological significance. The same 11 covariates were used in all of the binomial models, except presence of *T. granulosa*, a known predator on other amphibian early life stages, was not used in the model for *T. granulosa*.

Analysis of deviance and likelihood ratio tests were used to test the significance of each of the predictor variables. We calculated the change in the full model deviance ('residual' deviance) to the deviance of the model with a predictor variable omitted (Knapp, 2005). To provide a standardized estimate of the influence of each variable in the models, we calculated the percentage increase in deviance due to omission of each variable. The relationship between all significant variables ($P \leq 0.01$) and the probability of occurrence of the amphibians is depicted graphically in separate plots to show the relative influence of each predictor variable. The response curves are based on partial residuals and are standardized to have an average value of zero. We used the estimated fish effect in the binomial equations to approximate the change in the likelihood (i.e. odds ratio) of finding the different amphibians in the presence vs. absence of trout after having controlled for the effects of habitat and spatial variables (Hastie & Tibshirani, 1991).

Based on life history and population density differences among our study species, we anticipated differences in detection probabilities and therefore differences in the accuracy of the detection/non-detection data used in the regression models for each species. Although it was infeasible to resample every site, we did resurvey 31 sites in TA five times between 27 June and 1 September 2003 and used these data in the program PRESENCE (MacKenzie *et al*., 2002) to obtain a gross estimate of detection probabilities for the five species. We found that probabilities of detection were high for four species (*B. boreas*: 0.81, *R. cascadae*: 0.79, *P. regilla*: 0.79, and *T. granulosa*: 0.75) and relatively low for *A. macrodactylum* (0.47). Logistic regression models of wildlife–habitat relationships have been shown to be sensitive to even low levels of non-detection in occupancy models (Gu & Swihart, 2004; Mazerolle *et al*., 2005). Biases related to non-detection error are likely present in our regression analyses given our single-survey methodology. However, our focus was to cover a large number of sites over a large area (i.e. to census rather than sample sites) with the compromise of losing some accuracy associated with the habitat variables. We believe that any loss in accuracy in our habitat models is minimized by our large sample sizes.

Fish density relationships

In addition to testing whether fish presence in a water body is correlated with amphibian presence, we tested whether CPUE (number of fish caught per hour of gill net set) was related to the combined abundance of those amphibian species that were negatively correlated with fish presence in a water body (see Results). We first ran a linear regression to compare CPUE to actual fish density in four lakes to assess whether CPUE was an adequate surrogate for fish density. We then used a robust Poisson regression for the analysis and only included waters mapped on 7.5-min USGS quadrangles ($N = 417$) to eliminate most of the small ponds and wet meadows that were incapable of supporting fish. Covariates included CPUE, wilderness area, and water body perimeter for the analysis. We tested additional variables including fish species, percentage of near-shore silt, year of survey, month of survey, and maximum water depth, but we did not include them in the final model because they did not influence abundance of amphibians when analysed with the initial three covariates.

Our final analyses were to determine if relative fish abundance also correlated with the length and condition of the fish in the water bodies. Using the weight and length data collected from all netted fish, we first ran a simple linear regression to determine if fish were larger or smaller in lakes with different fish abundances. We then measured the variation in mass of individual fish in relation to CPUE while accounting for length of fish using the regression equation:

$$\log \mathrm{W} = \alpha + \beta \log \mathrm{L} + \mathrm{CPUE} + \varepsilon \tag{3}$$

where W = wet weight (mass), L = total fish length, and β = slope of L and represents the exponent of length ($\beta = 3$ for isometric growth) in the weight–length equation (LeCren, 1951). By controlling for length, W represents the weight of the fish when length is held constant and therefore represents the body condition (variation from the expected mass for a given length) of the fish.

RESULTS

We found brook, rainbow, or brown trout in 265 of the 728 sites surveyed (125 in TA, 95 in MM, and 45 in RW). Of water bodies deeper than 2 m, we found trout in 85% of the waters in the TA, 91% in the MM, and 97% in the RW. Amphibian species were less common than trout in the water bodies deeper than 2 m, but most amphibian species were more common than trout in shallow waters (Table 1). The presence of adult and/or post-metamorphic *R. cascadae* was fairly common in all the wilderness areas, whereas, actual *R. cascadae* breeding sites, as evidenced by the presence of egg masses or larvae, were less common. We found *R. cascadae* larvae in 23% of the water bodies > 2 m in the TA, 7% in the MM and 0% in the RW (Table 1). Overall, in water bodies > 2 m, *R. cascadae* larvae were about three times more likely to be found without trout than with trout, *A. macrodactylum* were 21 times and *P. regilla* were 1.7 times more likely to be

Table 1 Percent of shallow (< 2 m) or deep (> 2 m) water bodies where fish and amphibian species or life stage were found in each wilderness area

Species	TA < 2 m	TA > 2 m	RW < 2 m	RW > 2 m	MM < 2 m	MM > 2 m	Total % < 2 m	Total % > 2 m
Salvelinus fontinalis	11	77	32	80	10	76	18	78
Oncorhynchus mykiss	4	27	7	49	4	44	5	40
Salmo trutta	0	5	0	6	0	4	0	5
Rana cascadae larvae	38	23	8	0	15	7	20	10
Rana cascadae frogs	50	57	21	26	31	28	34	37
Pseudacris regilla	46	29	13	10	58	24	39	21
Ambystoma macrodactylum	9	8	16	0	1	0	9	3
Bufo boreas	10	32	5	10	1	10	5	17
Taricha granulosa	10	15	63	90	66	89	46	65

TA , Trinity Alps; RW, Russian Wilderness; MM, Marble Mountains.

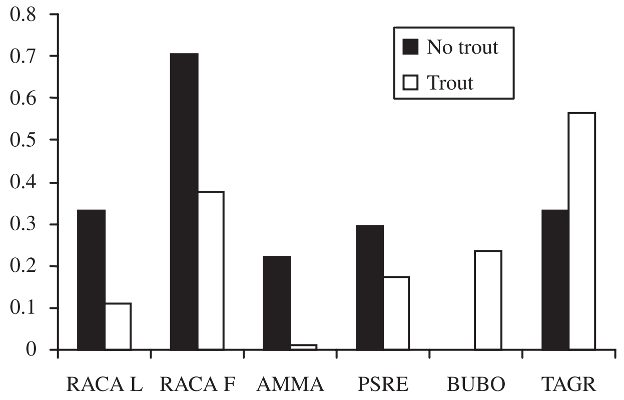

Figure 2 Proportion of water bodies greater than 2 m deep with amphibian species occupancy. Water bodies are categorized by whether trout were absent ($N = 27$) or present ($N = 191$). RACA L is *Rana cascadae* larvae, RACA F is post-metamorphic *R. cascadae* (adults and sub-adults), AMMA is *Ambystoma macrodactylum*, PSRE is *Pseudacris regilla*, BUBO is *Bufo boreas*, and TAGR is *Taricha granulosa*.

found without trout (Fig. 2). In contrast, *B. boreas* were only found in water bodies > 2 m with trout and *T. granulosa* was more often found in lakes with trout than in lakes without trout (Fig. 2).

Results of the logistic regression analysis to quantify the effect of trout presence/absence on the probability of finding amphibian species in a water body while accounting for habitat and isolation differences of the water bodies are presented in Table 2. The resulting models indicated that the distributions of *R. cascadae* (adults and larvae), *A. macrodactylum*, *P. regilla*, and *B. boreas* are correlated with trout after accounting for the influence of other predictor variables (Table 2). The direction of effect of trout was positive for *B. boreas* (Fig. 3) and negative for the other three species (Figs 4, 5, 6, & 7). On the other hand, the presence of *T. granulosa* appeared to be uncorrelated with the presence of trout (Table 2). Based on change in model deviance due to omission of individual variables compared to the full model, trout presence was the most important predictor variable for *A. macrodactylum*, second most important for *P. regilla* and tied for third most important for *R. cascadae* larvae (following month of survey and UTMs; Table 2). July and August were consistently the best months for detecting amphibians, and September was the worst (Figs 4, 5, 6, 7, & 8). Percentage of near-shore silt in a water body had a strong positive effect on the probability of finding most amphibians (although not significant for *A. macrodactylum* or *B. boreas*) and is likely an important habitat component for larval cover and possibly foraging (Figs 4,5,6, & 8). Wilderness area was a strong predictor for both *B. boreas* and *T. granulosa* (Figs 3 & 8). *Bufo boreas* was much more common in TA than MM or RW, whereas *T. granulosa* was much more common in MM and RW compared to TA. Although UTMs were a strong predictor variable in four models (Table 2), the graphical relationship between UTMs and the probability of a species occurrence is not provided because the complex three-dimensional figures did not alone provide insight into the habitat or trout relationships with a species occurrence. The significance of UTMs, however, confirms the importance of spatial dimensions as they relate to the occurrence of the three species/life stages indicated (Table 2), and reflects their uneven occurrence across these landscapes as described above.

Ambystoma macrodactylum appears to be particularly vulnerable to fish (Table 2). After controlling for the effects of habitat, temporal, and isolation variables, these salamanders were 44 times more likely to be found in fishless than fish-containing water bodies (odds ratio, approximate 95% confidence limits [CL]: 37–51). *Rana cascadae* larvae were 3.7 times (CL: 1.8–5.6) and *P. regilla* were three times (CL: 1.2–4.8) more likely to be found in fishless than fish-containing water bodies. In contrast, we found *B. boreas* to be 4.1 times more likely to be found in fish-containing than in fishless water bodies (CL: 1.7–6.6).

After finding that trout presence was significantly negatively correlated with the presence of three amphibian species, we ran robust Poisson regression models to assess whether density of fish also influenced the combined relative abundance of *R. cascadae*, *P. regilla*, and *A. macrodactylum* in a water body. An initial linear regression comparing CPUE to actual density of fish in four lakes where fish were completely removed showed that CPUE and density are highly correlated ($r^2 = 0.95$, P-value < 0.01) (K. Pope & S. Lawler, unpublished data). Using a Poisson semiparametric regression model with water body perimeter and wilderness area as covariates, we found that CPUE of fish was strongly negatively

Table 2 Results of generalized additive models developed for each amphibian species or life stage

Parameter	*Rana cascadae* frogs	*Rana cascadae* larvae	*Pseudacris regilla*	*Ambystoma macrodactylum*	*Bufo boreas*	*Taricha granulosa*
Null deviance	988	800	983	315	496	972
d.f.† (null model)	727	727	727	727	727	727
Model (residual) deviance	798	616	793	200	341	501
d.f.† (full model)	700	700	700	701	700	700
Deviance increase‡						
Trout presence	6 (3.2)*	16 (8.7)**	16 (8.4)**	28 (24.3)**	11 (7.1)*	1 (0.2)
Percentage of silt	16 (8.4)**	16 (8.7)**	15 (7.9)**	0.2 (0.2)	5 (3.2)	7 (1.4)*
Month	17 (8.9)*	19 (10.3)*	12 (6.3)*	11 (9.5)*	6 (3.8)	15 (3.1)*
Perimeter	27 (14.2)**	14 (7.6)*	6 (3.2)*	1 (0.8)	16 (10.3)**	4 (0.8)
Year	10 (5.3)	14 (7.6)*	27 (14.2)**	7 (6.1)	1 (0.6)	10 (2.1)*
No. of water bodies	22 (11.6)*	16 (8.7)*	10 (5.2)	11 (9.5)	2 (1.3)	2 (0.4)
UTMs§	28 (14.7)*	18 (9.7)*	8 (4.2)	12 (10.4)	35 (22.6)**	55 (11.7)**
Taricha granulosa presence	8 (4.2)*	5 (2.7)	1 (0.5)	0 (0)	1 (0.6)	
Wilderness area	0.2 (0.1)	5 (2.7)	1 (0.5)	2 (1.7)	22 (14.2)**	38 (8.1)**
Elevation	0.2 (0.1)	2 (1.1)	1 (0.5)	4 (3.5)	2 (1.3)	2 (0.4)
Maximum depth	2 (1.1)	1 (0.5)	3 (1.6)	2 (1.7)	2 (1.3)	5 (1.1)

Amphibians: all six species columns.

†d.f., degrees of freedom, ‡, deviance increase: increase in deviance resulting from dropping the selected variable from the model. The percentage increase in deviance is given in parentheses, and was calculated as (deviance increase/(null deviance – model deviance)) × 100 (Knapp, 2005). §UTMs, Universal Transverse Mercator grid coordinate. Asterisks indicate the statistical significance associated with each variable. $*P < 0.01$, $**P < 10^{-4}$.

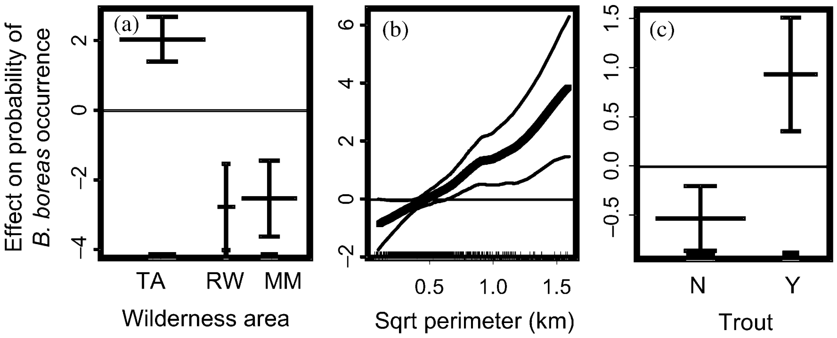

Figure 3 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Bufo boreas* as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) wilderness area, (b) water body perimeter, and (c) trout presence. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

correlated with the combined abundance of the three amphibian species ($F = 25.05$, d.f.$_1 = 405$, d.f.$_2 = 2$, $P = 4.9 \times 10^{-13}$) (Fig. 9).

To determine if trout density was also correlated with small body size and/or low body condition of trout in a water body, we used simple linear regressions. We found that trout were significantly shorter in lakes with high densities of trout than in lakes with low densities of trout ($t = 9.6$, SE = 0.0026, $P < 0.0001$). In addition, body condition of trout in lakes with high densities of trout was lower than in lakes with low densities of trout ($F = 10.17$, d.f.$_1 = 4285$, d.f.$_2 = 1.5$, $P < 0.0001$) (Fig. 10).

DISCUSSION

We found that, as predicted based on the known life-history defence strategies of the five amphibian species we analysed, the three palatable species were all negatively correlated with trout (Table 2), however, contrary to our prediction *P. regilla* was not the least affected by fish presence; adult *R. cascadae* was (Table 2). In contrast, the two unpalatable species were either uncorrelated with (presence of *T. granulosa*), or positively correlated with (presence of *B. boreas*) trout (Table 2). We found *B. boreas* four times more often in lakes with trout than in lakes without trout. Both our observations and previous experimental studies suggest that all life stages of *B. boreas* are unpalatable to fish (Wassersug, 1973; Kruse & Stone, 1984). Larvae were frequently observed swimming in large schools near trout with no response from the fish (K. Pope, pers. obs.).

Although we do not know definitively why presence of the western toad was positively correlated with trout, it is known that trout prey on predaceous aquatic insects such as diving beetles (*Dytiscus* sp.) and giant water bugs (*Lethocerus americanus*). Both insect species are predators on western toad larvae (Peterson & Blaustein, 1992), and their numbers can be reduced by fish

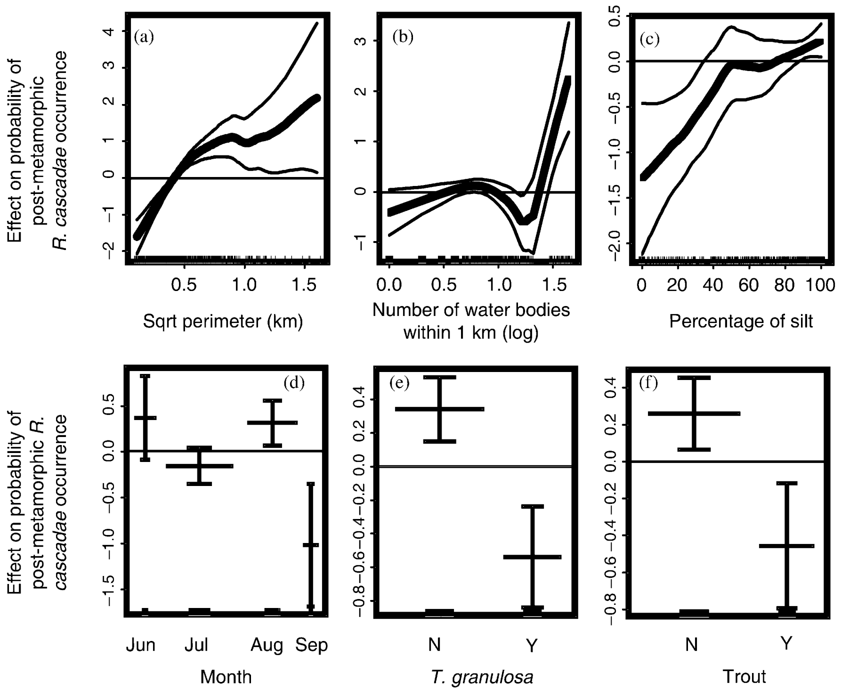

Figure 4 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Rana cascadae* frogs as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) water body perimeter, (b) number of water bodies within 1 km, (c) percentage of silt in the littoral zone, (d) month of survey, (e) *Taricha granulosa* presence, and (f) trout presence. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

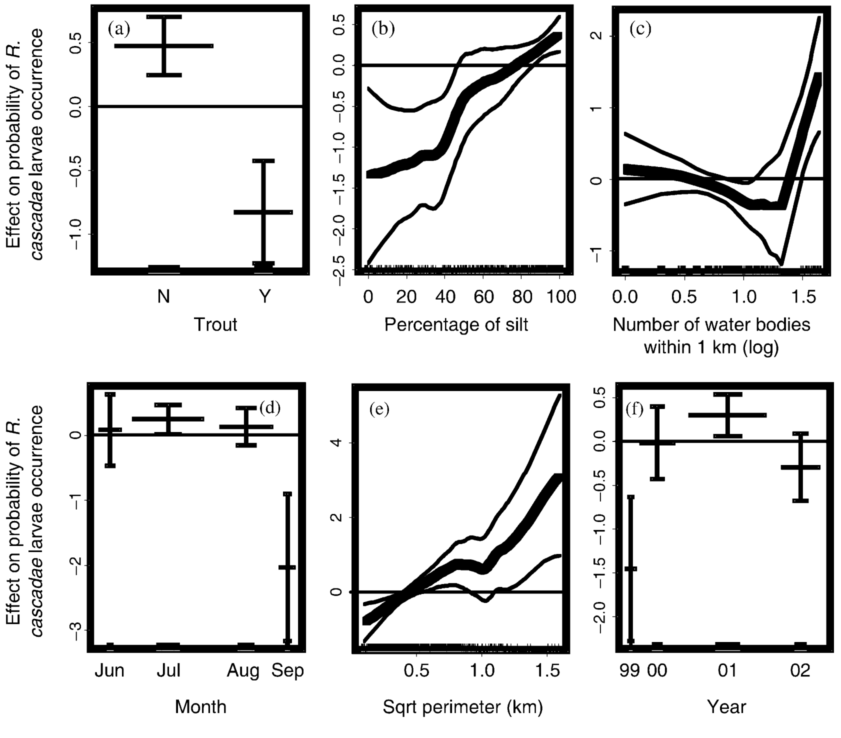

Figure 5 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Rana cascadae* larvae as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) trout presence, (b) percentage of silt in the littoral zone, (c) number of water bodies within 1 km, (d) month of survey, (e) water body perimeter, and (f) year of survey. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

presence in a lake (Knapp *et al.*, 2001; K. Pope & S. Lawler, unpublished data). Fish presence then would infer an indirect benefit to resident larval toad populations, which would experience enhanced survival in lakes with fish and fewer macroinvertebrate predators compared with lakes without fish and more macroinvertebrate predators. Similarly, Adams *et al.* (2003) found that non-native fishes increased bullfrog tadpole survival by reducing predatory macroinvertebrate densities.

Our results indicate that of the five species we examined, *A. macrodactylum* is the most sensitive to introduced trout. We encountered *A. macrodactylum* 44 times more often in water bodies without trout than with trout. One cautionary note on this result is that, because we did not account for probability of detection in our models, the strength of the parameter estimations from the logistic regression models may be negatively or positively biased. However, while we found *A. macrodactylum* to

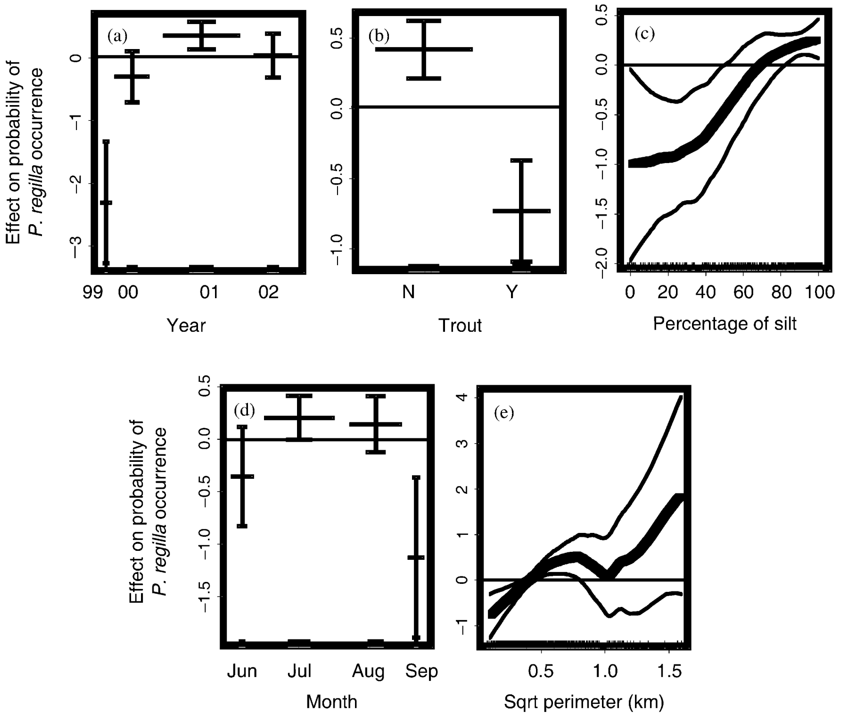

Figure 6 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Pseudacris regilla* as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) year of survey, (b) trout presence, (c) percentage of silt in the littoral zone, (d) month of survey, and (e) water body perimeter. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

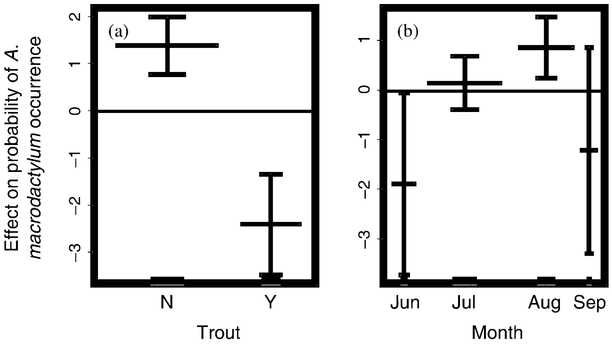

Figure 7 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Ambystoma macrodactylum* as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) trout presence and (b) month of survey. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

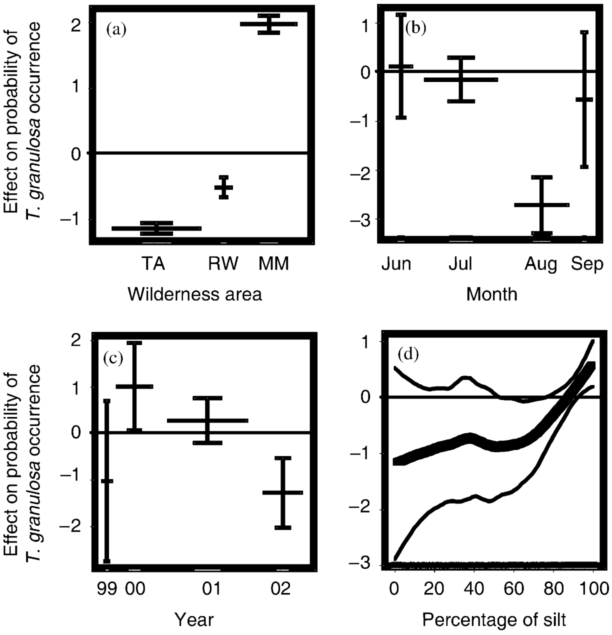

Figure 8 Estimated effect of each of the significant ($P \leq 0.01$) predictor variables on the probability of occurrence of *Taricha granulosa* as determined from the best generalized additive model (Table 2). Approximate 95% confidence intervals are included and hatch marks at the bottom of each graph represent data points. Variables include (a) wilderness area, (b) month of survey, (c) year of survey, and (d) percentage of silt in the littoral zone. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line.

have the lowest detection probability (0.47), we believe that the large sample size and strength of the relationship greatly reduce the chance of the general correlation being in error (see also Tyler *et al.*, 1998a,b; Pilliod & Peterson, 2001).

We predicted that *R. cascadae* would be highly sensitive to trout because they are highly aquatic even as adults (Dumas, 1966; O'Hara, 1981). Recent evidence, however, suggests that adult *R. cascadae* are able to identify fish threats (possibly from chemical cues) and will move to fishless waters to avoid them, or move to protected areas in lakes with fish, such as in enclosed shallow bays or behind logjams at the outlet of the lakes (J. Garwood & H. Welsh, unpublished data). In addition, the risk of predation

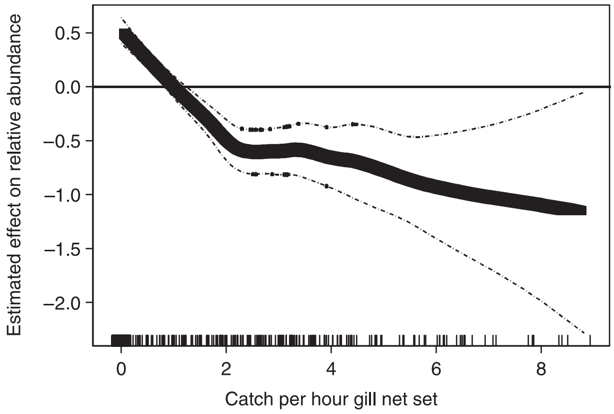

Figure 9 Estimated density effects of trout on the combined relative abundance of *Rana cascadae*, *Pseudacris regilla*, and *Ambystoma macrodactylum* (including approximate 95% confidence intervals). Horizontal line indicates the average effect level. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line. Hatch marks represent data points.

is less for adult frogs because trout are gape limited. This likely explains why we did not see as strong a negative correlation between trout and adult *R. cascadae* compared with the larvae.

The question then is why are *A. macrodactylum* larvae so sensitive to trout? It may be that they are not any more palatable than *R. cascadae* or *P. regilla* larvae, but that *A. macrodactylum* is better at hiding in habitats with trout compared to the other two species and therefore were not as readily detected. Although we cannot completely discount this alternative, our field crews did spend time looking under refuge objects and in silt for hidden individuals at all sites. In addition, Tyler *et al.* (1998a) found no differences in the percentage of larvae hidden in benthic substrates between fishless and fish-containing lakes in the North Cascades of Washington. One important life-history characteristic differentiating larval *R. cascadae* and *P. regilla* from *A. macrodactylum* that we did not originally take into account is that while *R. cascadae* and *P. regilla* larvae feed on algae and detritus along the shallow margins of the water bodies, *A. macrodactylum* larvae are predaceous and feed primarily on aquatic invertebrates and zooplankton. Even though all three species may be able to identify fish presence, feeding requirements may necessitate that *A. macrodactylum* larvae spend more time hunting in deeper areas where they are more susceptible to fish predation.

Our apparent finding of more detections of *R. cascadae* compared to *P. regilla* in some areas (Table 1) merits comment because it appears counter-intuitive based on the relative commonness of these two species where they co-occur. Recall that with *R. cascadae* we separated life stages for analysis, but with *P. regilla* we did not (see Methods), so the data in Table 1 are combined for that species. However, most of the *P. regilla* sample did consist of larvae so the only appropriate comparison here would be with *R. cascadae* larvae and *P. regilla*, in which case *P. regilla* did have more detections in all categories (Table 1). We believe that the higher detections of *R. cascadae* adults compared with *P. regilla* adults (data not shown) are an artefact of behaviour, detectability, and detection method (shoreline VES), and not a true reflection of their relative abundances in these areas. *Rana cascade* is less cryptic, diurnal, and frequents shoreline habitat, making it more readily detected than the cryptic and nocturnal *P. regilla* given our diurnal VES shoreline sampling.

We found consistent correlations between trout and amphibian distributions in all three wilderness areas. Moreover, each wilderness area supported trout in almost all water bodies that could support trout (permanent and deep). However, we did find notable differences in amphibian distributions among the three wilderness areas. In the TA, the five lentic amphibians that we studied were relatively common and widespread and appear unlikely to be at risk of extirpation. On the other hand, *A. macrodactylum* was only found at one site in the MM and both *R. cascadae* and *A. macrodactylum* were rare in the RW. Only five sites, all less than 2 m deep in the RW, supported *R. cascadae* breeding, and only 11 sites with *A. macrodactylum* were found. We acknowledge, and are hopeful, that we did not find all occurrences

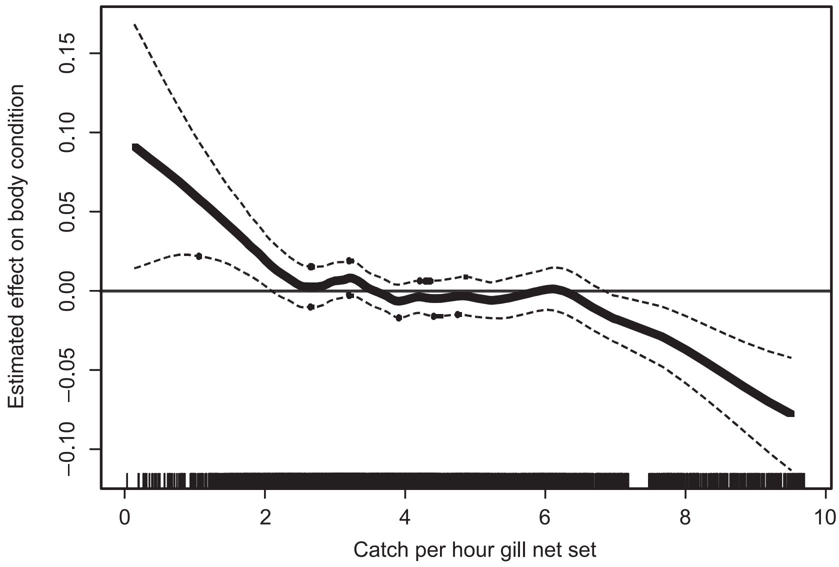

Figure 10 Estimated density effects of trout on body condition of trout, standardized so that average body condition for all sampled fish equals zero and values above zero represent higher than average body condition and values below zero represent lower than average body condition. Dotted lines represent approximate 95% confidence intervals, and horizontal line indicates the average effect level. Significance is indicated when 95% bounds fall completely above or below the average effect line. Hatch marks represent data points.

of amphibians in these wilderness areas using a diurnal single-visit visual encounter technique. However, even if we were to double the number of sites with presence in both the MM and the RW, *A. macrodactylum* would still be found in less than 10% of the surveyed water bodies. Although there is little documentation about the historical distribution and abundance of *R. cascadae* and *A. macrodactylum* in these wilderness areas, it is likely, based on their habitat associations and their present highly fragmented distributions, that they were not rare species in any of the three wildernesses. Based on evidence from the surveys reported here, however, we believe these species are currently in danger of extirpation in both the RW and the MM.

We are not sure why populations of *R. cascadae* and *A. macrodactylum* are more robust in TA compared to MM and RW. We did find a higher proportion of small and unmapped ponds and wet meadows in TA (55% of sites) than the other two wildernesses (27% of sites in the MM and 19% of sites in the RW). These additional shallow, mostly fishless waters may provide important alternative habitats for amphibians when fish occupy the large lakes and ponds. Prior research on seasonal movements of other high-elevation ranid frogs, and ongoing research on *R. cascadae*, suggest that they use a range of habitat types including permanent waters for over-wintering and breeding and shallower ponds and streams for feeding (Pope & Matthews, 2001; Pilliod *et al*., 2002; J. Garwood, unpublished data).

We found that high densities of fish were negatively correlated with the abundance of palatable amphibians and were negatively correlated with both length and condition of fish. These results support a growing body of evidence that introduced trout in wilderness lakes frequently may be food-limited. For example, Schindler *et al*. (2001) found that the maximum size and growth rate of trout were strongly negatively correlated with fish density in high-elevation Sierra Nevada lakes. By reducing or selectively eliminating stocking in high-elevation lakes, the resulting habitat improvement may allow for increased co-occurrence of trout and amphibians while simultaneously enhancing the health of the recreational fishery. New research has shown that approximately 70% of stocked lakes in the John Muir Wilderness of the Sierra Nevada contain self-sustaining populations of trout. Lakes with > 2.1 m^2 of spawning habitat, and at elevations < 3520 m, nearly always show evidence of trout reproduction (Armstrong & Knapp, 2004). The assumption that resident trout populations would go extinct without regular stocking is likely incorrect for the majority of high-elevation lakes in the western USA. Instead, supplemental stocking may provide no benefit to the fishery or create above-normal fish densities, resulting in small size and poor condition of fish. Population density is often negatively correlated with individual growth rates in stream and lake-dwelling salmonids (Donald & Anderson, 1982; Bohlin *et al*., 1994; Jenkins *et al*., 1999; Schindler *et al*., 2001). Therefore, if halting stocking results in decreased population density then we may expect to see an increase in fish size (but see Armstrong & Knapp, 2004).

Our results are consistent with a compelling body of evidence that fish drastically alter the aquatic community structure of mountain lakes in the western USA (reviewed by Kats & Ferrer, 2003). The evidence also suggests that elimination of stocking in some areas would likely improve conditions for amphibians (Kats & Ferrer, 2003; Vredenburg, 2004) with minimal impact on the recreational fishery, and may also increase the size and improve the condition of fish.

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