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BIODIVERSITY RESEARCH

Non-native salmonids affect amphibian occupancy at multiple spatial scales

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ABSTRACT

Aim The introduction of non-native species into aquatic environments has been linked with local extinctions and altered distributions of native species. We investigated the effect of non-native salmonids on the occupancy of two native amphibians, the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*), across three spatial scales: water bodies, small catchments and large catchments.

Location Mountain lakes at ≥ 1500 m elevation were surveyed across the northern Rocky Mountains, USA.

Methods We surveyed 2267 water bodies for amphibian occupancy (based on evidence of reproduction) and fish presence between 1986 and 2002 and modelled the probability of amphibian occupancy at each spatial scale in relation to habitat availability and quality and fish presence.

Results After accounting for habitat features, we estimated that *A. macrodactylum* was 2.3 times more likely to breed in fishless water bodies than in water bodies with fish. *Ambystoma macrodactylum* also was more likely to occupy small catchments where none of the water bodies contained fish than in catchments where at least one water body contained fish. However, the probability of salamander occupancy in small catchments was also influenced by habitat availability (i.e. the number of water bodies within a catchment) and suitability of remaining fishless water bodies. We found no relationship between fish presence and salamander occupancy at the large-catchment scale, probably because of increased habitat availability. In contrast to *A. macrodactylum*, we found no relationship between fish presence and *R. luteiventris* occupancy at any scale.

Main conclusions Our results suggest that the negative effects of non-native salmonids can extend beyond the boundaries of individual water bodies and increase *A. macrodactylum* extinction risk at landscape scales. We suspect that niche overlap between non-native fish and *A. macrodactylum* at higher elevations in the northern Rocky Mountains may lead to extinction in catchments with limited suitable habitat.

Keywords

***Ambystoma macrodactylum*, amphibian decline, biological invasions, fish stocking, landscape, mountain lake, *Rana luteiventris*.**

INTRODUCTION

Non-native fishes have contributed to the decline of amphibian populations throughout the world (reviewed by Kats & Ferrer, 2003). Populations of frogs and salamanders are often much smaller or have been extirpated from water bodies where non-native, predatory fish have been introduced compared with neighbouring fishless waters (e.g. Hayes & Jennings, 1986; Bradford, 1989; Braña *et al.*, 1996; Knapp & Matthews, 2000; Bosch *et al.*, 2006; Welsh *et al.*, 2006). This pattern is

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particularly apparent in montane lakes where fish were absent before human intervention. When fish are experimentally removed from these waters bodies, amphibian populations grow rapidly, approaching population sizes found in nearby fishless waters (Hoffman *et al.*, 2004; Vredenburg, 2004; Knapp *et al.*, 2007; Pope, 2008). Predation is the most likely mechanism by which non-native salmonids suppress amphibian populations (Hoffman *et al.*, 2004; Vredenburg, 2004), but competition, disease and predator avoidance may also be factors.

Most fish–amphibian studies have focused only on effects in individual water bodies. Yet the effects of non-native fish may extend beyond the scale of single water bodies and affect amphibian distributions within broader landscapes including areas where some water bodies remained fishless. These landscape-scale effects have only begun to be examined. For example, Pilliod & Peterson (2001) found that non-native salmonids suppressed frog populations in fishless water bodies in catchments where the only suitable overwintering habitats were occupied by fish. Frogs would leave fishless breeding sites in the fall, travel to deep, fish-occupied lakes to overwinter, and few would return the following spring compared to frogs that were able to travel to deep, fishless overwintering sites. Densities of adult and juvenile frogs (i.e. those that had overwintered at least once) in fishless water bodies could be predicted by the proportion of water body surface area in a catchment that contained fish. This and other studies (Bradford *et al.*, 1993; Knapp & Matthews, 2000; Knapp *et al.*, 2003) have suggested that non-native fish might adversely affect amphibian distributions within broader landscapes, but to date, none has examined whether non-native fish may decrease the probability of amphibian occupancy across entire catchments.

There are several ways in which fish might reduce amphibian persistence across a landscape. Fish may decrease the quality of certain critical habitats (e.g. breeding locations, areas with high prey abundance, places to survive winter) through excessive predation or by causing amphibians to avoid them (Resetarits & Wilbur, 1989; Kats & Sih, 1992; Hopey & Petranka, 1994; Pilliod *et al.*, 2002; Vredenburg, 2004). This can result in landscape-scale effects if amphibian populations in fishless water bodies experience predation or other negative fish-effects when individuals temporarily or seasonally move into neighbouring water bodies with fish (Pilliod *et al.*, 2002). Introduced fish may facilitate other amphibian predators, such as garter snakes, resulting in increased predation throughout a catchment (Pope *et al.*, 2008). If remaining fishless water bodies provide only marginal habitat for amphibians, then populations may be small and prone to extinction (Gilpin & Soule, 1986). Fish in streams or intervening lakes may interfere with animals' ability to travel among critical resources in a landscape, isolate populations in remaining fishless waters, or prevent recolonization (Bradford *et al.*, 1993; Knapp *et al.*, 2003). Thus, amphibian extinction risk would likely increase across the landscape in the presence of non-native fish (Sjogren, 1991).

The goal of this study was to investigate whether 50–100 years of stocking non-native predatory fish into high-elevation waters might affect amphibian distributions at multiple spatial scales and not just in the water bodies in which they were stocked. We compiled multiple original data sets from across the northern Rocky Mountains to test three hypotheses related to occupancy of the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*). First, we hypothesized that, in congruence with previous studies, these amphibians are less likely to occupy water bodies containing salmonids compared to fishless water bodies. Second, we hypothesized that these amphibians are less likely to occupy catchments where at least one water body contains fish compared with catchments that are devoid of fish. Third, given that the second hypothesis was supported, we hypothesized that the absence of amphibians from catchments with fish was a function of one of the following conditions: (1) amphibians were absent from the catchments before fish were introduced, (2) fish occupy all water bodies suitable for amphibians or (3) some remaining fishless habitats are suitable for amphibians, but fish increase amphibian extinction risk through various indirect processes. Catchments devoid of non-native fish were considered 'reference' catchments and allowed us to better understand amphibian habitat associations prior to fish introductions and whether fishless water bodies in catchments with fish provided suitable habitat for amphibians. Although we were not able to directly address all of these alternative hypotheses (e.g. there are no data on amphibian distributions prior to fish introductions), we examined the weight of evidence for each given the available data.

METHODS

Study area

The data for this study came from 10 mountain lake studies from 16 US National Forests, Glacier National Park and a few other private, state and federal lands across the northern Rocky Mountains (Fig. 1). The study area spanned western Montana (west of the Little Belt Mountains), central and northern Idaho (north of the Snake River), and eastern Oregon (Blue and Wallowa mountain ranges). Most, but not all, study catchments were selected randomly. Water bodies were defined as any lentic habitat > 0.1 ha (range 0.1–20 ha). We chose lakes and ponds ≥ 1500 m elevation to focus the analysis primarily on those water bodies that were historically fishless before salmonids were stocked. This is nearly twice the elevation cut-off used by Bahls (1992) to estimate that 95% of lakes above 800 m were historically fishless in 11 western states prior to the initiation of recreational fish stocking programmes in the early 1900s. Thus, we are confident that most lakes in our study were historically fishless prior to the initiation of stocking programmes. However, a few beaver pond complexes along riverine wetlands and a few low-gradient catchments in Montana might have had native bull trout (*Salvelinus confluentus*) and westslope

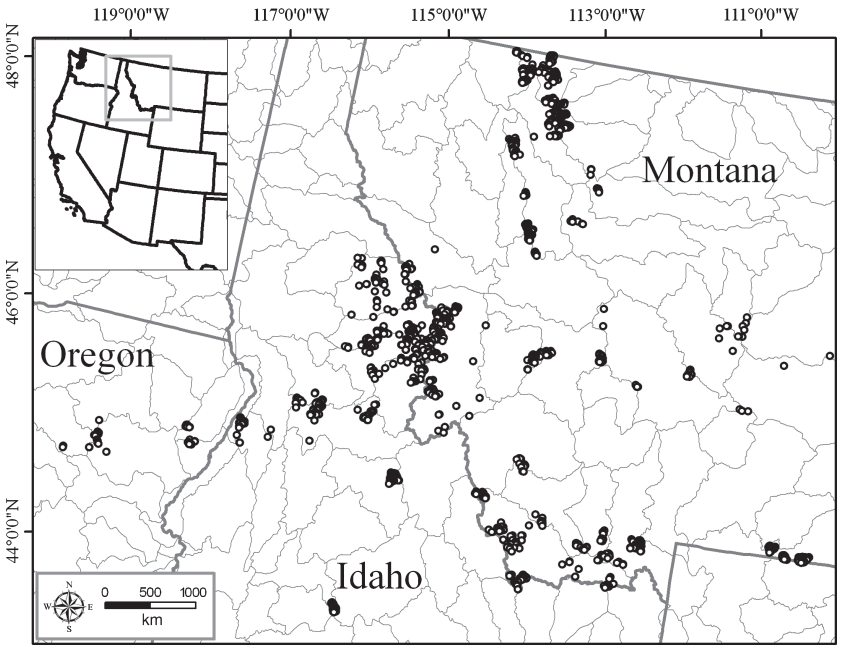

Figure 1 Location of water bodies surveyed in Idaho, Montana and Oregon between 1986 and 2002. Major sub-basins are shown for perspective.

cutthroat trout (*Oncorhynchus clarki*). In all, these represent < 1% of all water bodies sampled. Therefore, we considered the high-elevation water bodies used in this study as locations where amphibians likely had not been exposed to fish since post-glacial colonization, making them appropriate locations to understand the effects of non-native fish on amphibian decline and extinction risk.

Target species

Ambystoma macrodactylum and *R. luteiventris* are the two most common amphibians in the region. Both species respond to predatory fishes where they co-occur with them (Tyler *et al.*, 1998a; Pilliod & Peterson, 2001; Bull & Marx, 2002; Welsh *et al.*, 2006; Pearson & Goater, 2008), but differences in life history characteristics between *A. macrodactylum* and *R. luteiventris* could result in different sensitivities to predatory fish. Both amphibians breed in lakes and ponds ranging from sea level to nearly 3000-m elevation. Above 1500 m, both species deposit eggs from May to July and embryos hatch in 7–21 days (Pilliod & Fronzuto, 2005; Reaser & Pilliod, 2005). *Ambystoma macrodactylum* larvae feed on benthic and water column invertebrates and reach metamorphosis in 2 months to 3 years depending on depth, temperature and elevation (Pilliod & Fronzuto, 2005). In water bodies with fish, salamander larvae hide in protective cover to avoid predation, potentially resulting in reduced growth rates (Tyler *et al.*, 1998b). Adults and post-metamorphic juveniles live and hibernate terrestrially. Larvae of *R. luteiventris* typically feed on filamentous algae and other types of periphyton in the shallow margins of lakes and ponds and thus may be less exposed to predatory fish. Furthermore, *R. luteiventris* tadpoles metamorphose in 30–60 days and do not overwinter (Reaser & Pilliod, 2005). Recently metamorphosed, juvenile (1–3 years old) and adult frogs overwinter in water bodies that do not freeze to the bottom and have adequate dissolved oxygen (Bull & Hayes, 2002). These deeper water bodies are typically where introduced salmonids now occur (Knapp & Matthews, 2000; Pilliod & Peterson, 2001; Knapp, 2005).

Amphibian surveys

We delineated catchments using the Pfafstetter Coding System (Verdin & Verdin, 1999) in ArcGIS 9.0 (ESRI, Redlands, CA, USA). The Pfafstetter Coding System is a hierarchical classification of catchment boundaries on the basis of topology of land surface, especially junctions along a river network (Verdin & Verdin, 1999; Poppenga & Worstell, 2008). Higher levels represent ever-finer tessellations of the land surface into smaller catchments. We subdivided our landscape into large and small catchments (Fig. 2). Large catchments that were not subdivided into nested smaller catchments by the Pfafstetter Coding System were assigned to either the large-catchment or small-catchment data set to avoid the analytical issues of individual catchments appearing in both analyses. To determine which undivided catchments would be included in each analysis, we assigned undivided catchments as either 'small' or 'large' on the basis of its area. Catchments larger than the area of the smallest large catchment that was subdivided were included in the large-catchment analyses and catchments that were smaller than the area of the smallest large catchment that was subdivided were included in the small-catchment analyses.

We are confident that nearly all water bodies were searched within small catchments, but less confident that complete inventories were successful for large catchments because of their large extent and rugged topography. In most cases, water bodies were first identified through the examination of National Wetlands Inventory maps, aerial photographs and

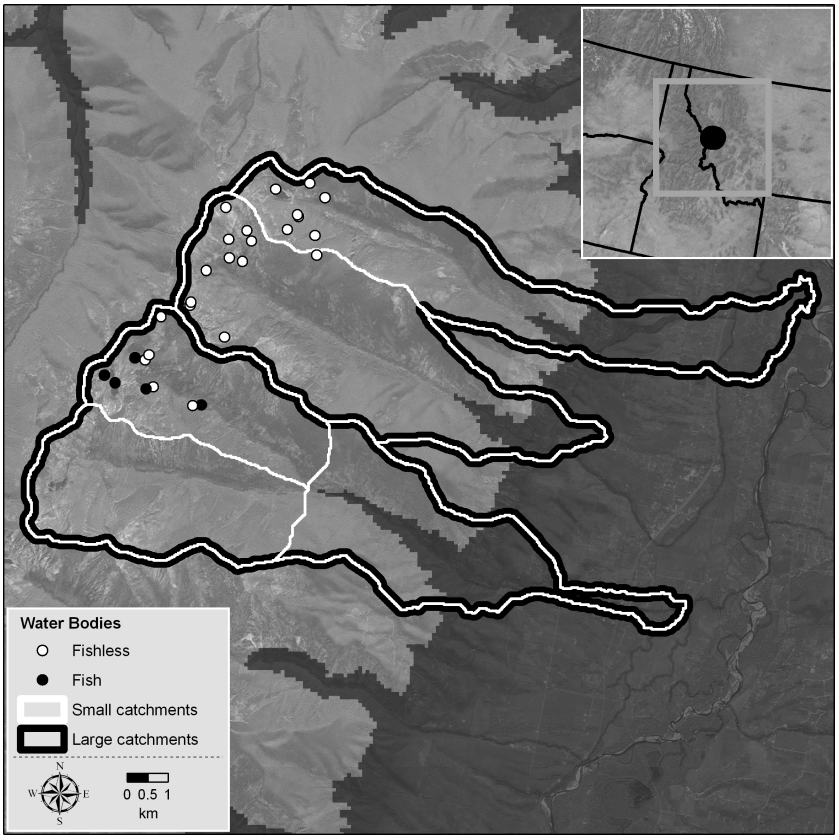

Figure 2 Example of small catchments nested within large catchments. Water bodies are indicated as with fish (fill circles) and without fish (open circles). The light grey background represents the proportion of catchments >1500 m elevation. The area of catchments <1500 m elevation (dark grey) were excluded from this study.

topographic maps prior to field visits. All potential wetland areas were searched in the field, and water bodies discovered incidentally were included in the study set. Any catchment that was not comprehensively surveyed was excluded from catchment-scale analyses. Water bodies that occurred in catchments where no amphibians (any life stage) or fish were detected were excluded from water body-scale analyses.

We defined occupancy of *A. macrodactylum* and *R. luteiventris* at a water body on the basis of reproduction (i.e. observing eggs or larvae) during visual encounter surveys (Crump & Scott, 1994; Thoms *et al.*, 1997). Surveys were conducted while amphibian larvae were expected to be present, usually from ice-out (June in most locations) through early September. Of 2267 water bodies surveyed, 81% were surveyed once, 15% were surveyed 2–5 times and 4% were surveyed > 5 times. A species was considered present in a water body if reproduction was detected during any survey and present in a catchment if reproduction was detected in any water body in the catchment during any survey. Although both species have conspicuous eggs and larvae, particularly in clear, oligotrophic mountain lakes, we recognize that occupancy determination could be affected by detection rates and breeding dynamics where species do not breed every year. We evaluated detection probabilities for each species by analysing a subset of our data where multiple visits were conducted within a year and over multiple years using the program PRESENCE. We used observed species occupancy, instead of estimated occupancy, in the final analyses.

Fish surveys

The occurrence of fish in a water body was determined by overnight gill net sets or visual observation and confirmed with state stocking records and fishery surveys. We hereafter use the capitalized word FISH to refer to the variable that denotes whether fish were present or not detected in a water body. We used program PRESENCE to estimate the detectability of fish at a subset of lakes with multiple visits to provide a measure of certainty.

Habitat descriptions

We recorded standardized habitat characteristics at each water body and refer to habitat variables used in models with capitalized abbreviations. During site visits, we used 1:24,000 US Geological Survey topographic maps or global positioning systems to record geographic coordinates (Universal Transverse Mercator, UTM) and elevation (ELEV) at the outlet of each water body. Site coordinates were converted to a common system to avoid problems with different datums and zones. We estimated maximum water depth at each water body (DEPTH) as 0–1, 1–2 and > 2 m using sonar, plumb-lines or visual inspection. Primary substrate of the littoral zone (SUBS) was defined as fine (organic, silt and sand) or coarse (gravel, cobble and boulder). We visually estimated the percentage of shoreline perimeter with emergent vegetation (VEG) as 0–5%, 6–25%, 26–50% and > 50%. Water temperature was not

measured directly because the diel and seasonal variability in water temperature is impossible to capture with spot measurements during 1–2 site visits that last only a few hours. As a surrogate for water temperature, we calculated the average solar radiation (SUN) striking one point in each water body using a modified solar radiation index model in a GIS (Kumar *et al.*, 1997). Solar index values were calculated as a brightness value (0–255) averaged across four times (10:00, 12:00, 14:00 and 16:00) on 4 days (6/15, 7/15, 8/15 and 9/15). This model did not adjust for shading from trees, but did account for shading from surrounding mountain ridges. Habitat variables collected by different investigators in different studies were recoded into common units or categories.

Data analysis

We analysed data at three nested spatial scales: water body, small catchments and large catchments. Analyses were restricted to water bodies and catchments within the range of the species; *A. macrodactylum* does not occur in the south-eastern part of the study area (Stebbins, 2003), so sample sizes for this species were slightly smaller.

Water bodies that support fish are often different than those without fish, which can confound analyses of co-occurrence. To address this discrepancy, we included a variable for fish presence into each of four habitat models, resulting in eight competing models. The habitat models were developed *a priori* using information on the habitat associations of these species from the literature and expert opinion (Anderson, 1967; Munger *et al.*, 1998; Tyler *et al.*, 1998a; Adams *et al.*, 2001; Bull & Marx, 2002; Murphy, 2002; Pilliod *et al.*, 2002; Palen *et al.*, 2005; Pearl *et al.*, 2007).

Water body models

Water body models related the local habitat characteristics of each water body to the probability of amphibian occupancy (i.e. a breeding population). We included a spatial location term for each water body in all water body models to account for expected autocorrelation in habitat features and the distribution of populations. This location variable was calculated as a smooth surface of UTM easting and northing values using a loess (locally weighted polynomial regression) smoother because of its advantages for spatially correlated data (Hobert *et al.*, 1997; Knapp *et al.*, 2003). Loess fits the data using weighted least squares, giving more weight to data nearest geographically to the point whose response is being estimated and less weight to data further away. We used a span window of 0.5 to define how much of the data was used to fit each local polynomial (Hastie & Tibshirani, 1990).

We examined eight water body models for each species. Habitat and Habitat + Fish models represented the global models and included all habitat variables. Temperature and Temperature + Fish models were hypothesized to be good predictors of *A. macrodactylum* and *R. luteiventris* breeding because the duration of warm water temperatures is important for water body productivity and growth rates for larval life stages (Smith-Gill & Berven, 1979). These models also included ELEV because of its importance to local climate and the distribution of multiple amphibian species across the West (Adams *et al.*, 2005). Cover and Cover + Fish models were hypothesized to be important to the breeding success of both species because they use emergent vegetation for oviposition (Bull & Marx, 2002; Palen *et al.*, 2005; Pearl *et al.*, 2007). In the Cover + Fish model, we included an interaction of vegetation (VEG) and fish presence (FISH) because vulnerable aquatic life stages can avoid predation when sufficient cover is available (Tyler *et al.*, 1998b). The Depth and Depth + Fish models examined the effect of habitat differences between shallow ponds and deep lakes. We included an interaction of ELEV and DEPTH in the *A. macrodactylum* models because the maximum water depth requirements for successful overwintering of larvae increase with elevation (Anderson, 1967). The ELEV by DEPTH interaction was not included in *R. luteiventris* models because its larvae do not overwinter and metamorphosed frogs can travel terrestrially to other nearby water bodies (Pilliod *et al.*, 2002).

Catchment models

Catchment models examined the relationship between landscape characteristics and amphibian occupancy (i.e. occurrence of at least one breeding population) of a catchment. We examined four pairs of catchment models at each landscape scale: small and large catchments. The presence or absence of fish in at least one water body in a catchment (FISHSTATUS) was added to each model to determine what additional variation could be explained by fish after accounting for landscape characteristics among catchments. The Elevation Model included a predictor variable for the average elevation (aELEV) of the catchment. The Isolation Model included a predictor variable for the average distance to nearest water body within a catchment (aDIST). The Size Model provided a measure of the amount of potential habitat per catchment, including total area of a catchment (AREA) and number of water bodies in a catchment (SITES). The Full Model included all variables. Smaller sample sizes in catchment analyses prohibited us from including a geographic location term in catchment models (i.e. UTM).

We did not expect linear relationships between species occupancy and covariates. Therefore, we used generalized additive models (GAMs) for analyses. GAMs are a nonparametric extension of generalized linear models that use a smoothing function to describe the relationships between predictor and response variables (Cleveland & Devlin, 1988; Hastie & Tibshirani, 1990). A cubic smoothing spline was applied to all continuous variables, except UTM, to allow for a nonparametric fit between predictor and response variables. We used loess smoothing with the UTM variable.

Selection of the best of the candidate models at each spatial scale was determined on the basis of differences in the second-order Akaike information criterion (AICc) and model weights

(w) (Burnham & Anderson, 2002). The best model from the set of models had the lowest AICc value and only models ≤ 2 AIC units from this top model were considered competitive. Model weights represent the probability that a model is the best of those being considered for the dataset (Burnham & Anderson, 2002). Model weights were summed separately for all models that contained fish and compared to those that did not contain fish to use the combined weight of evidence as a tool in determining the importance of fish as a predictor variable (Burnham & Anderson, 2002). We used coefficients from the highest ranked model to graph the effect of fish presence and other habitat and landscape characteristics on amphibian occupancy. The importance of variables was assessed by examining whether the 95% confidence intervals (CI) overlapped zero. Odds ratios for the fish parameter (FISH and FISHSTATUS) were calculated from the best supported model (Hosmer & Lemeshow, 1989). If the 95% confidence limits for odds of detecting amphibian reproduction included 1.0, then fish were considered to have little effect on amphibian presence. We estimated a single variance inflation factor (c) by dividing the goodness-of-fit chi-square statistic of the global model by its degrees of freedom (Burnham & Anderson, 2002). In general, model structure was acceptable and the data were not overdispersed ($\hat{c} \leq 1.3$). All GAMs were conducted in SPLUS 6.1.

Indirect effects of non-native fish on amphibian occupancy

To determine if the presence of non-native fish in at least one water body in a catchment (FISHSTATUS) has an effect on the probability of amphibian occupancy within fishless water bodies (i.e. an indirect effect of fish), we performed nonparametric multiplicative regression (NPMR) analyses for each species (McCune, 2006, 2009). These analyses allowed us to determine (1) the most important water body-level habitat variables (ELEV, SUN, DEPTH, SUBS and VEG) for predicting amphibian occupancy in fishless water bodies, (2) how these variables interact in non-additive, nonlinear ways to influence occupancy and (3) whether FISHSTATUS influences the probability of amphibian occupancy in fishless water bodies after accounting for differences in amphibian habitat quality.

The NPMR analyses were performed using the local mean model with Gaussian weighting functions in HyperNiche 2.06 software (McCune & Mefford, 2009). We assessed model fit using log likelihood ratios (logβ values) to evaluate the improvement of each fitted model over the naïve or null model (i.e. overall species occupancy rate in the data set). We included FISHSTATUS in all models and conducted a free search for all possible combinations of predictor variables and tolerances. Tolerance is the standard deviation of the Gaussian weighting function for a given predictor variable. A variable was included in the final model if its inclusion resulted in a ≥ 10% increase in logβ.

For the best model predicting occupancy of fishless water bodies for each species, we reported average neighbourhood size (N^*; average number of sample units contributing to the estimate of occupancy at each point on the modelled surface), tolerance for each predictor variable (low tolerance indicates that species occupancy is restricted to a narrow portion of the environmental or predictor gradient) and sensitivity for each predictor. Sensitivity is a measure of the relative importance of each predictor in estimating occupancy probability, where a sensitivity of one indicates that, on average, changing the value of the predictor by ± 5% of its range changes the response by an equal magnitude and a sensitivity of zero indicates that changing the predictor does not change the response value (McCune, 2009).

RESULTS

Between 1986 and 2002, we sampled 2267 water bodies for fish and amphibians in 149 large and 315 small catchments (Table 1). Fifteen large and 55 small catchments did not contain fish or amphibians. Small catchments ranged in size from 0.8 to 63.1 km^2 (median 9.3 km^2) and large catchments from 9.6 to 137.4 km^2 (median 27.0 km^2). There was a weak correlation between the size of large catchments and the number of water bodies within the catchment ($r^2 = 0.28$), but no comparable relationship for small catchments ($r^2 = 0.03$).

Fish were detected in 27% (607 of 2267) of the water bodies, 44% of the small catchments (140 of 315) and 60% (89 of 149) of the large catchments (Table 1). Although fish species composition was not recorded in all lakes, the following species were detected and generally agree with state stocking

Table 1 Number of water bodies and catchments sampled relative to fish presence.

		Fish		Amphibians		
Dataset	Spatial scale	Present	Not detected	Present	Not detected	Total
Within range of *Ambystoma macrodactylum*	Number of water bodies	492	1186	523	1155	1678
	Number of small catchments	113	109	126	96	222
	Number of large catchments	76	38	91	23	114
Within range of *Rana luteiventris*	Number of water bodies	607	1660	643	1624	2267
	Number of small catchments	140	175	177	138	315
	Number of large catchments	89	60	111	38	149

records for most areas: westslope and Yellowstone cutthroat trout (*Oncorhynchus clarki lewisi and Oncorhynchus clarki bouvieri*), rainbow trout (*Oncorhynchus mykiss*), golden trout (*Oncorhynchus m. aguabonita*), bull trout (*S. confluentus*), brook trout (*Salvelinus fontinalis*) and arctic grayling (*Thymallus arcticus*). Hybrid trout were also reported. Of the water bodies with fish, 74% were lakes > 2 m deep. Detection rate was 0.89 for water bodies visually surveyed for fish 2–5 times and 1.0 for lakes surveyed visually followed by overnight gillnet sets.

Effects of non-native fish on amphibian occupancy in water bodies

We detected evidence of reproduction (= occupancy) for *A. macrodactylum* at 31% (523 of 1678) and *R. luteiventris* at 28% (643 of 2267) of water bodies sampled (Table 1). The average single visit probability of detection given presence (P) was 0.74 (±0.12 SE) for *A. macrodactylum* and 0.91 (±0.07 SE) for *R. luteiventris* at a subset of water bodies where multiple visits were conducted within the same year.

Amphibian occupancy relative to fish presence in a water body varied by amphibian species. The estimated effect of fish presence on *A. macrodactylum* occupancy was negative in individual water bodies (Fig. 3a). *Ambystoma macrodactylum* was 2.3 (odds ratio 95% CI = 1.39–3.87) times more likely to be detected in fishless water bodies than in water bodies with fish. Habitat + Fish was the top-ranked model and received 95.9% of model weight, whereas the Habitat Model received none (Table 2). *Rana luteiventris* occupancy was unrelated to fish presence (Fig. 4a). The Habitat + Fish Model received the most support (w = 0.819), but frogs were just as likely to be detected in water bodies with fish than in fishless water bodies (Table 3, odds ratio = 0.78, 95% CI = 0.45–1.35).

Water body habitat characteristics were also important predictors of amphibian occupancy. Both species were more likely to occur in water bodies that were at lower elevations (i.e. below 2400 m), had more solar exposure (e.g. not in north-facing cirques), had predominantly silt, mud or sand substrates in the littoral zone and had at least 26% shoreline with emergent vegetation (Figs 3 & 4). *Ambystoma macrodactylum* had a weak negative association with water bodies > 2 m deep (Fig. 3d). *Rana luteiventris* was most likely to breed in water bodies 1–2 m deep (Fig. 4d) and was strongly associated with shoreline vegetation (Fig. 4f).

Effects of non-native fish on amphibian occupancy in catchments

The presence of fish in at least one water body in small catchments (i.e. catchment-level fish presence or FISHSTATUS) was negatively associated with the probability of *A. macrodactylum* occupancy in a catchment (Table 4, Fig. 5a). The Size + Fish status models were the top-ranked models for *A. macrodactylum* at the small catchment scale (w = 0.708; Table 4). Salamanders were more likely to occupy small catchments with > 3 water bodies and > 12 km^2 in area (Fig. 5b,c). The probability of salamander occupancy in small

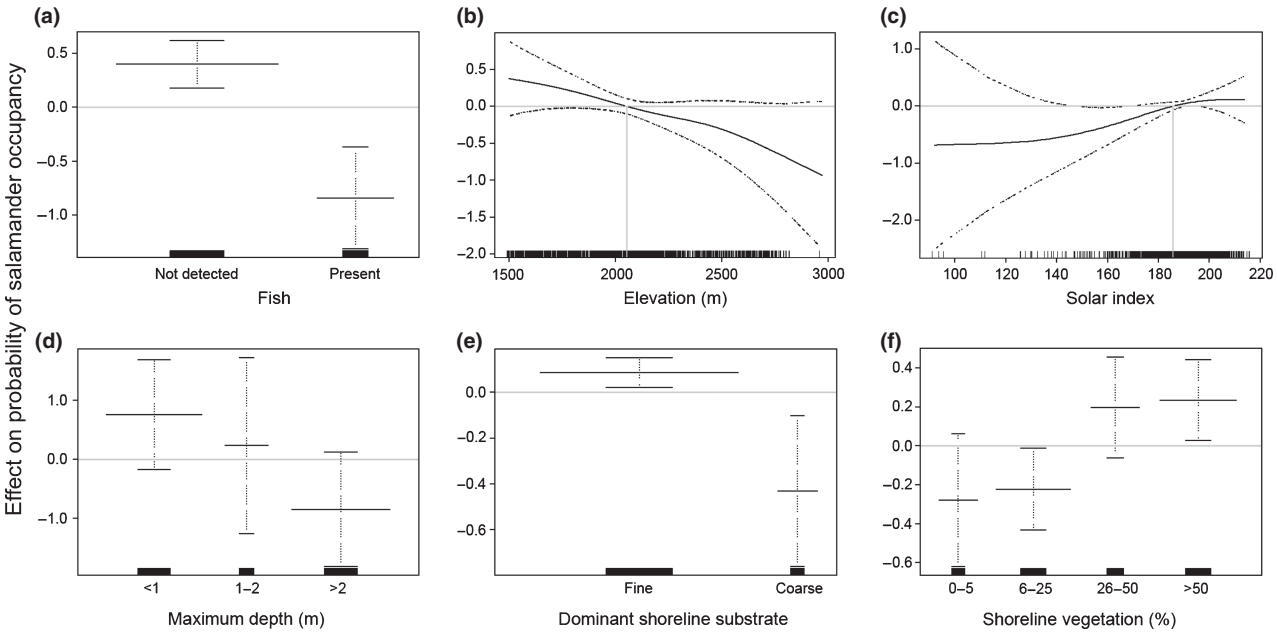

Figure 3 (a–f) Estimated effect of habitat variables on probability of *Ambystoma macrodactylum* occupancy (breeding) in 1536 water bodies in the northern Rocky Mountains. The dotted lines or error bars in each plot are approximate 95% pointwise confidence intervals (CI). Hatch marks at the bottom of each graph represent data points. Significance is indicated when estimated 95% CIs fall completely above or below the no-effect line at zero (light grey horizontal line). A vertical light grey line drawn down to the x-axis indicates an approximate threshold in the predictor variable where effects on occupancy transition from positive to negative or *vice versa*.

Table 2 Models predicting *Ambystoma macrodactylum* occupancy in water bodies.

Model name	Model parameters	k	Deviance	ΔAICc	W_i
Habitat + Fish	UTM + ELEV + SUN + DEPTH + ELEV:DEPTH + SUBS + VEG + FISH + VEG:FISH	24	1671.4	0.00	0.959
Temperature + Fish	UTM + ELEV + SUN + DEPTH + ELEV:DEPTH + FISH	17	1692.8	6.92	0.030
Depth + Fish	UTM + DEPTH + FISH	15	1698.9	9.02	0.011
Cover + Fish	UTM + SUBS + VEG + FISH + VEG:FISH	16	1728.0	40.16	0.000
Habitat	UTM + ELEV + SUN + DEPTH + ELEV:DEPTH + SUBS + VEG	20	1814.9	135.28	0.000
Cover	UTM + SUBS + VEG	12	1839.2	143.18	0.000
Depth	UTM + DEPTH	14	1840.3	148.43	0.000
Temperature	UTM + ELEV + SUN + DEPTH + ELEV:DEPTH	16	1837.1	149.27	0.000

Model description: n = 1536 water bodies, null deviance = 1970.27, $\hat{c}$ = 1.11.
AICc, Akaike information criterion; UTM, UTM easting and northing as a smooth surface; DEPTH, maximum water depth; ELEV, elevation; ELEV:DEPTH, interaction of DEPTH and ELEV; SUBS, dominant substrate in the water body; VEG, percentage of shoreline with emergent vegetation; SUN, solar radiation index; FISH, presence of non-native salmonids.

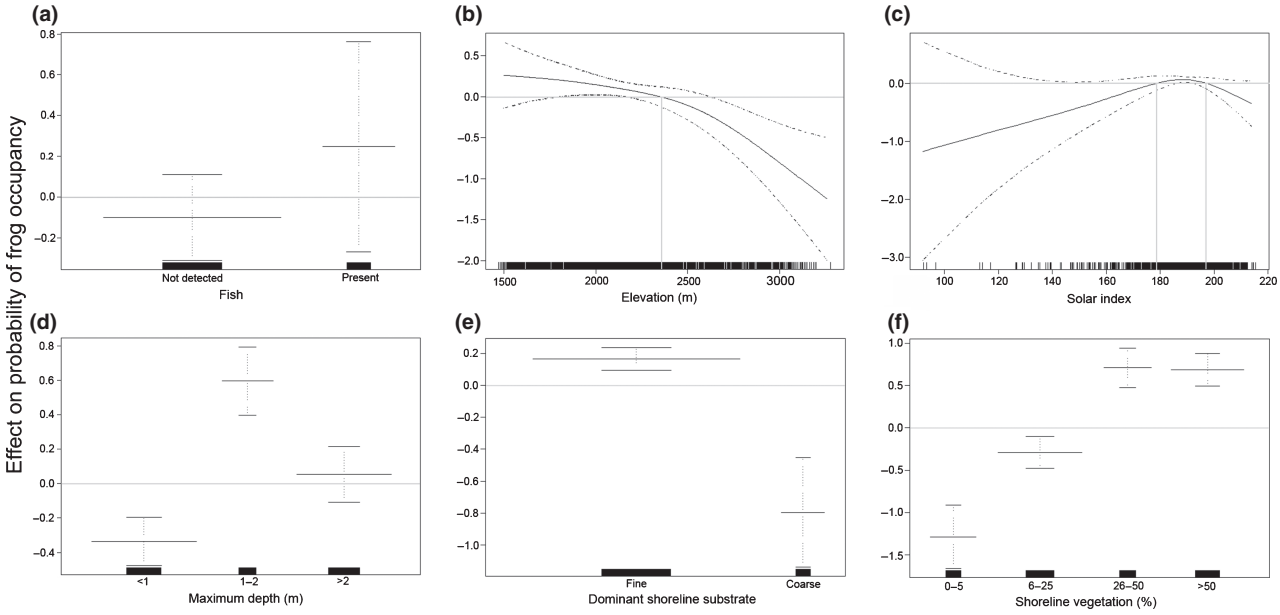

Figure 4 (a–f) Estimated effect of habitat variables on probability of *Rana luteiventris* occupancy (breeding) in 2093 water bodies in the northern Rocky Mountains. The dotted lines or error bars in each plot are approximate 95% pointwise confidence intervals (CI). Hatch marks at the bottom of each graph represent data points. Significance is indicated when estimated 95% CIs fall completely above or below the no-effect line at zero (light grey horizontal line). A vertical light grey line drawn down to the x-axis indicates an approximate threshold in the predictor variable where effects on occupancy transition from positive to negative or *vice versa*.

catchments increased logarithmically with the number of water bodies in a catchment (Fig. 6; $y = 0.1299\text{Ln}(x) + 0.4988$ for fishless catchments [$r^2 = 0.67$] and $y = 0.1507\text{Ln}(x) + 0.3275$ for catchments with fish [$r^2 = 0.71$]). There was model uncertainty for *A. macrodactylum* at the large-catchment scale and no influence of FISHSTATUS at this scale (Table 5; Table S1 in Supporting Information).

In contrast, the probability of *R. luteiventris* occupancy in small catchments was not associated with FISHSTATUS (Table S2, Fig. S2). The Size Model was the top-ranked model for *R. luteiventris* at the small-catchment scale (Table 5). The Size + Fish and Size models were both competitive models predicting the occupancy of *R. luteiventris* in large catchments, and FISHSTATUS was positively associated with frog occupancy at this scale (Table S3, Fig. S3).

Indirect effects of non-native fish on amphibian occupancy

FISHSTATUS, ELEV and DEPTH were the best predictors of *A. macrodactylum* occupancy in fishless water bodies (Table 6). This model represented a 20% increase in logβ over the model containing only FISHSTATUS and ELEV. The next best three factor model had a logβ 3% lower than the selected

Table 3 Models predicting *Rana luteiventris* occupancy in water bodies.

Model name	Model parameters	k	Deviance	ΔAICc	W_i
Habitat + Fish	UTM + ELEV + SUN + DEPTH + SUBS + VEG + FISH + VEG:FISH	21	2095.7	0.00	0.819
Habitat	UTM + ELEV + SUN + DEPTH + SUBS + VEG	17	2106.9	3.02	0.180
Cover + Fish	UTM + SUBS + VEG + FISH + VEG:FISH	17	2118.9	14.99	0.000
Cover	UTM + SUBS + VEG	13	2129.3	17.30	0.000
Temperature + Fish	UTM + ELEV + SUN + DEPTH + FISH	14	2289.3	179.33	0.000
Temperature	UTM + ELEV + SUN + DEPTH	13	2302.6	190.63	0.000
Depth + Fish	UTM + DEPTH + FISH	10	2364.1	245.97	0.000
Depth	UTM + DEPTH	9	2370.5	250.40	0.000

Model description: n = 2093 water bodies, null deviance = 2582.15, $\hat{c}$ = 1.01.
AICc, Akaike information criterion; UTM, UTM easting and northing as a smooth surface; DEPTH, maximum water depth; ELEV, elevation; SUBS, dominant substrate in the water body; VEG, percentage of shoreline with emergent vegetation; SUN, solar radiation index; FISH, presence of non-native salmonids.

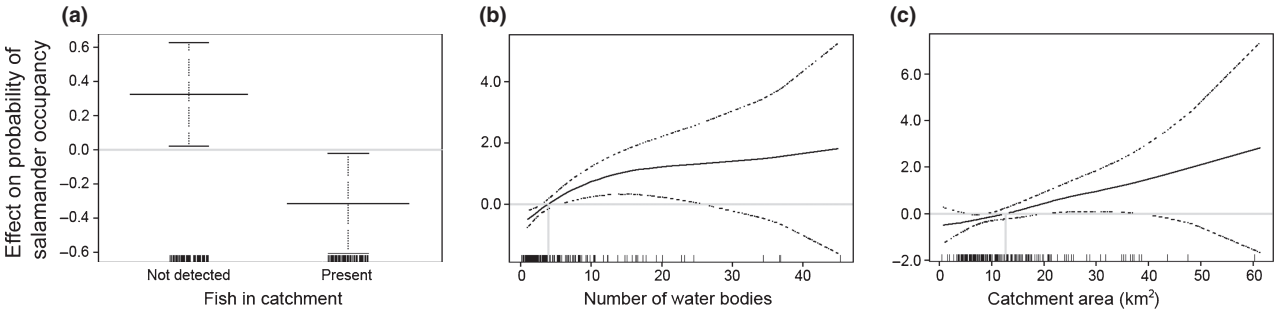

Figure 5 (a–c) Estimated effect of landscape variables on probability of *Ambystoma macrodactylum* breeding occurrence in 222 small catchments in the northern Rocky Mountains. The dotted lines or error bars in each plot are approximate 95% pointwise confidence intervals (CI). Hatch marks at the bottom of each graph represent data points. Significance is indicated when estimated 95% CIs fall completely above or below the no-effect line at zero (light grey horizontal line). A vertical light grey line drawn down to the x-axis indicates an approximate threshold in the predictor variable where effects on occurrence transition from positive to negative or *vice versa*.

model. The probability of *A. macrodactylum* occupancy in fishless water bodies was best predicted by a nonlinear interaction between ELEV and DEPTH (Fig. 7), with ELEV having a greater influence than DEPTH (Table 6; sensitivity 0.79 vs. 0.13). The highest probability of occupancy occurred between 1900 and 2400 m elevation in water bodies > 2 m deep and decreased in water bodies 1–2 m and < 1 m deep. For nearly all comparable combinations of ELEV and DEPTH, the probability of salamander occupancy in fishless water bodies was greater in fishless catchments than in catchments where at least one water body contained fish. Fish have a greater indirect effect on salamander occupancy at higher elevations (e.g. 2400–2500 m) in shallower water bodies. At lower elevations (e.g. 1500–1600 m), FISHSTATUS and DEPTH had little effect on the probability of salamander occupancy in fishless water bodies (Fig. 7).

The best model predicting the probability of *R. luteiventris* occupancy in fishless water bodies consisted of FISHSTATUS, VEG and DEPTH (Table 6). Adding DEPTH to the best two factor model (FISHSTATUS and VEG) increased logβ by 25%, whereas the next best model increased logβ by only 2% over the final model. *Rana luteiventris* occupancy in fishless water bodies was more dependent on VEG than on DEPTH (Table 6; sensitivity 0.38 vs. 0.03) and increased as VEG increased (Fig. 8). When VEG was < 25%, frog occupancy was higher in water bodies of intermediate depth and occupancy rates were low for both shallow and deep water bodies. However, when VEG was > 25%, occupancy rates were highest for water bodies > 1 m deep. In these deeper (> 1 m) water bodies with > 25% shoreline vegetation, the probability of frog occupancy was only slightly higher in catchments where fish were not detected than in catchments where fish were present. In catchments where fish were not detected, frog occupancy increased greatly in deep (> 2 m) water bodies as VEG increased beyond 25%. This increase was not observed in fishless water bodies in catchments with fish. In shallow (< 1 m) water bodies, the probability of frog occupancy increased with increasing VEG independent of whether fish were present within the catchment (Fig. 8).

DISCUSSION

This study adds to a growing body of evidence that the presence of non-native fish may be causing extirpations of

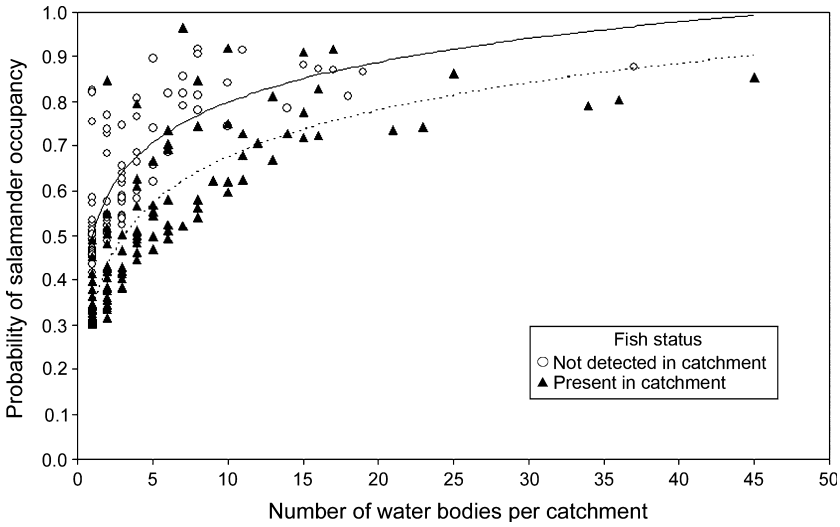

Figure 6 Generalized additive modelled probability of *Ambystoma macrodactylum* occupancy in small catchments as a function of the number of water bodies in a catchment (SITES) for catchments with and without non-native fish (FISHSTATUS). Lines represent logarithmic function fit to the data in catchments with fish (dashed line) and catchments where fish were not detected (solid line).

Table 4 Models predicting *Ambystoma macrodactylum* occupancy in small catchments.

Model Name	Model parameters	k	Deviance	ΔAICc	W_i
Size + Fish status	SITES + AREA + FISHSTATUS	5	273.6	0.00	0.708
Size	SITES + AREA	4	278.7	2.93	0.164
Full + Fish status	SITES + AREA + aELEV + aDIST + FISHSTATUS	10	265.9	3.86	0.103
Ful	SITES + AREA + aELEV + aDIST	9	270.8	6.64	0.026
Isolation	aDIST	3	292.8	16.02	0.000
Isolation + Fish status	aDIST + FISHSTATUS	4	291.4	16.68	0.000
Elevation	aELEV	2	302.8	22.96	0.000
Elevation + Fish status	aELEV + FISHSTATUS	3	301.4	23.64	0.000

Model description: n = 222 small catchments, null deviance = 303.69, $\hat{c}$ = 1.27.
AICc, Akaike information criterion; SITES, number of water bodies per catchment; AREA, size of the catchment; aELEV, average elevation of water bodies in catchment; aDIST, average distance to nearest water body within catchment; FISHSTATUS, presence of non-native salmonids in at least one water body per catchment.

Table 5 The best models selected from each set of models examined at each spatial scale for *Ambystoma macrodactylum* and *Rana luteiventris* occupancy. See Tables 2 and 3 for set of water body models and Table 4 and online supplementary material (Tables S1–S3) for full set of models at each catchment scale.

Species	Spatial scale	Number of models	Sample size	Top model at spatial scale	Σw (models with FISH)	Σw (models without FISH)	Effect of fish
A. macrodactylum	Water body	8	1536	Habitat + Fish	1.000	0.000	Negative
	Small catchment	8	222	Size + Fish status	0.811	0.189	Negative
	Large catchment	8	114	Size	0.250	0.750	Neutral
R. luteiventris	Water body	8	2093	Habitat + Fish	0.819	0.181	Neutral
	Small catchment	8	315	Size	0.378	0.622	Neutral
	Large catchment	8	149	Size + Fish status	0.953	0.047	Positive

amphibians in water bodies where fish have been introduced. More importantly, this study provides evidence that the introduction of non-native fish into mountain environments may also be extirpating some amphibians from entire catchments where fishless habitats still remain. These findings have important conservation implications because they indicate that non-native salmonids could negatively affect the distribution of some native amphibians across fairly large landscapes, possibly leading to range contractions.

Similar to other studies, we found *A. macrodactylum* was much less likely to breed in a water body if fish were present (Bahls, 1990; Tyler *et al.*, 1998a; Pilliod & Peterson, 2001; Bull

Table 6 Nonparametric multiplicative regression models predicting amphibian occupancy in fishless water bodies, based on water body habitat variables and whether fish were present in at least one water body in the surrounding catchment.

Response	*n* water bodies	**n* variables in final model	logβ	†*N**	‡Predictor 1	Predictor 2	§Tolerence	¶Sensitivity	Predictor 3	Tolerence	Sensitivity
Salamander occupancy	966	3	16.4	74	FISHSTATUS	ELEV	131 (10%)	0.79	DEPTH	0.8 (40%)	0.13
Frog occupancy	1410	3	42.1	91	FISHSTATUS	VEG	0.45 (15%)	0.38	DEPTH	0.3 (15%)	0.03

ELEV, elevation of water body (m); DEPTH, maximum water body depth (< 1, 1–2, > 2 m); VEG, percentage of shoreline with emergent vegetation (0–5%, 6–25%, 26–50%, > 50%); FISHSTATUS, presence of non-native salmonids in at least one water body in catchment (0, 1).

*The number of predictors was determined by adding a variable if doing so increased logβ by ≥ 10%.

†*N** is the average neighbourhood size, or the average number of water bodies contributing to estimates at each point on the response surface.

‡FISHSTATUS is a categorical predictor; therefore, it has no tolerance or sensitivity estimates.

§Lower tolerance values for predictors indicate a more restricted occupancy range relative to that predictor. The tolerance values are in same units as the original variable.

¶High sensitivity values indicate greater importance of a predictor relative to other predictors in the model.

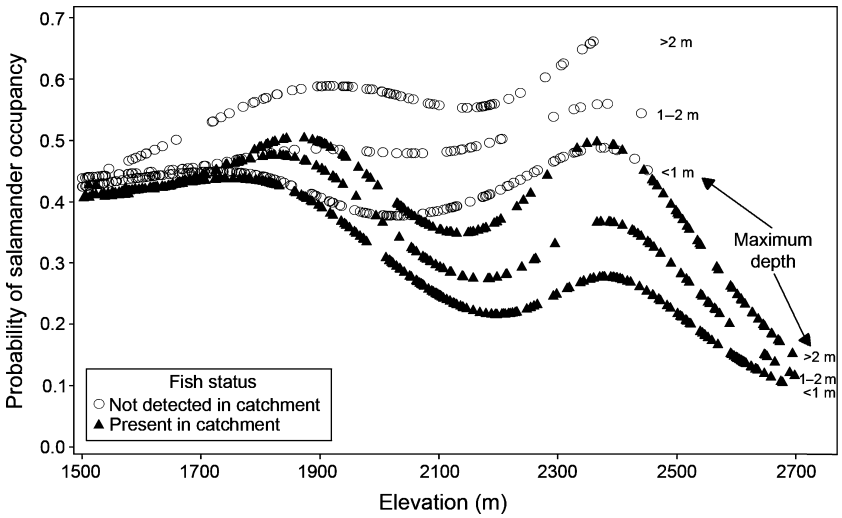

Figure 7 Nonparametric multiplicative regression modelled probability of *Ambystoma macrodactylum* occupancy in 966 fishless water bodies as a function of elevation. Separate probabilities are given for each combination of catchment fish status (FISHSTATUS or fish presence in a catchment) and maximum depth of the water body (DEPTH) resulting in six separate data series.

& Marx, 2002; Welsh *et al.*, 2006; Pearson & Goater, 2008). The habitat requirements of fish and *A. macrodactylum* overlap at high elevations in the northern Rocky Mountains (Howard & Wallace, 1985; Pilliod & Peterson, 2001; Pearson & Goater, 2008). In particular, fish and salamander larvae both require deeper water bodies (> 2 m) at higher elevations to survive winter. We speculate that, over time, this niche overlap has resulted in extinction of *A. macrodactylum* in deeper water bodies as fish predominantly occupy water bodies > 2 m deep and are known predators of this species (Tyler *et al.*, 1998b; Pearson & Goater, 2009). The confounding effects of fish and water body depth made it difficult to understand the importance of depth for *A. macrodactylum* at the water body scale, but the NPMR analyses of fishless water bodies (see Fig. 7) clearly show that the probability of salamander occupancy is highest in the deepest water bodies when fish are absent. The few salamander populations that are able to persist with fish may rely on cover provided by thick emergent vegetation along shorelines and submerged boulders and cobble (D.S. Pilliod, P.F. Bahls, unpublished data, Tyler *et al.*, 1998b; Pearson & Goater, 2009) or fish populations might be small.

Decreased probability of *A. macrodactylum* occupancy in small catchments where at least one water body contained fish appeared to be influenced by some interaction of available habitat and habitat suitability of remaining fishless water bodies. Catchments with fewer water bodies had lower probability of occupancy, especially when fish were present in the catchment. As hypothesized (alternative hypothesis a), this could be the result of historically low salamander occupancy in catchments now occupied by fish. Given the widespread distribution of salamanders across the northern Rocky Mountains and the distribution of these particular catchments (i.e. not at the very edge of the species range), we found no evidence to support this hypothesis. Alternatively (b), this landscape-level effect of fish presence could result if fish effectively eliminated all potential habitats for salamanders within a catchment (i.e. a direct water body-level effect manifested as a catchment-level effect). This would occur if remaining fishless habitats in catchments with fish were

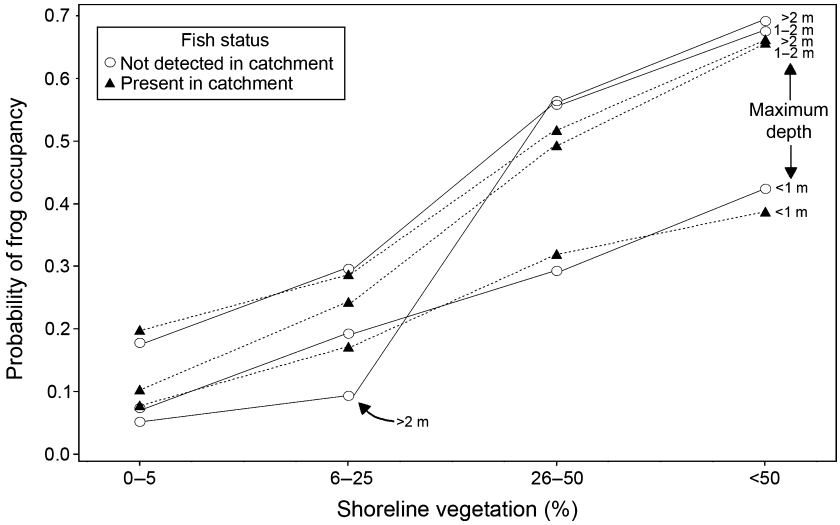

Figure 8 Nonparametric multiplicative regression modelled probability of *Rana luteiventris* occupancy in fishless water bodies as a function of shoreline vegetation (VEG). Separate probabilities are given for each combination of catchment fish status (FISHSTATUS or fish presence in a catchment) and maximum depth of the water body (DEPTH). Each of these six combinations is connected by lines for clarity. Solid lines indicate series where fish were not detected in catchments and dashed lines indicate series where fish were present in catchments.

unsuitable for salamanders. Our analyses of *A. macrodactylum* occupancy in fishless water bodies in catchments with and without fish indicated that suitable fishless habitats were available in fish-occupied catchments and thus this hypothesis also was not supported.

We found the strongest support for the third alternative hypothesis (c) that many remaining fishless habitats are suitable for amphibians, but the presence of fish in a catchment somehow increases extinction risk for amphibians through various indirect processes. In our analyses of water bodies in fishless catchments, we found that *A. macrodactylum* was most likely to occupy deep water bodies (> 2 m deep) at elevations ranging from 1900 to 2400 m. One could consider this a reference condition, because fish had never occupied these catchments. However, when we examined the probability of *A. macrodactylum* occupancy across this 'preferred' range of habitat characteristics in fishless water bodies in catchments with fish, we found that the probability of occupancy was lower than in our fishless reference catchments. The cause of this decreased probability of occupancy is unknown, but may be the result of indirect factors (e.g. isolation, disrupted metapopulation dynamics). Because catchments occupied by fish offer less available habitat compared with fishless catchments, fish stocking may act as a form of both habitat loss and functional isolation for *A. macrodactylum*, increasing extinction risk at the catchment scale. This combination of population extirpation in water bodies with fish followed by the increased isolation of remaining populations in fishless water bodies has been suggested previously as a possible cause of documented disappearances of amphibians from fishless water bodies (Bradford *et al.*, 1993; Knapp *et al.*, 2003). Greater distances between extant populations decrease the likelihood of recolonization in the event of local extinction. This effect is diminished as the number of water bodies in a catchment increases, a pattern observed for *A. macrodactylum* in small catchments and the likely explanation for the lack of a negative effect of fish status on *A. macrodactylum* in large catchments. Even in California where extensive declines of yellow-legged frogs (*Rana muscosa and Rana sierrae*) are well documented, extinctions from large catchments are rare (Knapp & Matthews, 2000; Knapp, 2005).

In contrast to *A. macrodactylum*, the presence of introduced salmonids had no negative effects on the occupancy of *R. luteiventris* at any spatial scale. *Rana luteiventris* are palatable to salmonids and fish can suppress the abundance of frog populations in water bodies where they co-occur (Pilliod & Peterson, 2001), yet populations have high resistance to extinction and appear to coexist with fish (Bull & Marx, 2002). The rapid development of *R. luteiventris* larvae allows the frogs to use a wide range of habitats, which we suspect limits their exposure to predatory fishes. Unlike *A. macrodactylum*, *R. luteiventris* was able to successfully breed in water bodies 1–2 m deep, habitats rarely stocked or inhabited by non-native fish. Where *R. luteiventris* and fish co-occur, tadpoles may be able to escape fish predation by using areas of the lake with shallow waters and complex habitat (e.g. dense emergent vegetation). The probability of frog occupancy greatly increased when > 25% of water body shoreline contained emergent vegetation, especially in water bodies > 1 m deep. We suspect this reflects a combination of breeding and overwintering habitat requirements for the species.

Differential effects of non-native fish on *A. macrodactylum* and *R. luteiventris* occupancy at different spatial scales may be explained by life history and population characteristics. Whereas both *A. macrodactylum* and *R. luteiventris* tend to have small effective population sizes (Funk *et al.*, 1999, 2005b; Davis & Verrell, 2005), *R. luteiventris* has higher fecundity than *A. macrodactylum* and may benefit from occasional 'boom' years of high recruitment. Further, the multi-year larval stage of *A. macrodactylum* at high elevations likely increases their exposure to predators. *Ambystoma macrodactylum* also has limited vagility (Tallmon *et al.*, 2000) compared to *R. luteiventris* (Pilliod *et al.*, 2002; Funk *et al.*, 2005a,b), which may result in a higher extinction risk in catchments than

R. luteiventris because declining local populations are less likely to be rescued by immigrants and recolonization rates are lower. Although overwintering habitats (i.e. deeper lakes, streams) of juvenile and adult *R. luteiventris* may be occupied by fish in some catchments (Pilliod & Peterson, 2001), the high vagility of the species (Pilliod *et al.*, 2002; Funk *et al.*, 2005b) may spread risk and reduce the probability of catchment-wide extinction.

Extirpation of native amphibians from high-elevation catchments in the northern Rocky Mountains has important conservation implications. Populations of *A. macrodactylum* and *R. luteiventris* have low gene flow between high-elevation catchments, and recolonization is most likely to occur from lower elevation portions of drainages (Tallmon *et al.*, 2000; Funk *et al.*, 2005b; Giordano *et al.*, 2007). Although possible, this process is slow and becoming less likely as low-elevation populations decline from loss of habitat in valley bottoms and decreased connectivity with mountain basins (Fisher & Shaffer, 1996; Funk *et al.*, 2005b). Climate change could further complicate this scenario as mountain snowpacks decline and hydrological patterns change (Cook *et al.*, 2004).

Although *A. macrodactylum* is considered 'secure' by the International Union for Conservation of Nature (IUCN, 2009), our data suggest that non-native fish may increase risk of extinction of high-elevation populations at landscape scales in the northern Rocky Mountains and conservation measures may be warranted in some situations. The potential for successful management of non-native fishes in montane environments is a rare opportunity in national and international efforts to reverse or mitigate the effects of non-native species (Kats & Ferrer, 2003). Amphibian populations can recover if fish die out following cessation of stocking (Funk & Dunlap, 1999; Knapp *et al.*, 2001, 2005; Eaton *et al.*, 2005). Experiments in California have demonstrated that non-native fish can be successfully removed from water bodies 1–2 ha in size, and native amphibian populations begin to recover within 1–2 years after fish elimination (Vredenburg, 2004; Knapp *et al.*, 2007; Pope, 2008). Our findings suggest that fish removal or altered fish management practices (e.g. cessation of stocking) implemented as conservation measures for high-elevation populations of *A. macrodactylum* in the northern Rocky Mountains may be most effective by targeting water bodies with the highest potential for salamander occupancy. Our analysis of salamander breeding habitat in fishless catchments suggests that water bodies targeted for fish removal should be < 2400 m elevation and have a maximum depth > 2 m.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Estimated effect of habitat variables on probability of *Ambystoma macrodactylum* breeding occupancy in 114 large catchments in the northern Rocky Mountains.

Figure S2 Estimated effect of habitat variables on probability of *Rana luteiventris* breeding occupancy in 315 small catchments in the northern Rocky Mountains.

Figure S3 Estimated effect of habitat variables on probability of *Rana luteiventris* breeding occupancy in 149 large catchments in the northern Rocky Mountains.

Table S1 Model results for long-toed salamander (*Ambystoma macrodactylum*) occupancy in 114 large catchments.

Table S2 Model results for Columbia spotted frog (*Rana luteiventris*) occupancy in 315 small catchments.

Table S3 Model results for Columbia spotted frog (*Rana luteiventris*) occupancy in 149 large catchments.

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BIOSKETCH

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