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RESEARCH ARTICLE

Linking the Distribution of an Invasive Amphibian (*Rana catesbeiana*) to Habitat Conditions in a Managed River System in Northern California

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Abstract

Extensive modifications of river systems have left floodplains some of the most endangered ecosystems in the world and made restoration of these systems a priority. Modified river ecosystems frequently support invasive species to the detriment of native species. *Rana catesbeiana* (American bullfrog) is an invasive amphibian that thrives in modified aquatic habitats. In 2004–2005 we studied the distribution of bullfrogs along a 98-km reach of the Trinity River below the Lewiston Dam to identify habitat characteristics associated with bullfrogs and to recommend actions to reduce their prevalence in the system. We also examined native amphibian distributions relative to bullfrogs and disturbance regimes. We used regression techniques to model the distribution of bullfrogs in relation to environmental conditions. Models assessing breeding habitat outperformed models assessing bullfrog presence. Top-ranked predictor variables of bullfrog distribution included water depth, percent rooted floating vegetation, and river km. Most breeding sites of bullfrogs were relict mine tailing ponds or inactive side channels created during restoration activities in the 1990s. Native species were more common in the lower reach where habitats were less modified, in contrast to the distribution of bullfrogs that dominated the upper, more modified reach. To control bullfrogs along a managed river, we suggest reducing the suitability of breeding sites by decreasing depth or reducing hydroperiod and increasing connection with the active river channel. Current management goals of restoring salmonid habitat and returning the river to a more natural hydrologic condition should aid in control of bullfrogs and improve conditions for native amphibians.

Key words: American bullfrog, bullfrog breeding habitat, dam effects, habitat models, lotic herpetofauna, Trinity River.

Introduction

Humans have extensively altered river systems worldwide through impoundments and diversions for water, energy, transportation, and flood control (Nilsson et al. 2005). Control of river systems has left floodplains among the most endangered ecosystems in the world and put them high on the conservation and restoration agendas of governments and organizations such as the International Union of the Conservation of Nature (Poff et al. 1997; Tockner et al. 2008). Natural floodplains are dynamic and diverse environments with high species diversity (Ward et al. 1999). Amphibians are thought of as indicators of stable floodplain habitat conditions (Joly & Morand 1994), yet are able to exploit the entire hydrodynamic gradient of natural floodplains and reach high diversity and density in these dynamic systems (e.g. Tockner et al. 2006).

In the western USA, river systems have undergone significant physical and biological changes, mostly due to flow manipulations for flood control and water exports (Dynesius & Nilsson 1994; Erskine et al. 1999). In addition to changes in flow regimes, hydraulic mining and channelization from urban or agricultural developments have resulted in greatly reduced riparian and in-stream habitat quantity and complexity, which eliminate important environmental attributes for biodiversity (Stromberg 2001). Human-modified aquatic ecosystems such as reservoirs often favor invasive species over native species (Rahel 2002; Johnson et al. 2008). Exotic species and degraded aquatic habitats can work synergistically to contribute to the decline of native species (D'Amore et al. 2010). Understanding how altered habitats aid in the persistence and spread of an invasive species can provide insight into how to focus restoration efforts to reduce survivability of the invader while improving conditions for native species.

Rana catesbeiana (American bullfrog) is an example of an invasive species that thrives in modified aquatic habitats of the western USA (Moyle 1973; Hammerson 1982;

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Hayes & Jennings 1986; Lind et al. 1996), where it often displaces native aquatic species due to competition and predation (Kiesecker & Blaustein 1997; Kupferberg 1997; Kiesecker & Blaustein 1998; Adams 2000; Pearl et al. 2004). A native to eastern North America, *R. catesbeiana* (hereafter, bullfrog), now ranges worldwide as a result of repeated introductions and invasions (Mahon & Aiken 1977; Stumpel 1992; Stebbins 2003). The worldwide expansion and negative effects of bullfrogs on native species have resulted in its inclusion in the list of the 100 worst invasive species (Lowe et al. 2001). Bullfrogs readily adapt to anthropogenic habitat modifications and are opportunistic feeders (Batista 2002; Carpenter et al. 2002; Cross & Gerstenberger 2002; King et al. 2002) that will prey upon threatened species including *R. draytonii* (California red-legged frog; Moyle 1973; D'Amore et al. 2010) and *Oncorhynchus kisutch* (coho salmon; Garwood et al. 2010).

Currently, many aquatic restoration projects are being designed to recover physical and biological processes that had been impacted by anthropogenic activities, often with a focus on recovering native species. To be successful, aquatic restoration projects where bullfrogs have invaded need to minimize or reduce habitat conditions which favor bullfrog persistence or eliminate bullfrogs (Adams & Pearl 2007). For example, D'Amore et al. (2009, 2010) successfully eradicated bullfrogs from ponds by hand removing, gigging (stabbing with a multi-pronged spear), and seining, to enhance site suitability for *R. draytonii*. In more complex systems such as river floodplains, system-specific habitat requirements of bullfrogs need to be determined in order to develop options to control or reduce the habitat attributes contributing to their persistence and expansion. Without this awareness, restoration activities have the potential to increase suitable habitats for bullfrogs, resulting in potential harm to native species.

The Trinity River in northern California has been extensively altered by human activity (Trush et al. 2000). The river basin was heavily mined beginning in the gold rush era of the mid-1800s with placer and sluice mining, followed by hydraulic mining. In the early- to mid-1900s, large-scale dredge mining devastated the river valley. The resulting tailing piles and ponds are still readily visible along the river channel and floodplain. The Lewiston Dam was built in 1963 to provide water for the Central Valley Project to irrigate farmland and for residential use in central and southern California. Damming of the Trinity River has reduced the duration and magnitude of flow, and has converted this once open, alluvial river to a channelized river, encroached by vegetation and isolated from its floodplain (Trush et al. 2000). Up to 90% of the water from the river was diverted to the Central Valley for several decades. These flow modifications resulted in significant losses in anadromous fish habitat leading to species declines and a Record of Decision (ROD) by the U.S. government for a Trinity River Mainstem Fishery Restoration Program (United States Department of Interior 2000). Based on the ROD, 48% of the water must remain in the Trinity River, and managed flows should better mimic the natural hydrograph. Unpublished historical accounts provide evidence that bullfrogs occurred along the river as early as the 1920s; however, the first documentation was not until 1990 (Wilson et al. 1991). The river below the dam still supports native fish such as coho salmon and amphibians such as the foothill yellow-legged frog (*R. boylii*), but at low densities (Lind et al. 1996; United States Department of Interior 2000).

The objectives of our study were to identify habitat features that allow for the persistence and spread of bullfrogs along a managed river system and to examine native amphibian and reptile distributions relative to habitat disturbance and bullfrog distributions. We assessed habitat conditions along a 98-km reach of the Trinity River below the Lewiston Dam where mandated restoration efforts are going on to improve conditions for anadromous fishes. Our goals are to inform restoration managers of specific habitat conditions to modify in order to reduce the distribution and numbers of bullfrogs along the river floodplain. We anticipate that our findings will also help refine the management strategy to improve conditions for other native species.

Methods

Study Area

We surveyed the mainstem of the Trinity River from just below the dam at river km 180 downstream to river km 82 (Fig. 1). Flows in this section of the river ranged from 62 m^3/second in the spring to 13 m^3/second in the late summer. We divided the study area into two reaches. The upstream reach (180–120 km) from the dam down to the North Fork was mined heavily from the gold rush era through the 1950s. Evidence of placer and sluice mining, hydraulic mining, and dredge mining are still common features in the upstream reach. The extensive mining tailings from dredge mining are of particular relevance to this study due to the persistent tailing ponds. The downstream reach from the North Fork down to Cedar Flat (120–82 km) is more confined with steeper banks and historically had smaller-scale placer mining on the gravel bars with some recreational suction-dredge mining continuing to present. The downstream reach retains much of its natural topography due to the bedrock geology and more natural hydrology due to cumulative tributary accretion, primarily downstream of Junction City (Fig. 1).

Data Collection

We conducted surveys from early summer through fall (June–September) of 2004 and 2005. In 2004, we conducted two surveys of the entire 98 km reach to map the distribution of bullfrogs and native herpetofauna and to record habitat conditions. In 2005, we focused on identifying and characterizing bullfrog breeding sites by conducting three surveys of all potential or known breeding sites found during the 2004 surveys and at 47 randomly selected and presumed non-breeding sites in the upper 60 km. We focused on this upper reach because it was the only stretch where bullfrogs were found during the 2004 surveys (see *Results*).

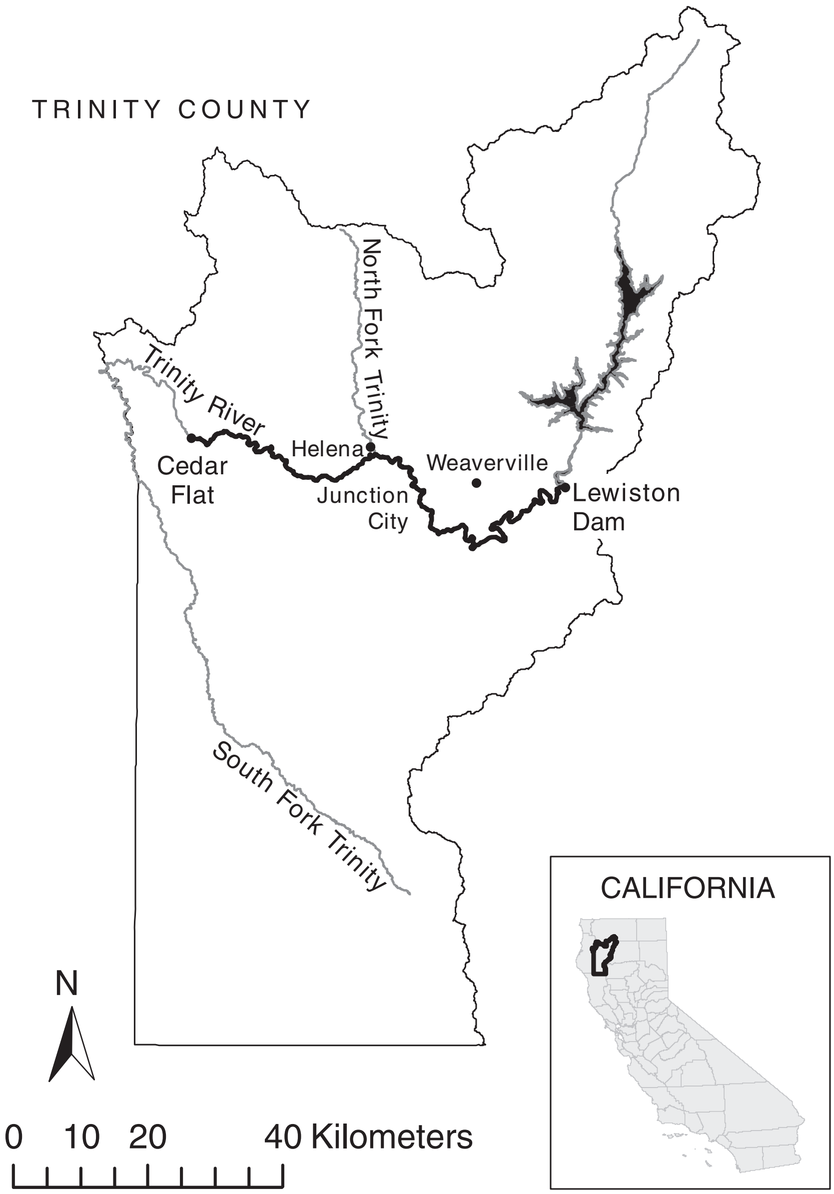

Figure 1. The location of the study area in Trinity County, California. The study was conducted on the mainstem Trinity River from Lewiston Dam (river km 180) downstream (west) to Cedar Flat (river km 82). The study area was divided into two sections, from the dam to the confluence with the North Fork Trinity River at Helena (river km 120), and from the North Fork down to Cedar Flat.

2004 Surveys. We conducted one round of survey during the high-flow period (06 June–08 July) and a second round during the low-flow period (03 August–23 September) to compare habitat changes between flows and to document seasonal changes in species distributions. High-flow surveys were conducted when flows were between 52.9 and 62.2 m^3/second, and low-flow surveys were conducted when flows were between 13.4 and 13.6 m^3/second. Prior to field surveys, we assessed high-resolution ortho-rectified color aerial photos with a vegetation map overlay to identify additional aquatic habitats adjacent to the river to visit on the survey. We surveyed all water bodies connected to the river or within its historic floodplain that had at least 5% lentic habitat, an area greater than 4 m^2, and a depth greater than 0.2 m. Sites were accessed by foot or using an inflatable kayak.

All habitats were surveyed between the hours of 10:00 and 19:00 using binocular and visual encounter surveys (Heyer et al. 1994). Binocular surveys involved scanning the surface of the water and counting the number of bullfrogs observed by life stage (adult, juvenile, larvae, egg mass). Visual encounter surveys were accomplished by walking or floating the shoreline and counting the number of species and individuals observed by life stage. Frogs were estimated as adults or juveniles based on body size. We counted all species by life stage; however, only presence/not-detected data were used for analyses.

We acquired site coordinates with a Garmin handheld GPS and then mapped them on vegetation maps with ArcGIS-derived river kilometers. Sites were spatially edited to determine accurate site locations in ArcGIS 9.1 using ortho-rectified color aerial photos and 1:24,000 digital raster graphics (DRG). Water bodies were considered independent from the river if there was a separation of at least 1 m of dry land at the time of the survey.

2005 Breeding Surveys. Due to the limited number of visits in 2004, poor water clarity, and difficulty with visual encounter surveys in heavily vegetated habitats, detecting larvae was challenging and we were not able to confirm breeding status at some sites. These were categorized as "unknown" breeding sites in the 2004 surveys. The primary objective for the 2005 surveys was to confirm breeding status at these sites and other potential breeding sites. We surveyed 19 "unknown" breeding sites identified during the 2004 surveys and 47 additional randomly selected sites. Each site was surveyed three times in 2005 to capture early, mid, and late summer activity with the anticipation of detecting first- or second-year bullfrog larvae. To aid in detection of aquatic larvae, we set four minnow traps overnight in the littoral zone of each potential breeding site. We used 40 $\times$ 22 cm collapsible, rectangular-framed, nylon mesh funnel traps as recommended by Adams et al. (1997). Three of the four traps at each site had a 28 cm^2 opening and the fourth had a 7 cm^2 opening.

Habitat Sampling. After each site was surveyed for animals, 18 habitat variables were measured or estimated (Table 1). In 2005, we additionally sampled water clarity, dissolved oxygen, and canopy cover. Due to the complexity of habitats and the inability to physically complete transects at all sites, we occularly estimated some site-specific habitat variables, such as the percent coverage of each vegetation type (Table 1). The same surveyor (T.F.) conducted all vegetation estimates. Maximum depth was measured to the nearest centimeter with a stadia rod. Water temperature was measured approximately 50 cm from the shore with a digital thermometer. We measured water clarity to the nearest centimeter using a transparency tube and secchi disc. Dissolved oxygen content was measured in parts per million with a Smart dissolved oxygen meter (res. $\pm$ 1.5% full scale, Milwaukee). If a site was deep enough, we measured dissolved oxygen at three depths: 6 cm, $^1/_2$ depth, and $^1/_4$ depth from bottom. Canopy cover was measured with a clinometer in four cardinal directions to get the angle to the horizon or angle of vegetation (Pearl et al. 2005). Four landscape-scale variables were collected: distance of site from main channel, distance of site to nearest bullfrog-occupied site, distance of site to nearest breeding site, and distance of site to nearest lentic site (Table 1). If feasible, we measured these variables in the field; if not (e.g. long distances between sites), we estimated distances from GIS coverages. All sites were descriptively categorized as either main channel, active side channel (watercourse with both inlet and outlet connected the main channel), inactive side channel (watercourse lacking either inlet or outlet from the main channel), backwater (inactive water body with neither inlet or outlet connected to the main channel), marsh (mostly still water containing aquatic vegetation such as cattails [*Typhia* sp.]), puddle (lentic depression less than 7 m^2), pond (lentic depression greater than 7 m^2), or tailing pond (dredge mining pond).

Table 1. Codes and descriptions of environmental variables used for building the habitat models for American bullfrogs.

Code	*Variable Description*
Local scale	
TEMP	Water temperature (°C) measured in littoral zone
DEPTH	Maximum water depth measured to 0.1 m with stadia rod
AREA	Site area (m^2) estimated by pace counts or visual estimates
LENTIC	Percentage lentic water
LOTIC	Percentage lotic water
O WATER	Percentage open water
O PERIM	Percentage open perimeter
G VEG	Percentage ground vegetation
S VEG	percentage shrub vegetation
T VEG	Percentage tree vegetation
G BAR	Percentage gravel bar
RF VEG	Percentage rooted floating vegetation
FF VEG	Percentage free floating vegetation
E VEG	Percentage emergent vegetation
HERB E	Percentage herbaceous emergent vegetation
WOODY E	Percentage woody emergent vegetation
OCCUPIED T1	SITE previously occupied by a bullfrog during high-flow survey (factor variable)
RIVER KM	River kilometer (km)
*DO	Dissolved oxygen measure using a SMART dissolved oxygen meter (res. $\pm$ 1.5% full scale)
*C COVER	Canopy cover, measured with a clinometer
*W CLARITY	Water clarity (cm) measured with a transparency tube
Landscape scale	
CHAN DIST	Distance to channel (m) estimated in the field or using ArcGIS
OCCUPIED DIST	Distance to a bullfrog-occupied site (m) estimated in the field or using ArcGIS
BREED DIST	Distance to a bullfrog breeding site (m) estimated in the field or using ArcGIS
LENTIC DIST	Distance to a lentic site (m) estimated in the field or using ArcGIS

* Variables used in bullfrog breeding models only (2005).

Data Analysis

Flow Models. To model the distribution of bullfrogs of any life stage with environmental variables, we used generalized additive models with logit-link functions (Guisan et al. 2002). Generalized additive models relax the distributional assumptions about the dependent variable (e.g. linear, quadratic, logistic) and also the relationship between the dependent and the predictor variables (Guisan et al. 2002). We conducted this modeling exercise separately for the high-flow and low-flow surveys due to the extreme seasonal changes we found in habitat characteristics and the possibility that bullfrogs associate with different habitats under the different conditions. Because of the potential for autocorrelation between the high-flow and low-flow surveys (i.e. if a bullfrog was present at a site during the high-flow survey, it might be more likely to be also present during the low-flow survey), we created a binomial variable "found at time one" (T1) used only in the late summer low-flow modeling. The binary response variable in all models was whether at least one bullfrog was detected at a site. River km was included as a variable in all models to account for spatial autocorrelation. Because no bullfrogs were detected below river km 120, we removed the lower 38-km stretch of the surveyed reach from the models. To prevent multicollinearity, which may confound the independent effect of predictor variables, we first ran a Spearman-rank correlation matrix for all pairwise combinations of variables. If the correlation coefficient (r) exceeded 0.70 for any pair, then only the variable with the highest correlation with bullfrog presence was used in that particular model (Berry & Felman 1985).

We developed primary models using variables collected at two spatial scales. The landscape model was developed from 10 a priori multivariate models using landscape-scale variables (Table 1). The local model was developed from 43 a priori multivariate models using environmental variables collected at the site (Table 1). For both high- and low-flow conditions, variables from the top-ranked landscape and local models (ranked using AICc; Akaike 1973; Burnham & Anderson 2000) were combined to form a multi-scale composite model. We determined the relative significance of the variables from each of the top-ranked models by examining adjusted deviance (D^2) and p-values when an individual variable was removed from the model. All modelings were conducted using S-Plus (2001).

Cross-validation. The high- and low-flow composite models were evaluated using a 10-fold cross-validation procedure. We randomly used 90% of the data set (training data) and estimated the model's parameters, then classified the remaining 10% (test data). We repeated this procedure 10 times (Fielding & Bell 1997). We then evaluated the distribution of predicted probabilities and classification rates (alpha $= 0.05$) for the original data (full data set model) and the test data set, to evaluate model stability (Manel et al. 2001). We further examined the stability of the original model using Cohen's kappa for chance-corrected classification rates, which provides a simple and effective statistic for evaluating or comparing models (Manel et al. 2001). We considered values of 0.1–0.4 to indicate unstable model performance, values of 0.4–0.6 to indicate moderate model performance, 0.6–0.8 to indicate stable model performance and 0.8–1.0 to indicate almost perfect model performance (after Manel et al. 2001).

Bullfrog Breeding Models. Using the 2005 breeding survey data, we developed 21 a priori multivariate models to predict breeding sites. A site was considered a breeding site if egg masses or ≥ 2 larvae were observed. Variables were selected based on the information published on bullfrog breeding habitat (Adams 2000; Stebbins 2003) and from the physical properties of the Trinity River that we deemed may influence breeding locations. We assessed the same suite of local environmental variables used in the flow models with the addition of three water quality variables (Table 1). We analyzed the breeding models using the same methods and criteria used for the flow models. In addition, we tested whether or not human-modified sites were used for breeding proportionately more than less-modified sites using a Yates Chi-square test. Finally, we used nonmetric multidimensional scaling (NMS) with a Sorenson distance measure to analyze the inter-relatedness of site types and habitat variables by ordinating sites in environmental space and overlaying the ordination with whether a site supported breeding or not. Ordination was conducted in PCOrd (McCune & Mefford 1999). On 50 runs, Monte Carlo test results showed three dimensions in the final solution and a low probability that a similar final stress in the NMS model could have been obtained by chance ($p = 0.02$). We used the analysis of similarities test (ANOSIM) to determine whether or not there were significant differences among habitat types supporting or not supporting breeding (Clarke & Warwick 1994).

Herpetofaunal Species Distribution. We combined high- and low-flow survey data for the 98-km study reach to compare native herpetofauna distribution with bullfrog distribution. We included *Bufo boreas* (western toad), *Pseudacris regilla* (Pacific treefrog), *Rana boylii* (foothill yellow-legged frog), *Thamnophis atratus* (aquatic garter snake), and *Actinemys marmorata* (western pond turtle) in this analysis. We first divided the river into 6 approximately equal 16-km increments and then calculated the mean number of native species per site surveyed within each increment. We also calculated the proportion of sites within each increment where bullfrogs were recorded. We used linear regression to assess the relationship between river km increments and bullfrog and native species distributions. In addition, we compared the distribution of the three native amphibians with the top-ranked environmental variables from the bullfrog models, river km, and bullfrog distribution using a generalized linear model.

Results

Bullfrog presence was recorded along the study reach from Lewiston Dam (river km 120) downstream to river km 60. Bullfrogs were recorded at 49 of 131 sites during the high-flow surveys and 44 of 145 sites during the low-flow surveys. Sites identified as occupied were consistently located adjacent to or within the floodplain of the channel; bullfrogs were only found in the main channel incidentally. Occupied sites tended to have still, deep water habitats with rooted floating vegetation and open shoreline vegetation (Table 2). Heavily modified sites such as tailing ponds were more likely characterized by these habitat features than less-modified sites (Fig. 2). Nine of the

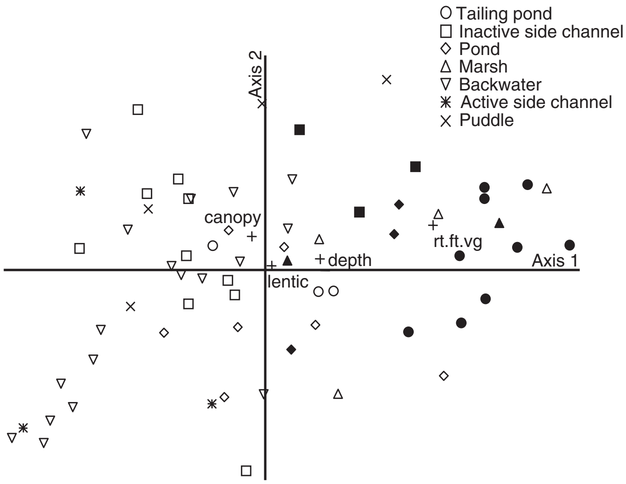

Figure 2. NMS ordination of sites surveyed during the 2005 breeding surveys. Sites are categorized by type and ordinated in environmental space using the top-ranked variables from the breeding GAM. The location of the cross symbols for the environmental variables shows their direction of influence on axes 1 and 2. Closed symbols represent sites where breeding was found. The variable rt.fl.vg represents rooted floating vegetation.

12 tailing ponds surveyed supported breeding, a much higher proportion than supported by the other more natural site types ($X^2 = 8.27,\ p = 0.004$, Fig. 2).

Flow Models

For both high- and low-flow conditions, the multi-scale model best predicted sites where bullfrogs were found (Table 2). Important variables in both models included percent rooted floating vegetation, maximum depth, river km, distance to an occupied site, and distance from channel (Table 2). Variables important in the low-flow but not high-flow model included water temperature, occupied at T1, and wetted surface area (Table 2).

The low-flow model explained a higher percent of the model deviance than the high-flow model (Table 2) with most of the improvements due to the inclusion of the temporal variable occupied at T1. This variable indicated the presence of a bullfrog at a site in the prior survey and accounted for 10% of the decrease in deviance, making it the third most significant variable. While both models correctly classified bullfrog presence with approximately 75% accuracy, the low-flow cross-validation model proved unstable compared to the full model (Table 3). Based on Cohen's kappa, model performance for correctly predicting bullfrog presence was low for the low-flow model and moderate for the high-flow model (Table 3).

Bullfrog Breeding

The top-ranked breeding model received strong support ($\text{AIC}_\text{w} = 0.9$) and explained 85% of the overall variation in the breeding site data. Variables in the top-ranked model in the order of importance included: Percent rooted floating vegetation, maximum water depth, percent lentic habitat, river km, canopy cover, and water clarity (Table 4). Maximum water depth was highly significant ($p < 0.01$) in the breeding model, accounting for 23% of the total deviance explained by the model (Table 4).

The top-ranked breeding model correctly classified bullfrog breeding sites with over 90% accuracy and the cross-validation test indicated substantial model stability (Table 3). Of the 66 sites surveyed in 2005, the full breeding model misclassified only two at the 0.5 cutoff, while the cross-validated results misclassified eight sites.

Results of the NMS grouped sites supporting breeding with specific habitat characteristics (Fig. 2). The ANOSIM test of similarity, however, did not strongly differentiate habitat types that supported breeding from those that did not ($R = 0.08$, $p = 0.07$). Tailing ponds and inactive side channels were the most common site types with features that supported breeding. Breeding was confirmed at 17 sites, just over half (52%) of which were perennial tailing ponds.

Herpetofaunal Species Distributions

The combined distribution of the native herpetofaunal species had a strong linear relationship with river km, and thus was inversely related to the distribution of bullfrogs (Fig. 3). Native species were more commonly found in the downstream reach (below river km 130), whereas bullfrogs were more common in the upstream reach closer to the dam. In the GLM assessing the distribution of native amphibians, river km was the only significant predictor of sites with native amphibians ($z = 4.277,\ p < 0.0001$). Presence of bullfrogs did not significantly predict sites with native species ($z = -0.218,\ p = 0.83$) and neither did maximum depth ($z = -1.83,\ p = 0.07$), percent lentic habitat ($z = 0.02,\ p = 0.98$), rooted floating vegetation ($z = 0.19,\ p = 0.85$), or shoreline canopy cover ($z = 0.005,\ p = 0.99$).

Discussion

The results of this study highlight the importance of considering the life history requirements of a target invasive species in light of the available physical habitat conditions and the distribution of native species when planning a below-dam restoration effort. Our research suggests that future management and control of bullfrogs along a managed river should focus on removing appropriate site conditions for breeding. Similar to many ranid frogs, bullfrogs appear to have more specific requirements for breeding compared to other life history functions. A common trait among many invasive species, including the bullfrog, is that they are generalists and consequently, may not show strong selection for specific habitat characteristics (Marvier et al. 2004; Evangelista et al. 2008). Postmetamorphic bullfrogs can adapt to a wide range of environmental conditions (Adams & Pearl 2007), which makes stable habitat associations challenging to identify and eradication of these life stages infeasible. On the other hand, breeding

Table 2. Top-ranked multi-scale generalized additive models for the high- and low-flow regimes for the 2004 surveys.

Model	*Variable*[a]	*Null Deviance*	*Residual Deviance*	*k*	*n*	*Adjusted $D^{2\,b}$*
Multi-scale high-flow	+LENTIC DIST*, +RF VEG*, +DEPTH*, +RIVER KM*, +CHAN DIST*, OCCUPIED DIST,	173.2	93.5	8	131	0.4
Multi-scale low-flow	+DEPTH*, TEMP*, +AREA* OCCUPIED T1*, −OCCUPIED DIST*, +RF VEG*, +CHANNEL DIST*, RIVER KM	177.9	64.6	10	145	0.6

Table includes the number of variables in the model (k), sample size (n) and the adjusted percent deviance explained (D^2).
[a] Direction of significant variables (+ = positive relationship; − = negative relationship).
[b] Adjusted $D^2 = 1 - (((n-1)/(n-k)) * (1 - (\text{null deviance} - \text{residual deviance})/\text{null deviance}))$.
* $p < 0.05$.

Table 3. Classification and Cohen's kappa results for full and cross-validation high- and low-flow models and bullfrog breeding model.

	% Classification at 0.5 Cutoff			*Kappa*[a]	
Top-ranked Models	*Predicted Classification*	*Full Model*	*Cross-Validation Model*	*Full Model*	*Cross-Validation Result*
Multi-scale high-flow[b]	Present	75.5	64.0		
	Absent	89.0	90.0	0.65	0.56
	Total	84.0	80.0		
Multi-scale low-flow[c]	Present	77.3	56.1		
	Absent	95.0	80.8	0.75	0.37
	Total	89.7	71.0		
Breeding Model[d]	Present	94.0	83.3		
	Absent	98.0	90.4	0.92	0.71
	Total	97.0	88.6		

[a] Kappa proportion of specific agreement (following Manel et al. 2001).
[b] June–July 2004.
[c] August–September 2004.
[d] June–September 2005.

Table 4. Variable significance and change in deviance for the top-ranked bullfrog breeding generalized additive model.

Predictive Variables	*Resulting Deviance*[a]	*Change in Deviance*[b]	*% Increase in Deviance*[c]	*Direction*[d]
LENTIC	23.41	12.42	19	+
RF VEG	33.80	22.80	35	+
W CLARITY	11.46	0.46	1	na
C COVER	12.91	1.91	3	−
DEPTH	25.86	14.87	23	+
RIVER KM	19.17	8.18	13	+

Percent increase in deviance shows the relative deviance explained by that variable.
[a] Resulting Deviance: residual deviance left in the full model after dropping that variable.
[b] Change in Deviance: resulting deviance − full model deviance.
[c] % Increase in Deviance: deviance increase/(null deviance − model deviance) * 100.
[d] Direction of Significant Variables (+ = positive relationship; − = negative relationship).

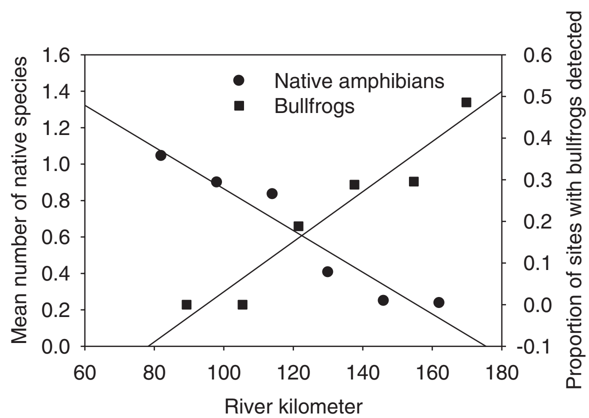

Figure 3. The relationship of amphibian distributions for each 16 km increment of the Trinity River study reach for the high-flow survey with the mean number of native species per site on the primary Y-axis and the proportion of bullfrog-occupied sites on the secondary Y-axis. Lines represent least-square regression lines where $R^2 = 0.93$ for native amphibians and $R^2 = 0.93$ for the proportion of bullfrogs.

sites were highly predictable and were characterized by still, deep water with rooted floating vegetation and open riparian canopies. Permanent water is essential for bullfrog reproduction in this region because tadpoles must often overwinter before reaching metamorphosis. Cook and Jennings (2007) also found deep water to be an important habitat condition for oviposition sites. Presence of rooted floating vegetation is likely an indicator of permanent water and an important component of breeding sites because it provides protection for bullfrog eggs, larvae, and metamorphic stages, which are the most vulnerable life stages to predators. Open canopy sites are likely favored because they receive more sunlight which increases water temperatures. Sun and warmth speed egg and larvae developmental rates (Skelly et al. 2002) and optimize thermoregulation. Green algae grow better under open canopy conditions and are a primary food source for many anuran larvae (Kupferberg 1997). Because bullfrogs breed in particular habitat conditions along the Trinity River, they can be controlled by site-specific restoration efforts.

Most of the bullfrog breeding sites on the Trinity River are the result of active and passive human modifications, a condition that links this bullfrog invasion to many other non-native species invasions (Marvier et al. 2004; Johnson et al. 2008; Vidra & Shear 2008; D'Amore et al. 2009, 2010). Most of the deep, lentic sites were remnant tailing ponds or inactive side channels with more permanent hydroperiods than active side channel sites. Tailing ponds also often had an open canopy structure due to the infertile tailing piles along the shoreline. Tailing ponds comprised over half of the breeding sites we found. These habitats were almost exclusively in the upper watershed where the river valley is wider than the gorge-like lower section and more conducive to the formation of side channels and the digging of dredge tailing ponds. The managed flows out of the Lewiston Dam have allowed for the hydrologic persistence of these features. Many of the inactive side channels were created during the 1990s' restoration attempt to mimic the historic side channel network. Under restricted flow releases, these sites remain isolated from the channel and allow the continued colonization by bullfrogs. Only one breeding site, at the Rush Creek Delta, was perennially connected to the river. A portion of this site has transitioned into a lentic marsh system due to the inability of the post-dam mainstem Trinity River to transport bedload from Rush Creek (McBain & Trush 2000). Without altering flows, habitat modification efforts to improve conditions for native species have had indirect negative impacts on many of these species by improving conditions for bullfrogs.

The current proposed and ongoing restoration efforts along the Trinity River combine returning the river to a more natural hydrologic condition with habitat modifications to benefit native species (United States Department of Interior 2000). Most projects have been specifically designed to improve conditions for native salmonids but will likely have the secondary benefits of reducing habitats suitable to bullfrogs and improving conditions for native amphibians. For example, bank-feathering projects designed to improve conditions for spawning salmonids also improve habitats for foothill yellow-legged frogs by removing established vegetated berms and creating meandering gravel bars that are also favored by foothill yellow-legged frogs for breeding (Lind et al. 1996). A study of a natural river system in Central Europe found a positive relationship between fish density and amphibian diversity which they attributed to the complex habitat structures found in natural systems such as vegetated islands and large woody debris dams (Tockner et al. 2006). These features provide protection to both fish and amphibians and facilitate the coexistence of these otherwise mutually exclusive groups (Gurnell et al. 2005).

Manipulating flows to produce active side channels, with shallow depths, gravel substrate, and a fast water component, would likely decrease bullfrog colonization while increasing habitat appropriate for native riverine species. Native amphibians, especially the lotic specialists such as the foothill yellow-legged frog, evolved with natural flow characteristics such as spring peak flows, which inform them of appropriate times to breed (e.g. Lind et al. 1996). Prior to incorporation of high spring water releases from Lewiston Dam that began in 2006, these conditions were only found in the lower reach where accretion from free-flowing tributaries created more natural-like flow conditions. The new spring peak releases will provide more natural cues to native species and will maintain open gravel bars, prevent rejoined side channels from becoming inactive and will prevent the accumulation of rooted floating vegetation favored by bullfrogs.

Unfortunately, ongoing restoration activities put a low priority on modifying remnant tailing ponds because these sites are isolated from the main channel and, therefore, have little association with salmonids, which are the key focus of the Trinity River Restoration Program. Given that 52% of the bullfrog breeding sites are old dredge tailing ponds that are isolated from the river channel, removing or restructuring these manmade habitat features to reduce depth and hydroperiod could help control bullfrog populations. According to our data, this would likely be most successful in a 20-km reach centered on Junction City where the majority of the tailing ponds support breeding habitat for bullfrogs.

Hopefully, with consideration of native herpetofauna in management decisions and reduction of bullfrog breeding habitats, the upper Trinity River may experience a rebound of native species diversity and abundance as recommended in the ROD (United States Department of Interior 2000). The overall goal should be to recreate dynamic habitat conditions more similar to a natural river system so that the stable lentic habitats favored by bullfrogs are reduced. Active floodplains support a high diversity of habitats allowing for colonization of a high diversity of species including native amphibians (Tockner et al. 2006).

Implications for Practice

- Anthropogenic modifications to riverine systems negatively affect native species and often create habitat conditions suitable to invasive species such as bullfrogs.
- To control bullfrogs on the Trinity River, efforts should focus on removing stable, deep, lentic habitats used for breeding.
- Without also altering flows to create a more hydrodynamic floodplain, habitat modification efforts to improve conditions for native species can have indirect negative impacts to native species by improving conditions for bullfrogs.
- Returning the river to a more natural hydrologic condition combined with linking inactive side channels to the

river and modifying tailing ponds to reduce depth and hydroperiod could simultaneously eliminate conditions that favor invasive species and create habitats favorable to native species.

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LITERATURE CITED

Adams, M. J. 2000. Pond permanence and the effects of exotic vertebrates on anurans. Ecological Applications **10:**559–568.

Adams, M. J., and C. A. Pearl. 2007. Problems and opportunities managing invasive bullfrogs: Is there any hope? Pages 679–693 in F. Gherardi, editor. Biological invaders in inland waters: profiles, distribution, and threats. Springer, Dordrecht, The Netherlands.

Adams, M. J., K. O. Richter, and W. P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. Pages 47–54 in D. H. Olson, W. P. Leonard, and R. B. Bury, editors. Sampling amphibians in lentic habitats. Northwest Fauna, Vol. 4. Society for Northwestern Vertebrate Biology, Olympia, Washington.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petran and F. Csaki, editors. International symposium on information theory. 2nd edition. Akademiai Kiadi, Budapest, Hungary.

Batista, C. G. 2002. *Rana catesbeiana* (bullfrog). Effects on native anuran community. Herpetological Review **33:**131.

Berry, W. D., and S. Felman. 1985. Multiple regression in practice. Sage Publications, Beverly Hills, California.

Burnham, K. P., and D. R. Anderson. 2000. Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York.

Carpenter, N. M., M. Casazza, and G. D. Wylie. 2002. *Rana catesbeiana* (bullfrog) diet. Herpetological Review **33:**130.

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

Cook, G. D., and M. R. Jennings. 2007. Microhabitat use of the California red-legged frog and introduced bullfrog in a seasonal marsh. Herpetologica **63:**430–440.

Cross, C. L., and S. L. Gerstenberger. 2002. *Rana catesbeiana* (American bullfrog) diet. Herpetological Review **33:**129–130.

D'Amore, A., V. Hemingway, and K. Wasson. 2010. Do a threatened native amphibian and its invasive congener differ in response to human alteration of the landscape? Biological Invasions **12:**145–154.

D'Amore, A., E. Kirby, and M. McNicholas. 2009. Invasive species shifts ontogenetic resource partitioning and microhabitat use of a threatened native amphibian. Aquatic Conservation: Marine and Freshwater Ecosystems **19:**534–541.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **226:**753–762.

Erskine, W. D., N. Terrazzolo, and R. F. Warner. 1999. River rehabilitation from the hydrogeomorphic impacts of a large hydro-electric power project: Snowy river, Australia. Regulated Rivers: Research and Management **15:**3–24.

Evangelista, P. H., S. Kumar, T. J. Stohlgren, C. S. Jarnevich, A. W. Crall, J. B. Norman III, and D. T. Barnett. 2008. Modelling invasion for a habitat generalist and a specialist plant species. Diversity and Distributions **14:**808–817

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24:**38–49.

Garwood, J. M., C. W. Anderson, and S. J. Ricker. 2010. Predation by an American bullfrog on a juvenile coho salmon in Humboldt County, California. Northwestern Naturalist (In press.)

Guisan, A., T. C. Edwards Jr, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distribution: setting the scene. Ecological Modeling **157:**89–100.

Gurnell, A. M., K. Tockner, G. E. Petts, and P. J. Edwards. 2005. Large wood delivers biocomplexity along river corridors. Frontiers in Ecology and Environment **3:**377–382.

Hammerson, G. A. 1982. Bullfrog eliminating leopard frogs in Colorado? Herpetological Review **13:**115–116.

Hayes, M. J., and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology **20:**490–509.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, D.C.

Johnson, P. T. J., J. D. Olden, and M. J. Vander Zanden. 2008. Dam invaders: Impoundments facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment **6:**357–363.

Joly, P., and A. Morand. 1994. Theoretical habitat templets, species traits, and species richness: amphibians in the Upper Rhone River and its floodplain. Freshwater Biology **31:**455–468.

Kiesecker, M. J., and A. R. Blaustein. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. Ecology **78:**1752–1760.

Kiesecker, M. J., and A. R. Blaustein. 1998. Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth and survival of native red-legged frogs (*Rana aurora*). Conservation Biology **12:** 776–787.

King, K. A., J. C. Rorabaugh, and J. A. Humphrey. 2002. *Rana catesbeiana* (bullfrog) diet. Herpetological Review **33:**130–131.

Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology **78:**1736–1751.

Lind, A. J., H. H. Welsh Jr, and R. A. Wilson. 1996. The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in northwesten California. Herpetological Review **27:**62–67.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2001. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Species Survival Commission, World Conservation Union, Auckland, New Zealand.

Mahon, R., and K. Aiken. 1977. The establishment of the North American bullfrog, *(Rana catesbeiana)* (Amphibia, Anura, Ranidae) in Jamaica. Journal of Herpetology **11:**197–199.

Manel, S., H. C. Wiliams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. The Journal of Applied Ecology **38:**921–931.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis **24:**869–878.

McBain, S., and W. Trush. 2000. Summary of the United States Secretary of Interior record of decision, December 19, 2000. Trinity River Restoration Program, Weaverville, California.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data version 4.08. MjM Software, Gleneden Beach, Oregon.

Moyle, P. J. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia **1973**: 18–22.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science **308:**405–408.

Pearl, C. A., M. J. Adams, R. B. Bury, and B. McCreary. 2004. Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. Copeia **2004**:11–20.

Pearl, C. A., M. P. Hayes, R. Haycock, J. D. Engler, and J. Bowerman. 2005. Observation of interspecific amplexus between western North American ranid frogs and the introduced Amercian bullfrog *(Rana catesbeiana)* and an hypothesis concerning breeding interference. The American Midland Naturalist **154:**126–134.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. Richter, R. Sparks, and J. Stromberg. 1997. The natural flow regime: a new paradigm for riverine conservation and restoration. BioScience **47:** 769–784.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics **33:**291–315.

Skelly, K. D., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology **83:** 983–992.

S-Plus. 2001. User's manual, version 6. Insightful Corporation, Seattle, Washington.

Stebbins, R. C. 2003. A field guide to western reptiles and amphibians. 2nd edition. Houghton Mifflin Company, Boston, Massachusetts.

Stromberg, J. C. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. Journal of Arid Environments **49:**17–34.

Stumpel, A. 1992. Successful reproduction of introduced bullfrogs *(Rana catesbeiana)* in northwestern Europe: a potential threat to indigenous amphibians. Biological Conservation **60:**61–62.

Tockner, K., I. Klaus, C. Baumgartner, and J. V. Ward. 2006. Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy). Hydrobiologia **565:**121–133.

Tockner, K., S. E. Bunn, G. Quinn, R. J. Naiman, J. A. Stanford, and C. Gordon. 2008. Floodplains: Critically threatened ecosystems. Pages 45–61 in N. C. Polunin, editor. Aquatic ecosystems: trends and global prospects. Cambridge University Press, London, England.

Trush, W. T., S. M. McBain, and L. B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. Proceedings of the National Academy of Sciences of the United States of America **97:**11858–11863.

United States Department of Interior. 2000. Record of decision for the Trinity River mainstem fishery restoration. Final environmental impact statement/environmental impact report. Trinity River Restoration Program, Weaverville, CA.

Vidra, L. R., and T. H. Shear. 2008. Thinking locally for urban forest restoration: a simple method links exotic species invasion to local landscape structure. Restoration Ecology **13:**217–220.

Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river systems: ecotones and connectivity. Regulated Rivers: Research and Management **15:**125–139.

Wilson, R. A., A. J. Lind, and H. H. Welsh Jr. 1991. Trinity River riparian wildlife survey - 1990. Final report prepared for the Wildlife Task Group, Trinity River Restoration Project. United States Department of Interior, Weaverville, California.