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ARTICLE

Land Use Associations with Distributions of Declining Native Fishes in the Upper Colorado River Basin

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Abstract
The upper Colorado River basin contains one of the most imperiled fish faunas in North America. Anthropogenic land use and nonnative species impacts are considered among the top reasons for imperilment. We determined the association of anthropogenic land use intensity (road density, percentage of converted land, and oil and gas well density), relative abundance of nonnative white suckers *Catostomus commersonii* and their hybrids, and natural landscape features with the occurrences of three native fishes in the Colorado River basin, Wyoming, that have declined throughout their ranges: flannelmouth sucker *C. latipinnis*, bluehead sucker *C. discobolus*, and roundtail chub *Gila robusta*. We found that flannelmouth suckers occurred more frequently in large, low-gradient stream reaches, but their occurrence was not associated with land use intensity or the relative abundance of white suckers and hybrid suckers. In contrast, bluehead sucker occurrence decreased with increasing intensity of each land use type within a 0.5-km stream buffer, which suggests that localized land use disturbances have negatively affected the species' distribution. Roundtail chub occurred more frequently in low-gradient stream segments with more riparian vegetation, but associations with land uses were more complex. Roundtail chub were negatively associated with road density in a 0.5-km buffer, but in contrast to our expectations they were positively associated with road density in the contributing watershed and with local oil and gas well density. We think that rocky substrates and pools—habitats preferred by roundtail chub and sometimes associated with oil and gas infrastructure—have concentrated the remaining individuals within their currently reduced distribution. The associations we identified highlight the potential role of land use in distributional declines and can help managers to determine whether proposed land use changes may affect existing populations. Spatial predictions of occurrence have already been used in regional fish conservation planning efforts in Wyoming.

The native ichthyofauna of the upper Colorado River basin ranks among the most imperiled in North America. Seven of the 14 native fish species are listed as imperiled by the American Fisheries Society Endangered Species Committee (Jelks et al. 2008), and four are listed as endangered under the U.S. Endangered Species Act. Six species are endemic to the Colorado River basin, and two taxa represent endemic subspecies of more widely distributed species. Nearly all native fishes in the upper Colorado River basin have declined in distribution, probably as a result of anthropogenic activities such as dam construction (Martinez et al. 1994; Van Steeter and Pitlick 1998; Osmundson et al. 2002), land conversion and water consumption (Richter et al. 2003), wetland drainage and creation (Beatty et al. 2009), deliberate suppression (Holden 1991; Wiley 2008), and the introduction of over 60 nonnative fish species (Olden et al. 2006).

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To date, most fish conservation activity has focused on four federally protected species (razorback sucker *Xyrauchen texanus*, bonytail *Gila elegans*, humpback chub *G. cypha*, and Colorado pikeminnow *Ptychocheilus lucius*; USFWS 2010) and the Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus*, a sport fish that occupies only 13% of its historical range (Young 2008). Other species have received comparatively little attention. Recently, however, state and federal agencies signed a rangewide conservation agreement with the goal of ensuring the long-term persistence of the roundtail chub *G. robusta*, flannelmouth sucker *Catostomus latipinnis*, and bluehead sucker *Catostomus discobolus* throughout their ranges (UDNR 2006). These species are commonly found in warmwater streams and rivers and often occur in pools with rocky substrates; juveniles use low-velocity areas, whereas adults are capable of using more fluvial habitats (Baxter and Stone 1995; Bezzerides and Bestgen 2002; Bower 2005). The maximum age of the roundtail chub is unknown (Bezzerides and Bestgen 2002), whereas the suckers can reach 18–26 years of age (Sweet et al. 2009). Although the roundtail chub, flannelmouth sucker, and bluehead sucker were once common to abundant in the upper Colorado River basin (Tyus et al. 1982), a recent assessment reported that the three native species occupy only 45, 45, and 50%, respectively, of their historical ranges (Bezzerides and Bestgen 2002). Their declines in distribution were attributed to habitat degradation from land use activities, streamflow alteration due to water use and dams, and negative interactions (including hybridization) with nonnative species. Recent fish surveys in Wyoming show that the nonnative white sucker *Catostomus commersonii* now numerically dominates fish communities across the basin, and other nonnative species can be locally abundant (Gill et al. 2007; Gelwicks et al. 2009). Oil and gas production has also increased substantially, exerting detrimental effects on some wildlife populations (Sawyer et al. 2009) and potentially affecting aquatic ecosystems and fisheries (Davis et al. 2009; Farag et al. 2010). Although these factors have been posited as reasons for distributional declines, no formal analyses have been conducted at the landscape scale.

Our goal was to identify how anthropogenic land use intensity and the abundance of nonnative white suckers and their hybrids are related to the distributions of roundtail chub, flannelmouth suckers, and bluehead suckers across the upper Colorado River basin in Wyoming. Our objectives were twofold: (1) to determine how occurrences of the three native species were related to anthropogenic land use intensity (road density, percentage of converted land, and oil and gas well density), relative abundance of nonnative white suckers and their hybrids, and natural landscape features; and (2) to make spatially explicit predictions of each species' occurrence probability across the landscape to inform fisheries management and conservation. Given their recent distributional declines, we hypothesized that the three species would show negative associations with each land use type and with the relative abundance of white suckers and their hybrids. The relationships we observed help to contextualize the reported declines in native species distributions in Wyoming, and model predications of occurrence have already been applied to conservation planning efforts in this region of rapid land use change.

METHODS

Fish collection data.—We used data from a 2002–2006 Wyoming Game and Fish Department fish survey of the upper Colorado River basin to meet our objectives (Figure 1). Stream sites were systematically sampled approximately every 8–16 km on all perennial streams (Strahler stream order = 1–9; watershed area = 0.5–24,500 km^2). Sample sites included the main-stem Green River, the largest Colorado River basin tributary in Wyoming. Because the survey was focused on warmwater fishes, the upstream extent of sampling per stream was terminated when the stream became dry or when the sampled fish community became dominated by salmonids (*Oncorhynchus* spp., *Salvelinus* spp., or *Salmo* spp.) or sculpins *Cottus* spp. In wadeable streams, fish sampling occurred in 200-m-long stream reaches isolated with block nets (5-mm mesh) or by natural barriers (e.g., dams constructed by North American beaver *Castor canadensis*). One gear type or a combination of gear types was used at each site to maximize sampling efficiency. Most sites were sampled with a shore-based electrofisher with one to four anodes (more anodes were used in larger streams) or a backpack electrofisher with one anode. Some deeper wadeable streams were sampled by use of an electrofishing unit (with up to three roving anodes) mounted on a cataraft. If electrofishing effectiveness was perceived to be poor by field crews during the first pass (e.g., fish were visibly evading capture), a second electrofishing pass or seine haul was completed. Seine hauls were occasionally made when residual pools were the only habitat type available. Nonwadeable streams were sampled with a raft electrofisher equipped with two fixed, boom-mounted anodes. Raft electrofishing samples were sometimes supplemented with periodic seine hauls in backwaters or other off-channel habitats to better represent small-bodied fishes.

All collected fishes were sorted by species and counted. Lengths and weights were taken for all flannelmouth suckers, bluehead suckers, and roundtail chub and for a minimum of 30 nonnative suckers (white suckers or hybrids). Hybrid suckers were identified by caudal peduncle depth, variation in scale size along the lateral line, and mouth morphology (see discussion by Quist et al. 2009). Unidentifiable fish were preserved in 10% formalin and were sent to the Larval Fish Laboratory at Colorado State University. Tissue samples (left pelvic fin) were taken from roundtail chub, flannelmouth suckers, bluehead suckers, and sucker hybrids and were preserved in 95% ethanol. Single-nucleotide polymorphisms were used to verify and correct phenotypic field identifications.

Environmental variables.—Natural landscape features and land use intensity were evaluated for their hypothesized effects on species occurrences at three different spatial scales: stream segment, 0.5-km segment buffer, and contributing watershed

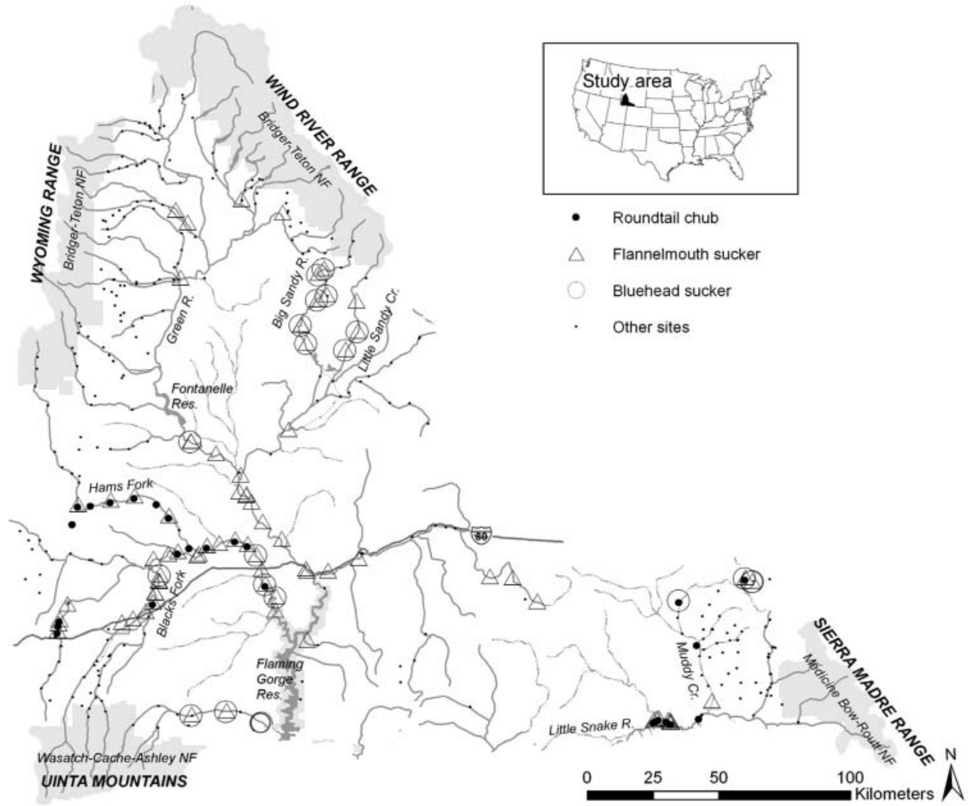

FIGURE 1. Fish sampling locations and occurrences of the flannelmouth sucker, bluehead sucker, and roundtail chub in the upper Colorado River basin, Wyoming (Res. = Reservoir; NF = National Forest). Inset shows location of the study area within the western United States.

(Table 1). We evaluated some variables at two scales, within a 0.5-km buffer and within the contributing watershed, because it is not known whether their influence is local (buffer) or accumulates downstream (contributing watershed; sensu Lammert and Allan 1999). At the segment scale, stream slope (%) and predicted mean annual streamflow (m^3/s; unit runoff method: RTI 2001) were determined for individual stream segments via the National Hydrography Dataset Plus (1:100,000 scale); predicted mean annual streamflow served as a measure of stream size that incorporated drainage area (USEPA and USGS 2006). Mean annual air temperature (°C) was determined with the Parameter–Elevation Regressions on Independent Slopes Model (PRISM) 800-m Normals data set (1971–2000; PRISM Climate Group, Oregon State University, Corvallis). Elevation (m) was determined with the 30-m National Elevation Dataset (U.S. Geological Survey, Sioux Falls, South Dakota). Instream habitat and fish distributions are known to change with the natural landscape features of stream slope, stream size, temperature, and elevation (Vannote et al. 1980; Brunger Lipsey et al. 2005). We included the natural landscape variables in our models (see below) to better understand how they influence our target species and to elucidate species–land use relationships that may be masked by variation due to natural factors. Road density (km/km^2), oil and gas well density (wells/km^2), and percent converted land were measured within a 0.5-km buffer and within the contributing watershed. Road density was measured by use of roads data from the Census 2000 Topologically Integrated Geographic Encoding and Referencing (TIGER) system (U.S. Census Bureau, Washington, D.C.), density of oil and gas wells was measured by using a 2004 database for wells in the western United States (USGS 2004), and converted land was determined based on three land cover classes (developed, pasture/hay, and cultivated crops) from the 2001 National Land Cover Data (U.S. Geological Survey, Sioux Falls). Roads, urban areas, cultivated lands and pasture, and oil and gas wells all potentially have negative effects on aquatic ecosystems and fishes (Angermeier et al. 2004; Burcher et al. 2007; Wenger et al. 2008; Davis et al. 2009).

We assessed riparian condition to detect potential influences of cattle grazing and flow alteration on instream habitat condition (Keller and Burnham 1982; Saunders and Fausch 2009). Riparian condition was quantified as the proportion of the floodplain with riparian vegetation. The floodplain was defined as areas within a specific distance and elevation of each stream segment, and the distances and elevations varied based on Strahler stream order (Ruefenacht et al. 2005). We used the Existing Vegetation Type data layer from the LANDFIRE Project (USFS 2009) to identify the following five riparian

TABLE 1. Summary statistics of environmental variables measured at 354 sites with presence or absence of native flannelmouth suckers (FMS), bluehead suckers (BHS), and roundtail chub (RTC) and nonnative white suckers and their hybrids (WHS). Variables were evaluated for inclusion in artificial neural networks, and the hypothesized association between each variable and species occurrence is noted.

			FMS		BHS		RTC		WHS			
Spatial scale	Variable	Statistic	Present ($n = 81$)	Absent ($n = 273$)	Present ($n = 20$)	Absent ($n = 334$)	Present ($n = 27$)	Absent ($n = 327$)	Present ($n = 181$)	Absent ($n = 173$)	Hypothesized association with FMS, BHS, RTC	Hypothesized association with WHS
Stream segment	Streamflow (m^3/s)	Mean	17.9	1.9	8.8	5.4	9.26	5.2	9.96	0.94	+	+
		Minimum	0.03	0.003	0.03	0.003	0.07	0.003	0.00	0.00		
		Maximum	87.4	93.8	69.4	93.8	20.35	93.8	93.76	12.94		
	Stream slope (%)	Mean	0.0018	0.0105	0.0049	0.0087	0.0017	0.0090	0.0040	0.0132	−	−
		Minimum	0.0000	0.0000	0.0005	0.0000	0.0006	0.0000	0.0000	0.0000		
		Maximum	0.0100	0.0900	0.0400	0.0900	0.0056	0.0900	0.0400	0.0900		
	Mean annual air temperature (°C)	Mean	4.0	3.1	3.7	3.3	4.4	3.2	3.51	3.1	+	+
		Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.00	0.0		
		Maximum	6.8	7.2	7.2	7.1	6.2	7.2	7.21	7.0		
	Elevation (m)	Mean	1,975	2,181	2,053	2,139	1,955	2,149	2,061	2,210	−	−
		Minimum	1,842	1,845	1,851	1,842	1,850	1,842	1,842	1,869		
		Maximum	2,231	2,728	2,318	2,728	2,175	2,728	2,426	2,728		
	Percent WHS[a]	Mean	24.0	7.8	17.3	11.1	21.9	10.6	22.5	0.0	−	
		Minimum	0.0	0.0	0.8	0.0	1.0	0.0	0.1	0.0		
		Maximum	89.5	100.0	89.5	100.0	58.0	100.0	100.0	0.0		
Buffer (0.5 km)	Road density (km/km^2)	Mean	1.55	1.41	1.08	1.46	1.34	1.45	1.47	1.41	−	+
		Minimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
		Maximum	6.52	11.09	2.37	11.09	4.13	11.1	6.52	11.09		
	Oil and gas well density ($wells/km^2$)	Mean	0.30	0.42	0.05	0.41	0.75	0.36	0.24	0.55	−	+
		Minimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
		Maximum	2.79	16.0	0.80	16.04	3.72	16.04	3.72	16.04		
	Percent converted land	Mean	6.7	5.8	1.8	6.3	9.1	5.8	8.0	3.9	−	+
		Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
		Maximum	59.7	59.7	16.1	59.7	57.5	59.7	59.7	49.6		
	Percent riparian vegetation	Mean	36.2	38.6	41.1	37.9	39.1	38.0	39.8	36.2	+	−
		Minimum	2.1	0.00	8.7	0.0	7.6	0.0	0.0	0.0		
		Maximum	79.8	96.5	69.0	96.5	79.8	96.5	87.4	96.5		
Contributing watershed	Road density (km/km^2)	Mean	0.85	0.82	0.88	0.83	0.94	0.82	0.84	0.82	−	+
		Minimum	0.17	0.01	0.53	0.01	0.71	0.01	0.06	0.01		
		Maximum	1.18	2.90	1.31	2.90	1.45	2.90	2.32	2.90		
	Oil and gas well density ($wells/km^2$)	Mean	0.18	0.27	0.11	0.26	0.19	0.26	0.14	0.37	−	+
		Minimum	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00		
		Maximum	0.71	16.33	0.46	16.33	0.52	16.33	0.99	16.33		
	Percent converted land	Mean	4.3	2.9	2.1	3.2	2.8	3.2	4.10	2.2	−	+
		Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.00	0.0		
		Maximum	16.6	100.0	12.1	100.0	12.9	100.0	100.0	73.1		

[a]The percent WHS variable was not evaluated for association with RTC occurrence or WHS relative abundance.

vegetation classes: introduced riparian vegetation, Rocky Mountain montane riparian systems, Rocky Mountain subalpine–montane mesic meadow, Rocky Mountain subalpine/upper montane riparian systems, and western Great Plain floodplain. The relative abundance of nonnative white suckers and their hybrids was calculated as a numerical proportion of all fishes collected at a site based on the fish survey data set (Wyoming Game and Fish Department). We focused on white suckers and their hybrids because they numerically dominate the fish communities in Wyoming and are considered an imminent threat to native suckers (McDonald et al. 2008; Gelwicks et al. 2009). Restricted distributions of other nonnative fishes prohibited their evaluation in a landscape-scale analysis (e.g., smallmouth bass *Micropterus dolomieu* occurred at 1% of the 354 study sites, channel catfish *Ictalurus punctatus* occurred at 2% of sites, and burbot *Lota lota* occurred at 1% of sites).

Neural network modeling.—We modeled the occurrence of flannelmouth suckers, bluehead suckers, and roundtail chub as a function of environmental variables by using artificial neural networks. Artificial neural networks are composed of interconnected elements ("neurons") that work in unity to solve a specific problem (Olden et al. 2008). When used on binary data (1 = presence; 0 = absence), artificial neural networks predict the probability of occurrence as a function of environmental variables. Since probabilities of species detection were unknown, model results represented a joint probability of species detection and occurrence (Elith and Leathwick 2009). Artificial neural networks are an effective ecological modeling technique for use when species prevalence is low, as is the case with our three target species. The effectiveness of neural networks stems in part from their ability to reveal nonlinear associations and complex interactions without a priori specification of model structure (Olden and Jackson 2002a).

An artificial neural network model was developed separately for each of the three native species by using the aforementioned environmental variables as predictor variables. We used the most common type of neural network for our analysis: a one-hidden-layer, supervised, feedforward neural network trained by backpropagation. In this type of neural network model, the input neurons of the network represent the predictor variables and are connected to neurons in a single hidden layer. Hidden-layer neurons are then connected to the output neuron that is the response variable (Ripley 1996). We first screened the predictor variables and removed those with *r*-values greater than 0.50 to reduce the likelihood of multicollinearity. Elevation was correlated with both stream gradient ($r = 0.594$) and mean annual air temperature ($r = -0.518$). Oil and gas well density within the contributing watershed was correlated with well density in a 0.5-km buffer ($r = 0.699$). Elevation and oil and gas well density within the contributing watershed were therefore omitted from the models. For each neural network model, we (1) standardized the data (i.e., mean = 0; SD = 1) before model fitting, (2) used entropy fitting because the response variable was binary (Olden and Jackson 2001), and (3) determined initial input weights and weight decay for each species by exploring how different values affected model performance. We determined model complexity by evaluating the predictive performance of different neural networks with 0 (no hidden layer) to 15 nodes in the hidden layer. Inclusion of more nodes in the hidden layer allows the model to fit more interactions and nonlinear patterns that might exist in the data. Predictive performance was determined with cross validation and the area under the curve (AUC) of a receiver-operating characteristic (ROC) plot. Cross validation was conducted 10-fold whereby the data set was divided into 10 subsets; the model was fitted to nine-tenths of the data, model validation was performed on the remaining one-tenth, and this process was repeated in turn for all 10 data subsets (Bishop 1995). The ROC plot was then constructed for the cross-validated model predictions. In a ROC plot, sensitivity is plotted against (1 − specificity) across the range of cut-points used to classify model-predicted probabilities of occurrence (0 = absent; 1 = present). The AUC of a ROC plot provides a measure of model discrimination (AUC = 0.5 represents no discrimination; AUC = 1.0 represents perfect discrimination; Hosmer and Lemeshow 2000). The AUC value also does not depend on selecting a single cut-point value to classify presence (versus absence) and is unbiased with respect to species prevalence (number of species occurrences) in the data set (Manel et al. 2001; Allouche et al. 2006). We identified the optimal number of nodes in the hidden layer as the point at which the AUC failed to increase when additional nodes were added.

Once the number of nodes in the hidden layer was determined, the final neural network was fitted by using all of the data. We determined the statistical significance of input–hidden-output connection weights and overall connection weight for each predictor variable by comparing the observed weights to a distribution of weights obtained by fitting the same network with the response variable randomly permuted 9,999 times (Olden and Jackson 2002b). This randomization approach is unbiased in elucidating the importance of predictor variables (Olden et al. 2004). The proportion of randomized weights, including the observed weight, that are equal to or more extreme than the observed value was used to determine one-tailed statistical significance at an α value of 0.10 based on our hypothesized direction of effect for each variable. We used a one-tailed test to reduce the chance of failing to detect the hypothesized relationships between species occurrences and each environmental variable (type II statistical error).

We used the final neural network models to predict probabilities of occurrence for each species across all stream segments in the Colorado River basin, Wyoming. The white sucker–sucker hybrid relative abundances used in model fitting were only available from the field data. Therefore, to make predictions in unsampled areas, we modeled relative abundance as a function of the same predictor variables evaluated for our target species by using a neural network model. We then used that model to make spatially explicit predictions of white sucker–sucker hybrid relative abundance for all segments in the stream network. These predicted values were used as inputs to model the probabilities of occurrence for the native suckers.

All environmental variables were measured and summarized with ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California). All analyses were run with R software (R Development Core Team 2008). Artificial neural networks were fitted with the R package nnet. The AUCs for the ROC plots were approximated with the R package Presence-Absence (Freeman and Moisen 2008). Model predictions were made with the "predict" function in R and were displayed with ArcGIS version 9.3.

RESULTS

All three native species were collected at less than 25% of the sample sites. Flannelmouth suckers were collected at 22.9% of the 354 sites sampled, bluehead suckers were collected at 5.6% of the sites, and roundtail chub were collected at 7.6% of the sites (Figure 1). All three native species tended to occur in relatively large, low-gradient streams at low elevations, but each species occurred across a wide range of environmental conditions (Table 1). White suckers and sucker hybrids occurred at 51% of the sites (i.e., at 181 sites), where their relative abundance ranged from 0.9% to 100% (mean = 22.5%; Figure 2).

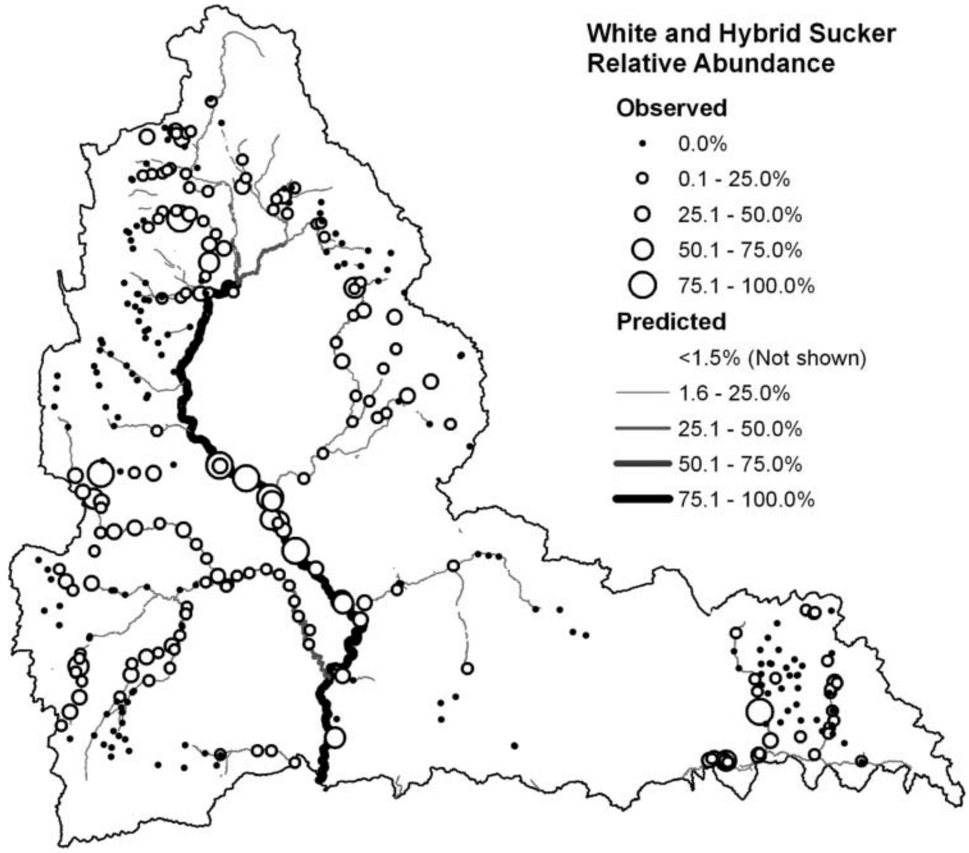

FIGURE 2. Observed relative abundance at sampling locations and spatially explicit model predictions of relative abundance for nonnative white suckers and hybrid suckers in the upper Colorado River basin, Wyoming.

Neural network models showed that different environmental variables affected the occurrence of the three native species in simple but different ways. Cross-validated predictive performance (i.e., AUC) showed little improvement as the number of hidden layer nodes in the neural network was increased beyond 0 or 1. The minimal improvement in AUC indicated a lack of interacting and nonlinear responses to the environmental variables. One-node models were best for flannelmouth suckers and bluehead suckers (AUC = 0.90 and 0.71, respectively), whereas the best model for roundtail chub was a zero-node model without a hidden layer (AUC = 0.83). The AUC values suggested that the roundtail chub and flannelmouth sucker models had excellent to outstanding discrimination ability and that the bluehead sucker model showed acceptable discrimination ability (Hosmer and Lemeshow 2000).

Only 2 of 10 variables were significantly associated with flannelmouth sucker occurrence ($P < 0.10$; Table 2). As hypothesized, flannelmouth sucker occurrence was strongly and positively related to streamflow and negatively related to stream slope (Figure 3). Land use variables and the relative abundance of white suckers and their hybrids were not significantly associated with flannelmouth sucker occurrence.

Bluehead sucker occurrence was significantly related to 4 of 10 environmental variables in the direction we hypothesized ($P < 0.10$; Table 2). Bluehead sucker occurrence showed a strong positive association with mean annual streamflow and was negatively associated with localized land uses, as we expected (i.e., road density, percentage of converted land, and oil and gas well density, each within a 0.5-km buffer; Figure 3).

Four of nine variables had significant associations with roundtail chub presence ($P < 0.10$; Table 2). As we hypothesized, roundtail chub were more likely to occur in relatively low-gradient streams with warmer annual air temperatures, lower road densities within a 0.5-km buffer, and more riparian vegetation in the floodplain (Figure 3). Road density in the watershed and oil and gas well density in a 0.5-km buffer had large positive input–hidden-output connection weights that would have been significant if we had used two-tailed statistical tests ($|\text{weight}| > 0.5$; see Table 2). Although we used one-tailed tests to maximize the power to detect our hypothesized negative associations for these variables, the large positive connection weights suggested that roundtail chub were more likely to occur where road densities in the entire watershed were higher and where oil and

TABLE 2. Input–hidden-output connection weights for the flannelmouth sucker (FMS) and bluehead sucker (BHS) neural network models and direct connection weights for the roundtail chub (RTC) and white sucker–sucker hybrid (WHS) neural network models. Weights show the relative magnitude and direction of effect for each variable. Results for a one-tailed permutation test are reported (9,999 permutations); significance (one-tailed $\alpha = 0.10$) was assessed based on the hypothesized direction of effect listed in Table 1.

	FMS		BHS		RTC		WHS	
Variable and spatial scale	Weight	P	Weight	P	Weight	P	Weight	P
Streamflow	27.059	<0.001	27.216	<0.001	−0.292	0.738	0.383	<0.001
Stream slope	−16.161	<0.001	−3.042	0.279	−5.660	<0.001	−1.438	<0.001
Mean annual air temperature	1.262	0.268	0.657	0.442	0.565	0.016	0.104	0.200
Percent WHS[a]	0.291	0.846	7.493	0.939				
Road density (0.5-km buffer)	−0.085	0.476	−7.860	0.064	−0.509	0.056	0.063	0.242
Oil and gas well density (0.5-km buffer)	0.891	0.723	−15.137	0.008	0.574	0.999	−0.006	0.535
Percent converted land (0.5-km buffer)	−1.373	0.260	−6.165	0.094	0.146	0.737	0.086	0.212
Riparian vegetation (floodplain)	0.241	0.460	−0.155	0.524	0.514	0.013	0.179	0.942
Road density (watershed)	−1.408	0.258	3.450	0.799	0.679	0.998	−0.054	0.600
Percent converted land (watershed)	0.704	0.693	−5.964	0.180	−0.151	0.403	−0.246	0.916

[a]The percent WHS variable was not evaluated for association with RTC occurrence or WHS relative abundance.

gas well densities within a 0.5-km buffer were higher. There were no associations between roundtail chub occurrence and streamflow or percent converted land at either the 0.5-km buffer scale or watershed scale.

Diagnostic tests showed that a zero-node neural network model was sufficient to predict relative abundance of white suckers and sucker hybrids, and the final model was fitted by using all predictor variables. Pearson's product-moment correlation coefficient (Pearson's r) between 10-fold cross-validated model predictions and observed relative abundance was 0.49. The model indicated that the relative abundance of white suckers and hybrid suckers was significantly higher in relatively large, low-gradient stream segments but was not significantly related to any land use variable ($P < 0.10$; Table 2; Figure 3). Model predictions showed that relative abundance was predicted to be higher in large, low-gradient streams (Figure 2).

Spatially explicit predictions of native species' probability of occurrence varied across the study area. Predictions for flannelmouth suckers ranged from 0.01 to 0.84 (mean = 0.10) and showed that this species was most likely to occur along large, low-gradient stream systems (Figure 4). Predictions for bluehead suckers were never greater than 0.20 (range = 0.001–0.20; mean = 0.04), indicating a low probability of occurrence throughout the basin in Wyoming. Predictions for roundtail chub ranged from 0 to 1 and showed low probabilities of occurrence for many stream segments (mean = 0.05), whereas a few segments where roundtail chub occurred and a few scattered segments in the north had high predicted probabilities.

DISCUSSION

We found that land use intensity had significant but simple and straightforward associations with the distribution (i.e., occurrence) of roundtail chub and bluehead suckers in the upper Colorado River basin, although the observed associations did vary across species and sometimes were in contrast to our expectations. Flannelmouth sucker occurrence, however, was only associated with environmental variables representing natural stream characteristics: mean annual streamflow (stream size) and stream slope. The lack of association between land use intensity and flannelmouth sucker occurrence is somewhat surprising because the species is considered to occupy only 45% of its historical distribution, and others have suggested that the negative effects of land use on aquatic habitats have influenced this species' decline (Bezzerides and Bestgen 2002).

Roundtail chub were negatively associated with road density in a 0.5-km stream buffer, which was consistent with our expectations. Culverts associated with road–stream crossings represent potential barriers to fish passage in the study area (Gelwicks et al. 2009), and population fragmentation threatens the persistence of roundtail chub populations in Wyoming (Compton et al. 2008). However, the roundtail chub appeared to be *positively* associated with road density at the watershed scale and with oil and gas well density within a 0.5-km stream buffer. We think it is unlikely that roads and oil and gas development per se are beneficial to roundtail chub, especially given the species' recent decline. Rather, roundtail chub occurrences could be associated with some factor that was omitted from our model but that is also associated with oil and gas development activity. Allan (2004) described how human influences on the landscape can covary with natural landscape features with which stream fishes are associated, thus leading to false conclusions regarding human impacts (e.g., that effects are positive) on aquatic ecosystems and stream fishes. For example, roundtail chub associate with deep pools and rocky substrates (Bower et al. 2008), and local rocky substrates could be influenced by underlying geology that is also amenable to oil and gas extraction. In

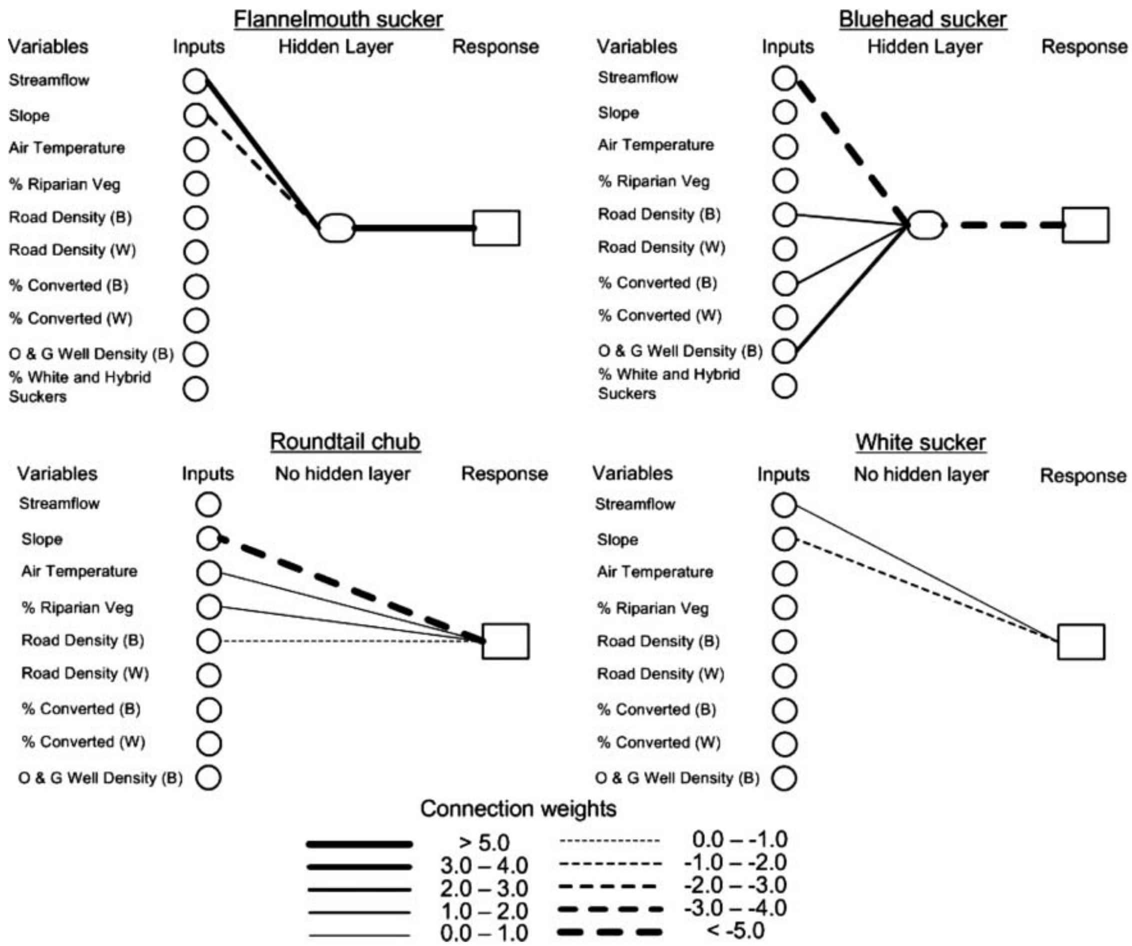

FIGURE 3. Neural interpretation diagrams for neural network models predicting flannelmouth sucker, bluehead sucker, and roundtail chub occurrences and white sucker–hybrid sucker relative abundance as a function of environmental variables in the upper Colorado River basin (Veg = vegetation;% Converted = percentage converted land; O & G = oil and gas). Variables (circles) connected to hidden neurons (ovals) or response variables (rectangles) significantly influence species occurrence or relative abundance (one-tailed $P < 0.10$). Input–hidden-output connection weight (see Table 2) and the direction of effect for each variable are determined as the product of input and output weights. Some environmental variables were measured at both the 0.5-km buffer scale (B) and contributing watershed scale (W).

addition, road and pipeline crossings are often constructed or fortified with rocky materials and create scour pools downstream. Reservoirs and water diversions have decreased the frequency of moderate floods that control channel morphology and instream habitat in many parts of the basin (Van Steeter and Pitlick 1998; Gaeuman et al. 2005). Decreased flood frequencies have limited the availability of natural pool habitats used by native fishes. Artificial structures can also inhibit fish passage (Compton et al. 2008; Gelwicks et al. 2009). Pools that are coincident with anthropogenic structures and fish passage barriers can concentrate fish from otherwise reduced or fragmented populations (Balkenbush and Fisher 1999). This can create the appearance that anthropogenic structures (e.g., those associated with oil and gas well infrastructure) are beneficial to native fishes when they actually have negative long-term effects. Regardless, the apparent positive associations between roundtail chub and oil and gas well density and road density at the watershed scale require further research, especially since our one-tailed statistical tests were not specifically designed to detect such associations (Ruxton and Neuhäuser 2010).

While artificial structures in streams may concentrate roundtail chub, they can also prohibit fish passage and threaten population persistence (Compton et al. 2008; Gelwicks et al. 2009). We did not directly address the effect of barriers in this study for two reasons: (1) although some barriers are known to prohibit passage (e.g., large dams), it is not clear exactly how small of a structure prohibits passage of our study species; and (2) detailed information on potential barriers is not available for our entire study area. Regardless, population fragmentation from impassible road culverts probably explains the negative association of roundtail chub and bluehead suckers with local road densities. This suggests that regional road–stream crossings should be inventoried, evaluated for fish passage, and modified where appropriate. In addition, small dams, grade control structures, and

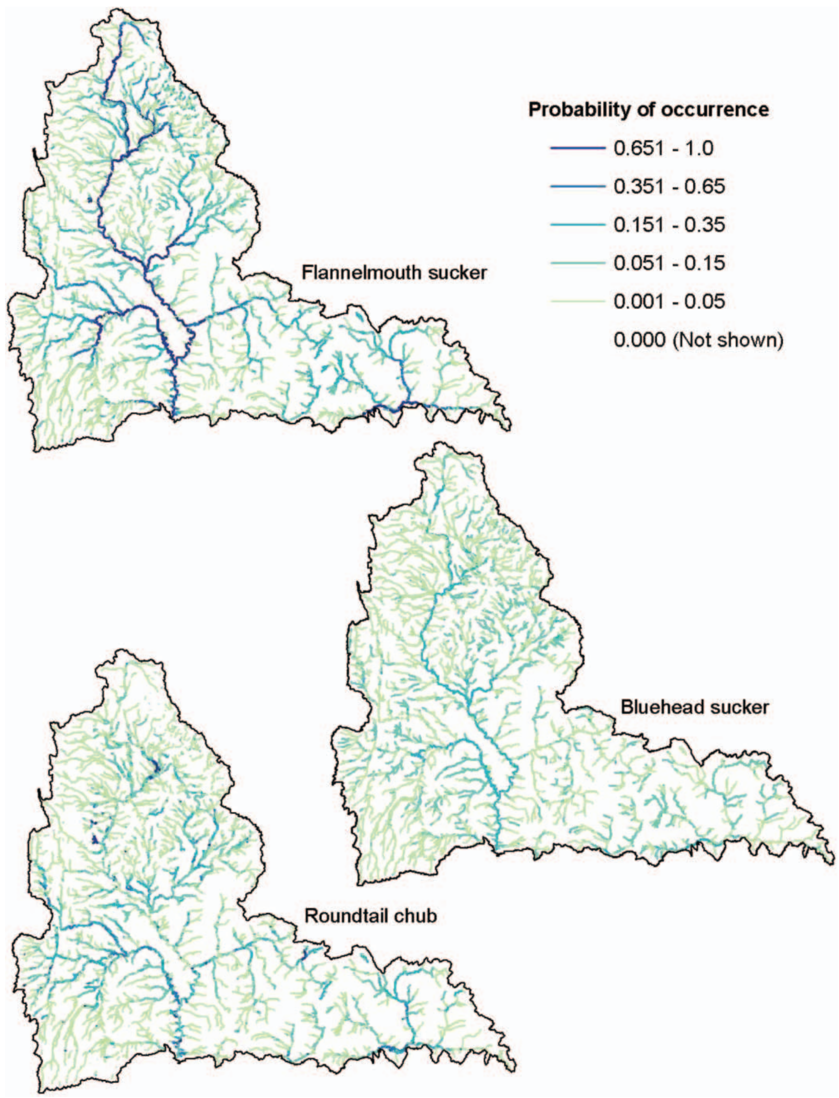

FIGURE 4. Spatially explicit predictions of occurrence probability for the flannelmouth sucker, bluehead sucker, and roundtail chub in the upper Colorado River basin, Wyoming. [Figure available in color online.]

water diversion structures have also altered regional stream habitats, causing fragmentation of and threatening the persistence of roundtail chub, flannelmouth sucker, and bluehead sucker populations, as was demonstrated in one Wyoming watershed (Compton et al. 2008). At a regional scale, the Flaming Gorge am has isolated the upper and lower portions of the Green River basin (Vanicek et al. 1970), and Fontenelle Dam has further divided the Green River. The explicit effect of fish passage barriers on the distribution of our study species at the landscape scale should be identified, but accomplishing this will be contingent on knowing exactly what constitutes a barrier (including behavioral barriers) and where they are located on the landscape (Fullerton et al. 2010).

We originally hypothesized a negative association between native sucker occurrences and white sucker relative abundance because of potential local extirpation due to hybridization (McDonald et al. 2008). We did not detect any significant negative associations, but the models showed that native suckers occurred more often in the relatively large, low-gradient streams where white suckers were also more abundant. The similarity of environmental preferences between native suckers and white suckers reinforces the threat of hybridization. Native sucker and white sucker populations do not segregate while spawning, and thus negative associations could emerge over time as native sucker populations become genetically introgressed and effectively extirpated from areas where white suckers remain abundant (Sweet and Hubert 2010). This also makes management problematic since white suckers are widely distributed, and it is not currently feasible to eliminate them basinwide or even from large river systems (Gelwicks et al. 2009).

Thus, effective management of native suckers will be contingent on establishing populations that are isolated from white suckers, and fish passage projects will have to balance between providing passage for native fishes and keeping nonnative invaders at bay (sensu Fausch et al. 2009). Efforts are currently underway in Wyoming to manage fish passage barriers, remove white suckers, and restore native fish assemblages in Muddy Creek (a tributary to the Little Snake River), Big Sandy River, and Little Sandy Creek (Gelwicks et al. 2009; Sweet et al. 2009).

The associations between land use and roundtail chub and bluehead sucker distributions should be further studied to better understand the mechanisms behind them. Some land use impacts to aquatic systems (e.g., from urbanization, agriculture, and road building) have a conceptual foundation, and negative associations between them and aquatic species are routinely observed (Wheeler et al. 2005; Burcher et al. 2007; Wenger et al. 2008). However, the exact mechanisms producing the negative effects are not always clear (sensu Wenger et al. 2009b), and the impacts have been understudied in southwestern Wyoming streams. In particular, the potential effect of oil and gas development on streams and fishes has only recently gained interest but has not previously been evaluated on a large scale in the Colorado River basin (Davis et al. 2009; Farag et al. 2010). Evaluating how natural stream features and land uses structure the local habitats preferred by roundtail chub and bluehead suckers (e.g., pools and rocky substrates; Bower et al. 2008) will lead to a better understanding of how land use is linked to these species' recent declines. For example, land use in Iowa negatively influenced fish assemblages by altering the physical habitats with which certain species were associated (Rowe et al. 2009a, 2009b). The long life span of suckers may also delay the negative effects of land use activities, nonnative species, and population fragmentation on sucker distributions across the landscape (Compton et al. 2008; Sweet et al. 2009). If so, the magnitude of the negative associations we observed between certain land uses and native species is likely to have been underestimated, particularly for oil and gas development, which has accelerated over the last decade.

Modeling fish distributions as a function of environmental variables can provide important insights into factors that control species occurrence on the landscape. Distribution models often have good predictive ability when developed across large spatial extents (large regions) because large-scale characteristics of landscapes are thought to control occurrences of native species (Poff 1997), whereas local abundance is thought to be controlled more by local habitat conditions (Dauwalter et al. 2008). This is one reason why models that predict species occurrences often outperform and have better predictive capability than models predicting relative abundances or densities (Stanfield et al. 2006; Brewer et al. 2007). For example, our native species presence–absence models had better predictive performance (AUC = 0.71–0.90) than our white sucker–hybrid sucker relative abundance model (Pearson's $r = 0.49$). Similarly, Stanfield et al. (2006) predicted presence–absence of rainbow trout *O. mykiss* as a function of landscape-scale variables with good accuracy (86% correct classification rate) for Lake Ontario tributaries, but their model predicting rainbow trout density had poorer predictive performance for the same region ($r^2 = 0.49$). Although we did not directly assess how current native fish distributions differ from historical distributions (Hoagstrom et al. 2009), the associations we observed can be still be used to determine the role of land use in the purported distributional declines.

The spatial resolution and temporal era of the data we used in our models may have influenced our results, particularly for rapidly changing land uses. Species occurrences from 2002 to 2006 may not entirely reflect the influence of 2000-era roads and 2004-era oil and gas wells. For example, the number of oil and gas wells increased 14% annually from 2004 to 2006 (from 2,339 to 3,035 wells) in Sublette County, Wyoming (Wyoming Oil and Gas Conservation Commission 2009). Aquatic species can show stronger relationships to historical rather than present-day land uses (Harding et al. 1998; Wenger et al. 2008), particularly for long-lived species like the flannelmouth sucker and bluehead sucker (Sweet et al. 2009). Additionally, Hawbaker and Radeloff (2004) found that 1:100,000-scale TIGER data underrepresented roads, particularly secondary roads, by up to 50% in northern Wisconsin. These secondary roads may affect aquatic resources more so than primary roads because they are often poorly designed and maintained (Waters 1995). We suspect that secondary roads in Wyoming were also underrepresented in the TIGER data since many were built in association with the recent oil and gas development activity.

Neural network models have the ability to detect complex relationships between species and their environments without a priori specification of model structure. For this reason, they often outperform other statistical modeling techniques (e.g., generalized linear models) that require careful a priori specification of interactions and nonlinear relationships (Olden and Jackson 2002a). Neural network models have been used successfully to model fish distributions (presence–absence) as a function of environmental variables in both lakes and streams (Vander Zanden et al. 2004; Steen et al. 2006). When species relationships with environmental variables are not complex, other approaches such as generalized linear models can perform as well as artificial neural networks (Steen et al. 2006). Our results suggested that the relationships between occurrences of our study species and environmental variables were relatively simple (i.e., additive and linear on a logit scale) and that a generalized linear model would probably have yielded similar results. However, our use of artificial neural networks safeguarded against misspecification of model structure before analysis since information on exactly how these species' occurrences are related to certain environmental variables is sparse relative to more intensively studied fishes, such as salmonids (Cooke et al. 2005). As a consequence, the use of generalized linear models could have resulted in misspecified models with poor predictive performance.

Despite the need for a mechanistic understanding of how land uses influence these declining species, the associations and model predictions can inform conservation and management decisions. Fisheries managers often comment on proposals for land management projects that potentially affect aquatic resources (Stern et al. 2010). The associations we observed can generally be used to anticipate the manner in which road building or oil and gas development in leased areas will affect these native species. This is especially true for bluehead suckers, which were only collected at 5.6% of sample sites and showed negative associations with every land use. However, since the models also showed good to excellent predictive capability (i.e., AUC = 0.71–0.90), the spatial predictions can also be used (i.e., in cases where field data are absent) to aid managers in determining whether native fishes are likely to occur in areas of proposed land management changes (Dauwalter and Rahel 2008). These informed decisions will be particularly important when land development is considered in drainages that have been designated as native fish restoration priorities (e.g., Muddy Creek, Big Sandy River, and Little Sandy Creek; Gelwicks et al. 2009).

Spatially explicit predictions of occurrence probability can also be used in conservation planning. Our predictions have already been used to help identify Wyoming watersheds for a new conservation initiative of the National Fish and Wildlife Foundation (2009). Watersheds were identified based on proximate distributions of Colorado River cutthroat trout and our three study species (Dauwalter et al. 2011). Data for each Colorado River cutthroat trout population in the basin were spatially complete (Hirsch et al. 2006), but data for the three warmwater species were not. Hence, our model predictions were used to estimate potential distributions and identify specific watersheds where conservation efforts could benefit coldwater and warmwater fishes. Model predictions of occurrence are a common input into spatial conservation planning analyses as an indicator of potential species distributions in situations where field data are absent (Elith and Leathwick 2009; Wenger et al. 2010). For example, Wenger et al. (2009a) used known and predicted species distributions to prioritize the Conasauga River basin, Tennessee–Georgia, for native fish conservation and restoration. Rigorous conservation plans must be proactive and should consider current species distributions and potential distributions relative to impending land use changes, including oil and gas development, which is forecasted to increase in our study area and across the Intermountain western United States (Copeland et al. 2009).

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