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Distribution modelling to guide stream fish conservation: an example using the mountain sucker in the Black Hills National Forest, USA

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ABSTRACT

1. Conservation biologists need tools that can utilize existing data to identify areas with the appropriate habitat for species of conservation concern. Regression models that predict suitable habitat from geospatial data are such a tool. Multiple logistic regression models developed from existing geospatial data were used to identify large-scale stream characteristics associated with the occurrence of mountain suckers (*Catostomus platyrhynchus*), a species of conservation concern, in the Black Hills National Forest, South Dakota and Wyoming, USA.

2. Stream permanence, stream slope, stream order, and elevation interacted in complex ways to influence the occurrence of mountain suckers. Mountain suckers were more likely to be present in perennial streams, and in larger, higher gradient streams at higher elevations but in smaller, lower gradient streams at lower elevations.

3. Applying the logistic regression model to all streams provided a way to identify streams in the Black Hills National Forest most likely to have mountain suckers present. These types of models and predictions can be used to prioritize areas that should be surveyed to locate additional populations, identify stream segments within catchments for population monitoring, aid managers in assessing whether proposed forest management will potentially have impacts on fish populations, and identify streams most suitable for stream rehabilitation and conservation or translocation efforts.

4. When the effect of large brown trout (*Salmo trutta*) was added to the best model of abiotic factors, it had a negative effect on the occurrence of mountain suckers. Negative effects of brown trout on the mountain sucker suggest that management of recreational trout fisheries needs to be balanced with mountain sucker conservation in the Black Hills. However, more spatially explicit information on brown trout abundance would allow managers to understand where the two species interact and where recreational fisheries need to be balanced with fish conservation.

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KEY WORDS: mountain sucker; GIS; distribution modeling; logistic regression; presence–absence; brown trout; aquatic conservation; Black Hills

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INTRODUCTION

The distribution and abundance of organisms are often influenced by factors operating across spatial scales (Frissell *et al*., 1986; Wiens, 2002). Understanding which factors are important at a particular scale is important because it can allow managers to focus their efforts at the spatial scales where they are most likely to effect change in the populations of interest (Dauwalter *et al*., 2007). Historically, the factors affecting the distribution of stream fish were evaluated at a local scale (Fausch *et al*., 2002). Water depths, velocity, substrate and cover were often measured within short reaches of a stream ($\sim$200 m) and then related to the presence and abundance of fish (Kozel and Hubert, 1989). However, aquatic biota are often influenced by factors operating at large spatial and temporal scales (Durance *et al*., 2006; Hughes *et al*., 2006). With the advent of geographic information systems (GIS) and the increased availability of large-scale spatial data, managers have an improved ability to evaluate the effects of large-scale variables on fish distributions and abundance (Creque *et al*., 2005). Because large-scale data are available for large geographic areas, a GIS can be used to predict the occurrence of fish in areas that have not been sampled (Filipe *et al*., 2002; Fisher and Rahel, 2004).

Large-scale predictors of fish occurrence and abundance provide two important advantages over field-based predictors. Large-scale factors, such as those at the regional, catchment, or stream segment scale often act as controls on the distribution of local habitats (Isaak and Hubert, 2001). This link between large and small spatial scales often results in relationships between fish and large-scale controlling variables (Pusey *et al*., 2000; Dauwalter *et al*., 2007; Dauwalter *et al*., in press). Brewer *et al*. (2007) showed that the distribution of smallmouth bass (*Micropterus dolomieu*) in Missouri, USA was associated with catchment topography and soils, whereas local abundances were associated with stream size, channel slope, and groundwater influx. Unlike field-based predictors, large-scale predictors can be mapped over large geographic areas using a GIS. This allows statistical models to be applied to large, unsampled areas and presented spatially as maps. These spatially explicit predictions of occurrence and abundance are beneficial to management, especially when management decisions need to be made with limited data on species distributions (Peterson and Vieglais, 2001). Statistical models based on spatially extensive data allow areas of suitable habitat to be identified quickly without costly field studies. Such models also make it is easier to identify large areas with suitable habitat that then can be targeted for conservation or restoration efforts (Rodríguez *et al*., 2007). For example, Wall *et al*. (2004) modelled the distribution of Topeka shiner (*Notropis topeka*) by using large-scale geospatial data, and combined its predicted distribution with land protection information to identify areas that should be given high conservation priority. Brewer *et al*. (2007) used their models to predict the distribution of smallmouth bass throughout Missouri, and suggested that predictions could be used to identify stream segments of management interest where smallmouth bass populations were not meeting their natural potential.

Species distributions can also be influenced by biotic interactions (Poff, 1997). Species may be absent from streams with suitable habitats because of competition with, or predation by, other fish. For example, knowledge of how and when species interact is useful to managers who need to balance management or conservation efforts between interacting species. In Japanese streams, white-spotted charr (*Salvelinus leucomaenis*) and Dolly Varden (*Salvelinus malma*) were mostly segregated along a temperature gradient, but density compensation caused by interspecific competition affected their abundances in stream pools when they occurred in sympatry (Fausch *et al*., 1994). Although biotic interactions between stream fish have been shown many times, they are rarely included in models that predict fish occurrences and, hence, distributions. This is because extensive spatial data on fish distributions are often lacking. However, accounting for species interactions in distribution models can have important conservation and management implications, such as when managers need to determine priorities for sport fish management versus native fish conservation (Dudgeon and Smith, 2006).

The mountain sucker (*Catostomus platyrhynchus*) is native to western North America and has experienced declines in abundance and distribution in parts of its range (Decker, 1989; Patton *et al*., 1998). Aside from a few descriptions of habitat where the mountain sucker has been collected, little is known about the factors that influence its distribution. The objectives of this study were to: (1) identify large-scale abiotic factors associated with the occurrence of mountain suckers in stream segments of the Black Hills National Forest in South Dakota and Wyoming, USA; (2) predict where mountain suckers are likely to occur within the stream network in the Forest; and (3) examine the effect of large brown trout on the presence of mountain sucker after the effects of abiotic factors are determined. Predicting where mountain suckers are likely to occur will help to identify streams in the Black Hills National Forest that are of conservation interest. Furthermore, understanding how brown trout influence the distribution of mountain sucker will help managers to decide where maintenance of recreational trout fisheries needs to be balanced with the conservation of a native fish species.

METHODS

Study area

The Black Hills of South Dakota and Wyoming are a dome-shaped uplift with Precambrian igneous and sedimentary formations representing basement rocks that are exposed at the core of the uplift, and are surrounded by Palaeozoic and Mesozoic sedimentary rock formations that form a concentric ring around the core (Williamson and Carter, 2001). Elevations range from 980 to 2380 m, mean annual precipitation is 47 cm but can be as high as 74 cm in the north, and mean annual air temperature is 6.6°C with cooler temperatures at higher elevations (Williamson and Carter, 2001). Land uses in the Black Hills are ranching, grazing, logging, recreation, and mining. Changes in the forest ecosystem occurred with European settlement, as cattle grazing increased and wild fires were suppressed (Brown and Sieg, 1999). Physical and chemical characteristics of surface waters in the Black Hills vary with local geology and land use (Williamson and Carter, 2001), and locally elevated concentrations of nutrients, metals, trace elements, and dissolved solids are present from historical and recent mining activities (Rahn *et al*., 1996; Hamilton and Buhl, 2000; May *et al*., 2001). The sedimentary Madison Limestone and Minnelusa formations at high elevations in the west comprise the Limestone Plateau region (Figure 1) that is a recharge zone where streams seldom have stream flow except where perched springs occur (Carter *et al*., 2005). At low elevations these formations, in addition to the Minnekahta formation, create the Loss Zone where many streams lose all or most of their surface flow as they flow north and east off the Black Hills (Williamson and Hayes, 2000; Carter *et al*., 2005). The Black Hills represent the eastern extent of the distribution of the mountain sucker. It was historically distributed across the Black Hills, and its distribution has not changed much except for some local population declines and a possible range reduction in the south (Isaak *et al*., 2003). In this area the mountain sucker is listed as vulnerable and sensitive by private conservation groups and government agencies (Belica and Nibbelink, 2006). Both South Dakota and Wyoming have identified the mountain sucker as a species of great conservation concern (WGFD, 2005; SDGFP, 2006). The mountain sucker has also been identified as a Management Indicator Species for the Black Hills National Forest because of its distribution across the Forest and its sensitivity to human activities and land management (SAIC, 2005).

Factors influencing mountain sucker occurrence

The occurrence of mountain suckers in the Black Hills National Forest was modelled using data from a 1:24 000 scale stream network and an existing database of fish collections. Each stream segment on the network was attributed with four abiotic predictor variables. Fish collection data were spatially linked to stream segments. Logistic regression was used to model the presence–absence of mountain suckers at each site using the predictor variables. Multiple models that included different combinations of variables were compared using several diagnostic methods to identify the model that predicted mountain sucker occurrences best. The best model was then applied to the entire stream network to predict probability of occurrence for all stream segments in the Black Hills National Forest. Finally, a variable regarding the abundance of brown trout was added to the best model to evaluate the effects of a potential predator on mountain sucker occurrence.

Stream network

An existing GIS database of streams in the Black Hills National Forest was used to evaluate the effects of four abiotic predictors of mountain sucker occurrence. The stream network was created by the Black Hills National Forest to be used in forest planning. It originated from 1:24 000 scale topographic maps, and was available in the Universal Transverse Mercator, Zone 13 coordinate system and North American Datum 1983 datum. Streams were divided into segments, often lengths of stream between tributary confluences, that were typically 1 to 10 km in length.

Each segment in the stream network was attributed with information on stream permanence, stream order, elevation, and slope that represent characteristics of streams at the segment scale. The permanence of stream segments was classified as perennial or intermittent (perennial = 1, intermittent = 0) based on original topographic map classifications, but classifications were updated by forest biologists using field data. Stream permanence can be important to fish that are sensitive to stream flow patterns (Travnichek *et al*., 1995). Stream order is a measure of stream size ranging from first order for the smallest streams to higher orders for larger streams. The stream order of each segment was determined using the Strahler (1957) method, whereby stream segments without tributaries are first order, segments below the confluence of two first-order segments are second order, and so on, where segments below the confluence of segments of the same order are assigned the next higher order. Stream flow, temperature, physical habitat and energy sources often change with stream size and influence the distribution of fish (Vannote *et al*., 1980). Stream slope ($\mathrm{m\,km^{-1}}$) was computed as the change in elevation over each stream segment divided by segment length. Stream slope is often correlated with physical habitat characteristics that are important to stream fish, and can be used as a surrogate for instream habitat conditions (Isaak and Hubert, 2000). Elevations (m) of segment nodes were obtained from a 10 m digital elevation model, and were averaged for segment elevation. Elevation is often used as a surrogate for stream temperatures that influence fish distributions (Rahel and Nibbelink, 1999).

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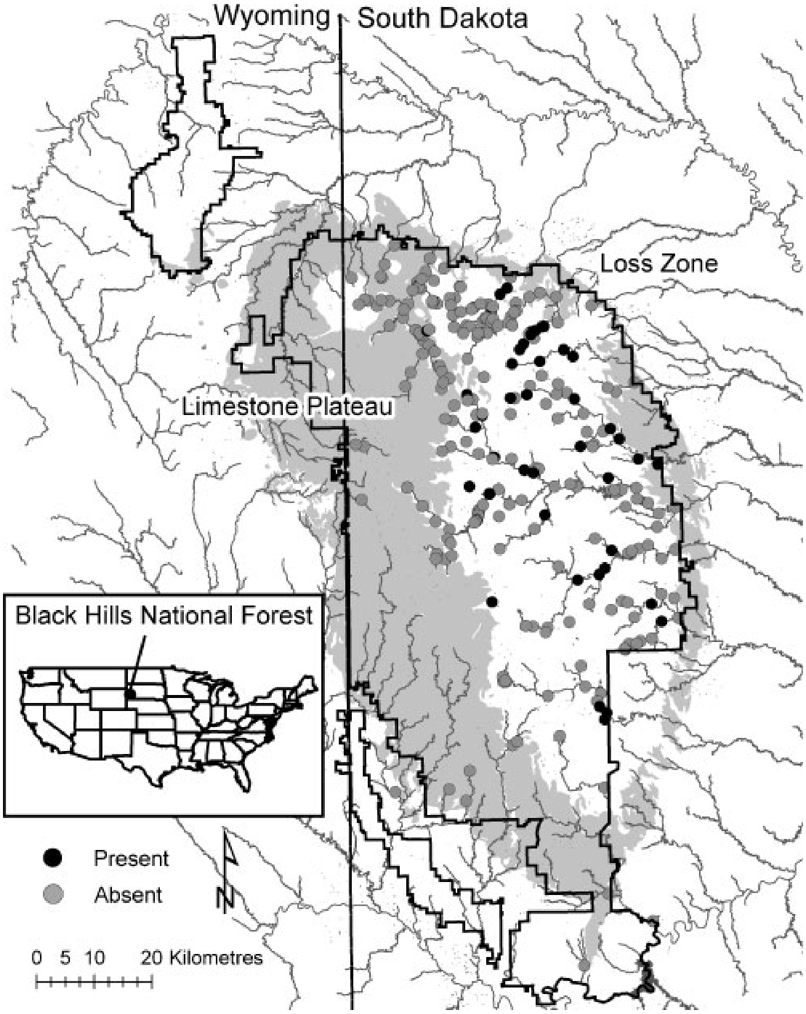

Figure 1. Fish collection sites where mountain suckers were present and absent when sampled from 1988 to 2004 at streams in the Black Hills National Forest, South Dakota and Wyoming. Only third order and larger streams are shown. Madison Limestone, Minnelusa, and Minnekahta geologic formations are shown in grey. They represent zones where streams are often intermittent at high elevations in the western Limestone Plateau region, or at low elevations in the Loss Zone in the north and east as streams flow off of the Black Hills.

Fish collection data

Existing fish collection data were used to determine the presence of mountain suckers in streams in the Black Hills National Forest. South Dakota Department of Game, Fish, and Parks sampled fish at 289 stream sites in the Black Hills National Forest from 1988 to 2004. They estimated abundance of fish within a 100 m stream reach using a three-pass removal estimate (Zippin, 1958). Three-pass capture probabilities for mountain suckers were estimated for a subset of these data and they ranged from 0.20 to 1.00 with a median of 1.00 (mean = 0.91). Because capture probability (q) and the number of individuals present (n) determine detection probability $d = 1-(1-q)^n$ (Bayley and Peterson, 2001), mountain suckers were very likely to be detected during electrofishing even if only one individual was present in the reach. If a site was sampled during multiple years, only data from the most recent year were used. The spatial location of each site was represented in a GIS database, and ArcGIS 9.1 GIS software (ESRI, Inc., Redlands, California) was used to spatially link sampling sites to the stream network.

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Modelling presence–absence

Multiple logistic regression was used to model the effects of the abiotic predictor variables on mountain sucker presence at a stream site. Logistic regression is similar to linear regression except that it predicts a binary response ($0 = \text{absence}$, $1 = \text{presence}$) from one or more predictor variables (Hosmer and Lemeshow, 2000). Logistic regression was used to model the presence–absence of mountain suckers because it has been shown to be as accurate or more accurate in predicting the presence of stream fish when compared with other modelling techniques that can predict a binary response (Steen *et al.*, 2006).

Several logistic regression models were constructed and evaluated to determine which model was the most parsimonious. First, all four predictor variables and first-order interactions between stream order, segment slope, and elevation were included in a global model. This global model was the largest model (contained the most predictors), and, hence, would fit the data best. To ensure that this largest model fitted the data, lack-of-fit of the global model was assessed using a Hosmer–Lemeshow test (Hosmer and Lemeshow, 2000). Discrimination ability of the global model was evaluated using two methods: a receiver operating characteristic (ROC) curve and *k*-fold cross-validation. The ROC curve is a plot of sensitivity versus 1-specificity over the entire range of possible probabilities (0 to 1) used to classify an observation as present or absent. The area under the curve provides a measure of discrimination ability ranging from 0.5 for no discrimination to 1.0 for complete discrimination (Hosmer and Lemeshow, 2000). Independent model validation was done using *k*-fold cross-validation (Boyce *et al.*, 2002). The data set was partitioned into $k=$ five sets, and the global model was fitted to 80% of the dataset and the remaining 20% was used for cross-validation. The cross-validated dataset was partitioned into five bins, and Spearman rank correlation was used to compare the association between the median (independently) predicted probability of occurrence and the percentage of observations with mountain suckers present among bins. This process was repeated five times for each 20% of the original dataset, and correlations were averaged to test for model fit. An r^2 measure of fit was not used because they are not recommended (Hosmer and Lemeshow, 2000), and a 2×2 classification table was not used because they rely on an arbitrary threshold probability to classify presence and can be biased when species occur infrequently (Pearce and Ferrier, 2000; Olden *et al.*, 2002). Whether or not a stream segment was perennial was assumed to influence mountain sucker presence, as it would for most fish species, and the stream permanence predictor variable was included in all candidate models to estimate effect size (Johnson, 1999). The set of candidate models consisted of the global model and models with all combinations of variables in the global model (with stream permanence always included) and first-order interactions. All models were evaluated for plausibility (Burnham and Anderson, 2002). Akaike's Information Criterion corrected for small sample bias (AIC_c) was used to quantify parsimony in each model; that is, which model explained the most variation in the data with the fewest parameters. Akaike weights (w_i) were computed to determine the probability that a given model is the best model (Burnham and Anderson, 2002). Model averaging was conducted if needed using models within 4 AIC_c units of the best model and w_i were used as model weights. Parameters not included in a specific model were given a value of zero for that model during averaging (Burnham and Anderson, 2002). All statistical analyses were done using SAS Version 9.1 statistical software (SAS Institute, Inc., Cary, North Carolina).

Mapping occurrence probabilities

The model that predicted the probability of mountain sucker occurrence best was used to predict probabilities of occurrence for each segment in the stream network in the Black Hills National Forest. Since each stream segment was attributed with the predictor variables evaluated in logistic regression models, the attributes of each stream segment could be included in the model to predict occurrence probabilities, which ranged continuously from 0 to 1 for each segment. The predicted occurrence probability for each segment was placed in a new field in the attribute table of the GIS database for the stream network. This allowed occurrence probabilities to become spatially explicit and predicted across the forest. Spatially explicit probabilities of occurrence were computed and displayed using ArcGIS 9.1 software (ESRI, Inc., Redlands, California).

Effect of brown trout on mountain sucker occurrence

The density of large brown trout ($\geqslant 20$ cm) was also evaluated for any effect on mountain sucker occurrence. The size threshold was identified in the South Dakota Game, Fish, and Parks' database and represents trout likely to be predatory on the mountain sucker. This biotic effect was modelled after modelling the effects of abiotic factors because brown trout densities were not known for much of the stream network. If brown trout density was evaluated in the initial models, it would have prohibited modelling mountain sucker occurrence for the majority of streams in the forest where no data on brown trout density were available. After the final model or best set of candidate models was selected describing how abiotic factors affected the probability of mountain sucker occurrence, then a brown trout density variable was added.

Models with and without a brown trout density variable were compared using AIC$_c$ as described above. If brown trout density had a plausible effect, then its coefficient was estimated for the best model or by using model averaging.

RESULTS

Factors influencing mountain sucker occurrence

The network of streams within the Black Hills National Forest contained 9374 stream segments with the majority (7498) representing small, intermittent streams. Stream orders ranged from 1 to 7, with 4713 segments being first order, 2341 second order, and the remainder third order or higher. Elevations ranged from 923 to 2108 m, and averaged 1550 m. Segment slopes ranged from 0 to greater than 600 m km^{-1}, with an average of 44 m km^{-1}.

Mountain suckers were present at 49 of the 289 sites that were sampled for fish in the Black Hills National Forest (Figure 1). Mountain suckers were never collected within first-order streams, and were collected in only five of 69 reaches that were classified as intermittent (Table 1). They were collected in reaches at all but the highest slope values sampled, and across a wide range of elevations.

The occurrence of mountain suckers at a site was influenced by the four abiotic variables in complex ways. There were no strong correlations indicating redundancy among the three continuous variables and all were included in the global model ($|r|_{\max} = 0.59$). The global model did not show lack of fit (Hosmer–Lemeshow: $\chi^2 = 5.56$, df = 8, $P = 0.697$) and had an ROC = 0.76. An ROC between 0.7 and 0.8 indicated that the model had an acceptable ability to discriminate between sites with and without mountain suckers (Hosmer and Lemeshow, 2000). The *k*-fold cross-validation resulted in a mean Spearman correlation among five bins of $r_s = 0.955$, indicating very good fit of models to the data (Boyce *et al.*, 2002). Model selection criteria showed that of the 40 candidate models examined, the model with stream permanence, stream slope, stream order, elevation, and first-order interactions

Table 1. Summary of stream characteristics where mountain suckers were present versus absent in stream sites of the Black Hills National Forest, South Dakota and Wyoming

Variable	Mountain sucker	*n*	Mean	SD	Range
Perennial	Present	44			
	Absent	176			
Intermittent	Present	5			
	Absent	64			
Slope (m km^{-1})	Present	49	15.8	11.9	2.6–63.0
	Absent	240	27.5	22.6	0.2–124.2
Stream order (Strahler)	Present	49	3	1	2–5
	Absent	240	3	1	1–5
Elevation (m)	Present	49	1521	149	1189–1883
	Absent	240	1552	188	975–1952
Brown trout (n ha^{-1})	Present	49	143	283	0–1388
	Absent	240	213	484	0–3587

Table 2. Linear predictor functions of logistic regression models used to assess mountain sucker probability of occurrence in streams of the Black Hills National Forest, South Dakota and Wyoming. Only models within 10 ΔAIC$_c$ units of the best model are presented. The effect of brown trout density on mountain sucker presence was evaluated by adding it to the most plausible model based solely on stream characteristic effects

Model	log(*L*)	AIC$_c$	ΔAIC$_c$	w_i
Stream characteristic effects				
Perennial + Slope + Order + Elevation + S × O + S × E + O × E	−110.34	237.20	0.00	0.851
Perennial + Slope + Order + Elevation + P × S + P × O + P × E + S × O + S × E + O × E	−109.27	241.49	4.28	0.100
Perennial + Slope + Order + Elevation + S × E + O × E	−114.95	244.30	7.10	0.024
Perennial + Slope + Order + Elevation + S × O + S × E	−115.78	245.95	8.75	0.010
Brown trout effect on mountain sucker occurrence				
Perennial + Slope + Order + Elevation + S × O + S × E + O × E + BrownTrout	−108.39	235.43	0.00	0.709
Perennial + Slope + Order + Elevation + S × O + S × E + O × E	−110.34	237.20	1.78	0.291

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Table 3. Parameter estimates (b_i), standard errors (SE), and 95% confidence intervals for logistic regression models, with and without a brown trout effect, predicting probability of mountain sucker presence in streams of the Black Hills National Forest, South Dakota and Wyoming. The brown trout excluded model is the best model from Table 2 based only on physical stream characteristics. Parameter estimates for the brown trout included model are an average of those of the best model without brown trout and the same model with brown trout in Table 2

Variable	Brown trout excluded			Brown trout included		
	b_i	SE	95% CI	b_i	SE	95% CI
Intercept	41.9968	11.4553	19.0862, 64.9074	41.2519	11.2937	18.6645, 63.8393
Perennial (Yes = 1; No = 0)	0.4097	0.6063	−0.8029, 1.6223	0.4908	0.6100	−0.7292, 1.7108
Slope (m km^{-1})	−1.1917	0.3036	−1.7989, −0.5845	−1.1924	0.3058	−1.8040, −0.5808
Stream order (Strahler)	−7.5843	2.3433	−12.2709, −2.8977	−7.4615	2.3064	−12.0743, −2.8487
Elevation (m)	−0.0255	0.0072	−0.0399, −0.0111	−0.0252	0.0070	−0.0392, −0.0112
Slope × Stream order	0.0592	0.0218	0.0156, 0.1028	0.0603	0.0213	0.0177, 0.1029
Slope × Elevation	0.0006	0.0002	0.0002, 0.0010	0.0006	0.0002	0.0002, 0.0010
Stream order × Elevation	0.0042	0.0015	0.0012, 0.0072	0.0042	0.0015	0.0012, 0.0072
Brown trout (n ha^{-1})				−0.0007	0.0006	−0.0019, 0.0005

among slope, stream order, and elevation had the minimum AIC$_c$ and was the most plausible model (Table 2). No other model had ΔAIC$_c < 4$. Hence, model averaging was not done and only the best model was used. The best model showed good ability to discriminate between sites where mountain suckers were present versus absent (ROC = 0.76) and based on the Akaike weights had a probability of 0.85 of being the best model. Parameter estimates suggested that mountain suckers were more likely to be present in perennial streams, but the effects of stream slope, elevation, and stream order were complex and depended on the values of other variables (Table 3; Figure 2). For example, mountain suckers were more likely to be present in large streams when gradient is high but small streams when gradient is low (Figure 2(C)). Mountain suckers were more likely to be present in large streams at high elevations but small streams at low elevations (Figure 2(D)). They were also more likely to be present in high gradient streams at high elevations and low gradient streams at low elevations (Figure 2(E)).

Mapping occurrence probabilities

The best model (i.e. model with minimum AIC$_c$) based only on habitat data was used to estimate a probability of mountain sucker occurrence for each individual segment in the stream network for the Black Hills National Forest. The model predicted that the majority of streams had a low probability of having mountain suckers present (Figure 3). In fact, 76% of the 8132 km of streams in the Forest had a probability between 0 and 0.05 of having mountain suckers present, with many kilometres of stream having a probability near zero. By contrast, only 2% of the stream kilometres had a high probability (>0.5) of mountain sucker occurrence. These stream segments were distributed throughout the Forest, with a small concentration in the south (Figure 4).

Effect of brown trout on mountain sucker occurrence

Brown trout were collected at 103 of 289 sites in the South Dakota Department of Game, Fish and Parks database, and densities ranged from 9 to 3587 ha^{-1}. Of the 49 sites where mountain suckers were present, brown trout were present at 21. The model that included brown trout density was more plausible than the best model consisting of only abiotic characteristics of streams (Table 2). However, there was still a probability of 0.29 that the model without the brown trout variable was the best. When model parameters were averaged across the two models using Akaike weights (w_i), the estimated effect of large brown trout on mountain sucker presence in streams was negative (Table 3).

DISCUSSION

Existing data from GIS databases were used to examine how segment-scale characteristics of streams were related to the occurrence of mountain suckers in the Black Hills National Forest, South Dakota and Wyoming, USA. In doing so, we demonstrated how models that provide insights regarding the distribution of fish can be developed from existing databases. These models can be used to guide sampling efforts for management and to predict the potential distributions of fish within a geographic area. Information on which stream segments appear to have the best habitat for a species can also be used to guide fish conservation and management efforts.

Within the mountainous region of the Black Hills, the distribution of mountain suckers in streams appears to be determined, at least in part, by large-scale physical factors that interact in complex ways. It was assumed that mountain suckers would occur more often in perennial streams and

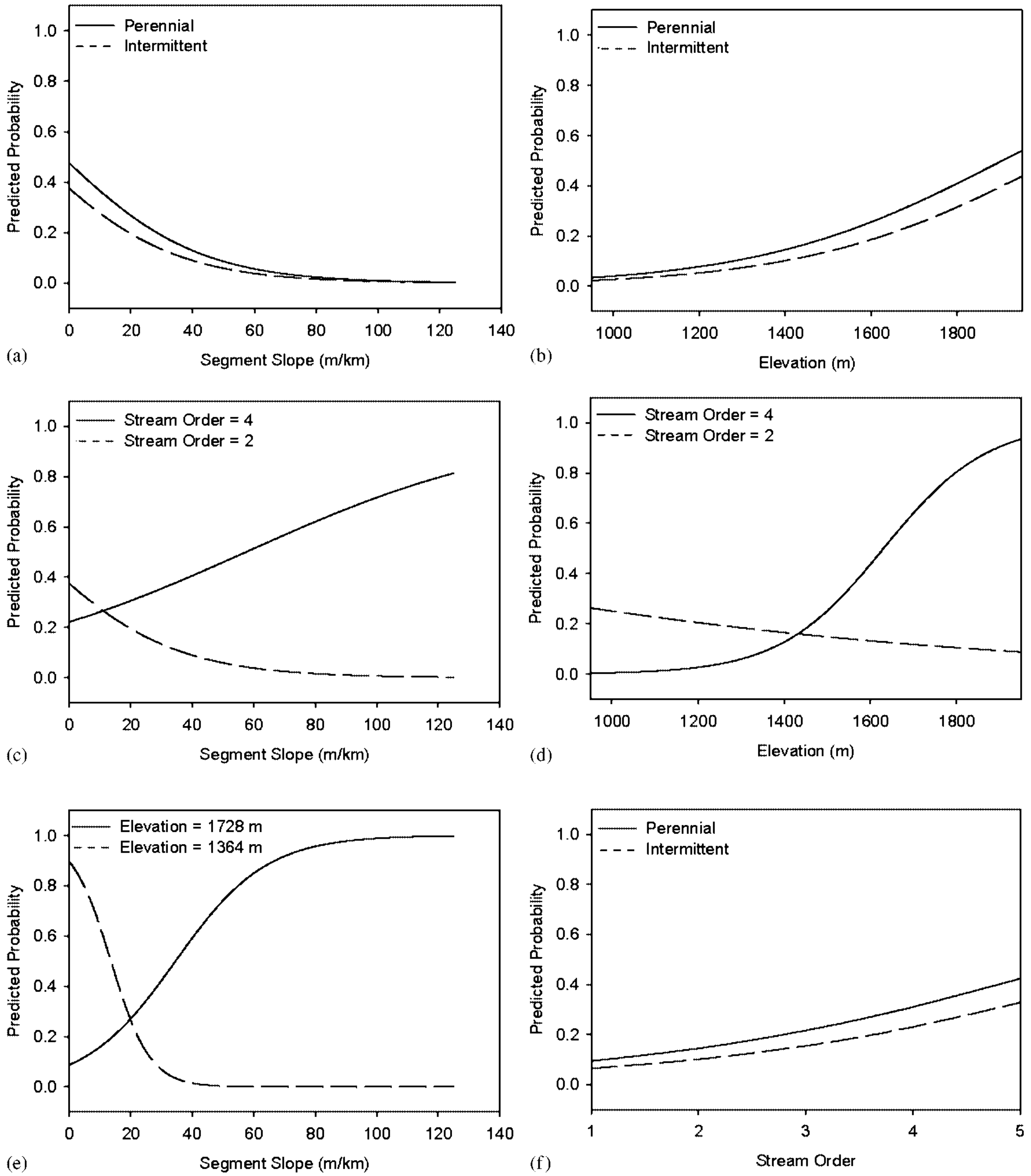

Figure 2. Predicted probability of occurrence of mountain suckers at stream sites differing in stream permanence, stream slope, stream order, and elevation in the Black Hills National Forest, South Dakota and Wyoming. Probabilities for variables that interacted with other variables (stream order, slope, elevation) are predicted at the mean ± 1 SD values of those variables to show their interaction; all remaining variables were held at their mean value.

stream permanence was included in every candidate model. Although the standard error of the stream permanence parameter estimate was large, exploratory data analyses showed that stream permanence alone explained mountain sucker presence but not as well as a model with the additional parameters of stream order, slope, elevation, and their

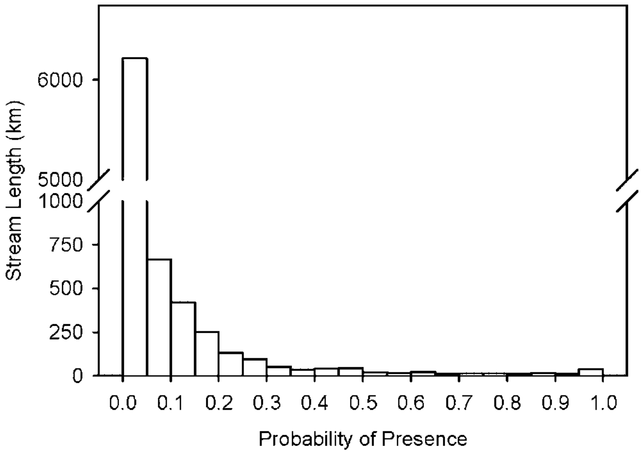

Figure 3. Total stream length in the Black Hills National Forest in relation to the predicted probability of mountain sucker presence.

interactions. Including these additional parameters probably led to a large standard error for the stream permanence parameter estimate in the best model despite its known effect (Hosmer and Lemeshow, 2000). The importance of stream permanence also suggests that mountain suckers are found in larger streams (that are typically perennial), and indeed mountain suckers were not collected in any first-order streams. However, springs, loss zones where streams flow subsurface at the periphery of the Forest, and other geological formations also determine stream permanence in the Black Hills (Carter *et al.*, 2005). The importance of perennial streams to the mountain sucker magnifies the value of maintaining hydrologic conditions that permit stream permanence, especially since water and land-use practices can alter stream hydrology (Allan and Flecker, 1993; Poff *et al.*, 1997).

Individually, stream order, stream slope, and elevation are often related to the distribution of stream fish (Brunger Lipsey *et al.*, 2005). However, the effects of these variables on the occurrence of mountain suckers were complex. At higher elevations mountain suckers were more likely to be found in larger streams with higher gradients. At lower elevations around the periphery of the Black Hills National Forest mountain suckers were more likely to be collected in smaller, low-gradient streams. These interacting effects suggest that regional-scale and stream-segment-scale factors affect local-scale stream habitats that influence mountain sucker occurrence. Larger high-gradient streams at higher elevations are likely to have the cool and clear water conditions in which mountain suckers are typically found (Baxter and Stone, 1995). However, at lower elevations around the Forest boundary the larger streams become warmer and more turbid (Williamson and Carter, 2001; Carter *et al.*, 2005). Thus, at low elevations, cool, clear water may only be present in perennial tributary streams with suitable gradients. Shading and increased springflows often cause smaller streams to have cooler and clearer waters (Vannote *et al.*, 1980). However, this effect would diminish as streams flow out onto the Northern Great Plains and even smaller tributaries become warm and turbid. This would explain why mountain suckers are found only in streams in or near the Black Hills in this geographic region (Bailey and Allum, 1962). Other catostomids have been shown to have similar patterns of occurrence. In Missouri, USA, the shorthead redhorse *Moxostoma lepidotum* is most abundant in larger, downstream sections of cool and clear rivers in the Ozark region, but it is more abundant in smaller streams of the prairie region where streams are typically warmer and more turbid than in the Ozarks (Pflieger, 1997).

The model identified the large-scale abiotic conditions where mountain suckers occur, a characteristic of most statistical models (Guisan and Zimmermann, 2000). The model could also be applied in a spatially explicit context because data for the predictor variables were available for every segment in the stream network. Spatially explicit predictions of occurrence probabilities can aid species conservation and management in three ways (MacKenzie, 2005). First, model predictions can guide sampling efforts aimed at assessing contemporary fish distributions. For example, the mountain sucker has historically occurred throughout the Black Hills, but recent analysis of existing fish-collection data suggested a possible reduction in distribution in the southern Black Hills (Isaak *et al.*, 2003). Model predictions can guide new sampling efforts directed at validating this range reduction. Sampling crews can target stream segments where mountain suckers are most likely to occur in the area where their range is thought to have contracted. This can be especially helpful in areas that historically have been underrepresented during field sampling

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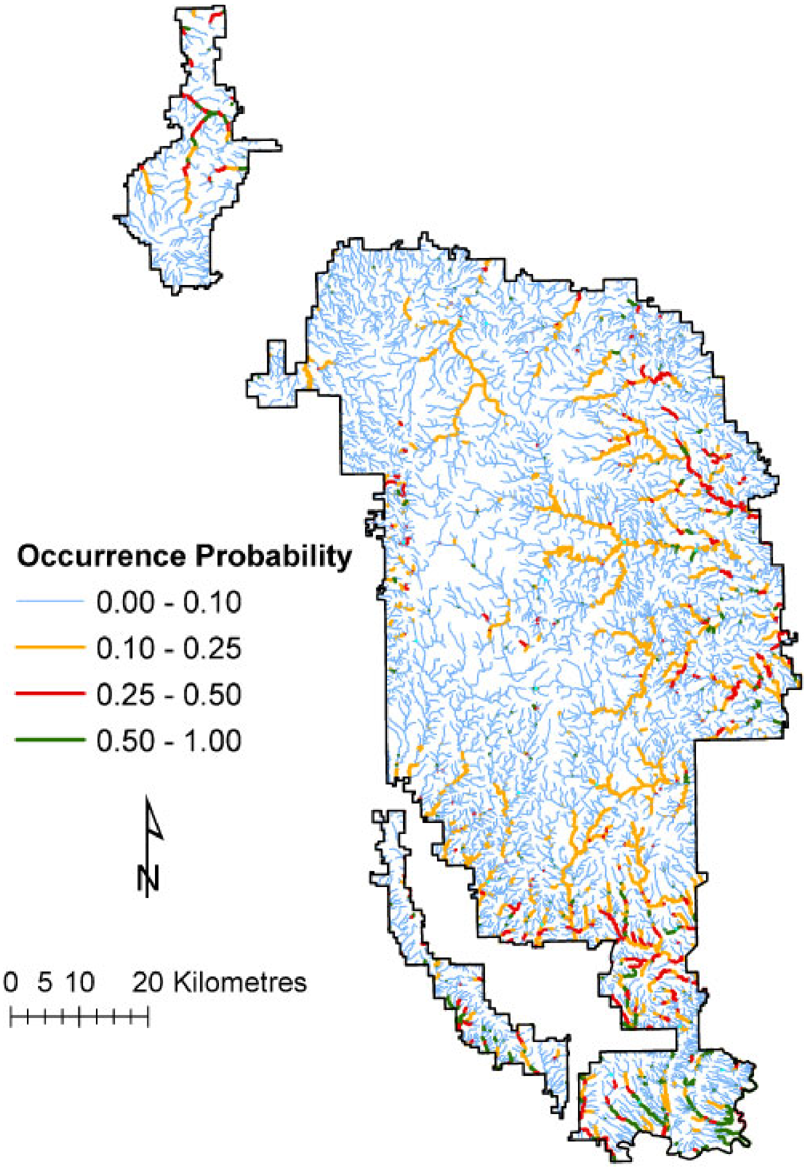

Figure 4. Predicted probabilities of mountain sucker presence for stream segments on the Black Hills National Forest, South Dakota and Wyoming, USA.

efforts, such as the southern Black Hills. In addition, the Black Hills National Forest is initiating a monitoring plan for mountain suckers that assesses its change in distribution over time. The plan calls for detecting changes in mountain sucker occurrence in catchments over time, and sampling within catchments will occur in stream segments where mountain suckers have the highest probability of occurrence.

A second way large-scale models can be useful is in helping managers assess the potential impacts of proposed land management activities on aquatic biota when resources to conduct field studies are not available. Spatially explicit predictions allow managers to assess the likelihood of species occurrence in the project area, and to conduct field studies only when a species of conservation concern is likely to occur there. Again, this is especially true on the southern section of the Black Hills National Forest where recent field data on fish are lacking. The Black Hills National Forest assesses the impact of proposed land management (e.g. timber sales, recreation, grazing allotments) on aquatic ecosystems, fish habitat, and fish populations. Spatially explicit predictions will give managers a better understanding of whether mountain suckers are likely to occur near and be affected by proposed projects.

A third way that spatially explicit model predictions can be used is to prioritize stream segments for conservation efforts. The predictor variables in the model represent segment-scale factors that often control local stream habitat conditions. Thus, if mountain suckers are absent from a stream segment that has a high predicted probability of occurrence then stream rehabilitation or restoration efforts could be targeted at those reaches because the segment-scale conditions are in place for mountain suckers to occur (Filipe *et al*., 2002). Many streams in the Black Hills have had localized impacts on physical habitat from logging, grazing, and reservoir construction (Modde *et al*., 1986). In addition, historical and recent mining activity has resulted in contaminated water and sediments at concentrations that can adversely affect both aquatic and terrestrial organisms (Rahn *et al*., 1996; May *et al*., 2001), sometimes far downstream from the mine activity (Walter *et al*., 1973; Hesse *et al*., 1975). Model predictions could also be used to avoid restoration of mountain sucker populations in streams where segment-scale characteristics indicate that local habitat conditions are likely to be unsuitable for mountain suckers, such as in the large number of small intermittent streams in the Black Hills National Forest. Eikaas *et al*. (2005) used spatially explicit predictions of species occurrences to forecast the effects of land-use change on the amount of habitat for two New Zealand stream fish. Areas or catchments with a high number of streams with predicted occurrences can also be set aside as conservation areas. Filipe *et al*. (2004) used species distribution models, the conservation status of fish, and a GIS to identify the conservation priority of catchments in the Guadiana River basin, Portugal. Others have used predicted species occurrences to identify stream segments and catchments that should be given priority for the conservation of particular species (Wall *et al*., 2004) or conservation of freshwater biodiversity (Argent *et al*., 2003; Sowa *et al*., 2007). Thus, spatially explicit information and GIS are valuable tools for managers who need to identify areas that are to have a fish conservation emphasis (Fisher and Rahel, 2004).

As discussed above, the model offers insight into the abiotic factors affecting the distribution of mountain suckers and can aid in mountain sucker conservation and management. Like any model, however, it must be applied cautiously outside the range of data used in development. Many streams to the east of the Black Hills are at lower elevations than the data used to develop the model. Predicted probabilities of occurrence based on the model developed would be high for these small, low-gradient, and low-elevation streams on the north-western Great Plains where they are known not to occur (Bailey and Allum, 1962). Streams to the west may be within the elevation range of the data used, but are outside of the Black Hills and, consequently, have a different geologic setting and different temperature regimes and instream habitat. This mismatch arises because the model predictions are applied beyond the geographic extent for which the model was developed, and application of the model to these streams would be inappropriate. Caution must also be used when predictions are applied to stream segments with slopes outside the range used in model development (i.e. $>120\,\mathrm{m\,km^{-1}}$). Although probability of occurrence in large streams increased with slopes up to $120\,\mathrm{m\,km^{-1}}$ (Figure 2(C)), it seems unlikely that probabilities would continue to remain high as slopes increased further because fish have difficulty living in torrential flows (Kruse *et al*., 1997). This illustrates the well-known caveat against extending statistical models beyond the range of the data used to develop them.

The density of brown trout negatively influenced the occurrence of mountain suckers. Model selection, the sign of the coefficient in the model, and other studies all suggest that brown trout negatively affect the occurrence of mountain suckers (Decker and Erman, 1992). Brown trout were introduced into Black Hills streams, and populations are generally sustained by natural reproduction and recruitment, but some streams are supplementally stocked for recreational fishing (USDA Forest Service, 2005). Brown trout have been known to replace native salmonids in streams (Waters, 1983), and larger brown trout are frequently piscivorous (Baxter and Stone, 1995). The Black Hills National Forest has reported the loss of mountain sucker populations where brown trout fisheries are maintained (USDA Forest Service, 2006). Spatially explicit modelling of mountain sucker occurrence could be used to identify candidate streams for non-native fish removal (Novinger and Rahel, 2003). For example, model predictions could be used to identify stream segments that have conditions suitable for mountain suckers, and brown trout populations could be eradicated before mountain sucker populations are restored. Predictions could also be used to identify suitable stream segments that are isolated from streams with established brown trout populations. Isolation could occur due to natural features such as intermittent stream segments or steep stream slopes that represent natural dispersal barriers (Eikaas *et al*., 2006), or man-made features like road culverts (Warren and Pardew, 1998). Eikaas *et al*. (2006) found that the distributions of diadromous New Zealand fish were influenced by steep stream slopes that restricted upstream migration. Likewise in New Zealand, native galaxiid fish are often restricted to portions of stream above anthropogenic or natural barriers that prevent colonization by piscivorous non-native brown trout (Townsend and Crowl, 2001). Hence, isolated streams could be the focus of isolation management for mountain sucker populations or other fish of conservation concern (Novinger and Rahel, 2003).

Although brown trout negatively influenced the occurrence of mountain suckers, this relationship was evaluated only within a 100-m stream reach where fish sampling occurred. The effects of biotic interactions on species occurrences is expected to decrease as spatial scale increases (Angermeier *et al*., 2002; Pearson and Dawson, 2003). Thus, the effect of brown trout on mountain sucker occurrence needs to be evaluated at the segment scale. In addition, spatially comprehensive data on brown trout abundance is lacking; data currently exist only for individual sites that have been sampled for a variety of reasons. However, predicting the abundance of stream salmonids, including brown trout, can be difficult (Stanfield *et al*., 2006). Spatially explicit predictions of brown trout abundance for the entire stream network would allow for more informed conservation and management decisions. Streams that are predicted to have suitable mountain sucker habitat and few or no brown trout would be better candidates for conservation activities than streams that are predicted to have high brown trout abundance. Understanding how biotic interactions influence species distributions across scales and including them in models would improve predictions of species occurrences across large geographic areas and result in better informed conservation and management decisions (Guisan and Thuiller, 2005).

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