Reach and catchment-scale characteristics are relatively uninfluential in explaining the occurrence of stream fish species

M. R. Wuellner*†, R. G. Bramblett*, C. S. Guy‡, A. V. Zale‡, D. R. Roberts* and J. Johnson§

*Department of Ecology, Montana State University, P. O. Box 173460, Bozeman, MT 59717-3460,U.S.A., ‡United States Geological Survey, Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, MT 59717, U.S.A. and §Confluence Consulting, Inc., 1115 North 7th Avenue, Suite 1, P. O. Box 1133, Bozeman, MT 59771-1133, U.S.A.

The objectives of this study were (1) to determine whether the presence or absence of prairie fishes can be modelled using habitat and biotic characteristics measured at the reach and catchment scales and (2) to identify which scale (*i.e.* reach, catchment or a combination of variables measured at both scales) best explains the presence or absence of fishes. Reach and catchment information from 120 sites sampled from 1999 to 2004 were incorporated into tree classifiers for 20 prairie fish species, and multiple criteria were used to evaluate models. Fewer than six models were considered significant when modelling individual fish occurrences at the reach, catchment or combined scale, and only one species was successfully modelled at all three scales. The scarcity of significant models is probably related to the rigorous criteria by which these models were evaluated as well as the prevalence of tolerant, generalist fishes in these stochastic and intermittent streams. No significant differences in the amount of reduced deviance, mean misclassification error rates (MER), and mean improvement in MER metrics was detected among the three scales. Results from this study underscore the importance of continued habitat assessment at smaller scales to further understand prairie-fish occurrences as well as further evaluations of modelling methods to examine habitat relationships for tolerant, ubiquitous species. Incorporation of such suggestions in the future may help provide more accurate models that will allow for better management and conservation of prairie-fish species.
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INTRODUCTION

Conservation of biodiversity in freshwater systems is of global and national importance (Richter *et al.*, 1997; Ruiz & Peterson, 2007). The importance of water to both aquatic and terrestrial animals is accentuated in semi-arid regions such as the

†Author to whom correspondence should be addressed at present address: Department of Natural Resource Management, South Dakota State University, Box 2140B, Brookings, SD 57007-1696, U.S.A. Tel.: +1 605 688 5963; email: melissa.wuellner@sdstate.edu

North American Great Plains. The prairie biome is arguably the most endangered ecoregion in North America, and the risk of extirpation for many aquatic organisms there is greater than in other regions (Samson & Knopf, 1994; Ostile *et al.*, 1997). Changes in prairie stream habitats and fish assemblages have occurred post-European settlement, primarily associated with the large-scale conversion of the landscape to agriculture. Specific anthropogenic stressors that may affect prairie fishes include altered hydrology, lowered groundwater tables, reduced connectivity, altered turbidity, pollution and introduced species (Cross & Moss, 1987; Samson & Knopf, 1994). Research and management of prairie-stream fish assemblages are, however, often of low priority because of their low angling and economic importance relative to fisheries in other regions (Matthews, 1988; Samson & Knopf, 1994). Therefore, a paucity of basic information on fish occurrences and species responses to habitat gradients exists for many North American Great Plains streams. A 2002 analysis of the Montana Fish, Wildlife and Parks database of the Montana River Information System identified >28 000 km of unsampled streams throughout the state; the majority of these were small prairie streams (Montana Fish, Wildlife and Parks, unpubl. data).

Streams of the North American Great Plains are ecologically important, although they have been historically ignored relative to other systems. Prairie streams are a stronghold of fish biodiversity in the North American interior west; for example, native fish species richness in prairie streams is about three times higher than in similarly sized Rocky Mountain streams (Brown, 1971; Rahel & Hubert, 1991). Additionally, prairie streams offer unique opportunities to study disturbance ecology of fishes as these systems are dynamic with unstable flow regimes and widely fluctuating habitat characteristics (Matthews, 1988; Dodds *et al.*, 2004). For these reasons, several state and federal natural resource management agencies in the Great Plains have made the management and conservation of prairie streams and fishes a priority over the past decade.

Effective conservation of fishes relies on an understanding of their ecology, including how the presence or absence of fishes responds to habitat gradients (Wiens, 1989; Schlosser, 1991; Fausch *et al.*, 2002). Species–habitat models developed at different spatial scales offer different ecological insights (Rabeni & Sowa, 1996; Allan *et al.*, 1997; Fausch *et al.*, 2002). For example, catchment-scale analyses can provide information on biogeography (Darlington, 1957; Jackson & Harvey, 1989), effects of extrinsically regulated abiotic factors (Rabeni & Sowa, 1996; Fausch *et al.*, 2002; Gido *et al.*, 2006; Mullen *et al.*, 2011), availability of refugia (Labbe & Fausch, 2000; Fausch *et al.*, 2002) and dispersion barriers for fishes (Gido *et al.*, 2006). In contrast, smaller-scale analyses can provide insight on the importance of certain meso and microhabitat characteristics and the influence of biotic interactions on fish assemblage structure (Rabeni & Sowa, 1996; Labbe & Fausch, 2000; Jackson *et al.*, 2001; Fausch *et al.*, 2002; Quist *et al.*, 2005). Because each scale provides unique information on the ecology of fishes, management and conservation efforts require knowledge of the factors that influence fish occurrences at multiple scales (Labbe & Fausch, 2000; Fausch *et al.*, 2002).

Information regarding the influence of catchment and reach-scale characteristics on presence or absence of Great Plains fishes is limited, particularly in the north-western region (Matthews, 1988; Bramblett *et al.*, 2005; Mullen *et al.*, 2011). Statistical models that relate the presence of fishes to these characteristics elsewhere have provided information on fish occurrences and habitat that are necessary to develop

and prioritize conservation strategies (Warren *et al.*, 2000; Ruiz & Peterson, 2007). No such models have been developed for the north-western Great Plains. Therefore, the objectives of this study were (1) to determine whether the presence or absence of prairie fishes can be modelled using habitat and biotic characteristics measured at the reach and catchment scales and (2) to identify which scale best explains the presence or absence of prairie fishes: reach, catchment or a combination of variables measured at both scales.

MATERIALS AND METHODS

STUDY AREA

The study area included the Great Plains of Montana, which cover about two-thirds of the state and include parts of the Missouri and Yellowstone River drainages (Fig. 1). Two ecoregions occur in this area: the North-western Glaciated Plains and the North-western Great Plains (Omernik, 1987). Low precipitation and soil moistures for months to years are a 'significant ecological condition' in the northern Great Plains (Sauchyn *et al.*, 2003). The North-western Glaciated Plains and the North-western Great Plains ecoregions have similar semi-arid climates and receive <40 cm of rainfall annually (Slagle, 1984). Patterns of precipitation influence the frequency and duration of flooding and drying cycles (Matthews, 1988). During spring, local or montane snowmelt may flood some prairie streams, creating longitudinal and lateral connectivity (Matthews, 1988; Dodds *et al.*, 2004). Many prairie streams lack montane headwaters, however, and have only local low-elevation snowmelt discharge or during dry years may have none. Generalized rainfall or local thunderstorms may flood streams as well (Matthews, 1988). Many prairie streams regularly cease to have
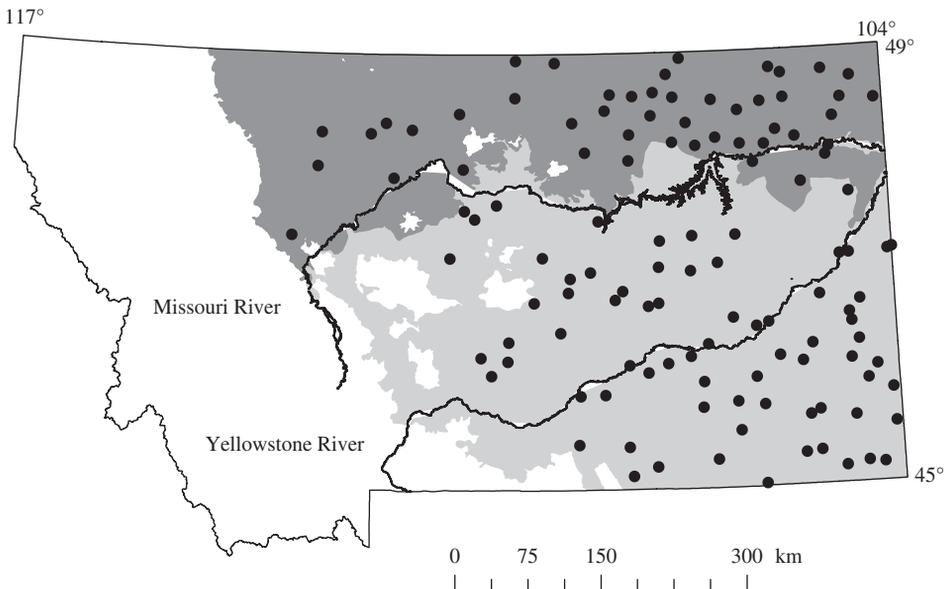
FIG. 1. Study area and 120 sample reaches in the Great Plains of Montana from which fish occurrence models were developed. ■, the North-western Glaciated Plains ecoregion; □, the North-western Great Plains ecoregion.

surface flow during summer and early autumn because of increased rates of transpiration and evaporation resulting from warm ambient temperatures (Matthews, 1988; Fausch & Bestgen, 1997; Dodds *et al.*, 2004). As a result, prairie streams are often intermittent (Matthews, 1988) and water quality is variable between streams (Appendix). Groundwater inputs and the depth of scoured pools may be important factors in maintaining patches of fish habitation during dry periods. Physical, chemical and biotic characteristics are variable among individual streams at both the reach and the landscape scales (Appendix). Dominant land use in both ecoregions includes grazing and row-crop agriculture but oil extraction is common in some areas. Human population density, however, rarely exceeds three individuals km^{-2} in this region (http://2010.census.gov/); thus, anthropogenic disturbance is less obvious in this region compared to other areas of North America (Bramblett *et al.*, 2005).

SITE SELECTION AND FISH SAMPLING

Sample sites ($n = 120$) were randomly selected from second to sixth-order (Strahler, 1957) streams. Only one site was sampled per stream and no sites were sampled on more than one occasion. Sampled streams ranged from 0·1 to 19·0 m in wetted width, were dominated by low-gradient pools with fine substrata, had little woody debris and often had high conductivities, temperatures and turbidities (Appendix). Main-stem dams were rare, but headwaters of many streams had abundant earthen stock pond dams.

Sites were sampled from July to mid-September every year from 1999 to 2004 and fishes were collected by seining. The length of the sampling reach varied. During 1999–2001, the reach sampled was 40 times the mean channel width (range of stream lengths: 150–500 m), which had been demonstrated to be adequate to capture 90% of the fish species present in a stream (McCormick & Hughes, 1998). During 2002–2004, sample reaches were 300 m long, a length demonstrated to be sufficient to capture 100% of fish species present in Wyoming prairie streams (Patton *et al.*, 2000), which are similar to streams in eastern Montana. Seines used varied in length (4·6, 6·1 or 9·1 m) depending on stream widths. Mesh size was 6·4 mm, which generally retains fishes >40 mm in total length (L_T). Fishes were identified to species and counted in the field. Up to 10 individuals of each species sampled per site were preserved in formalin as voucher specimens, and all voucher specimens were examined in the laboratory to verify field identifications.

REACH AND CATCHMENT-SCALE CHARACTERISTICS

Habitat characteristics measured at the reach scale included physical, chemical and biotic characteristics (Appendix). Physical and chemical features of the habitat were measured following the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Programme protocol (Kaufman & Robison, 1998). Eleven transects crossed the wetted width of the stream and were evenly spaced within the defined fish sampling reach. Habitat features measured at each transect and between transects were used to compute 30 metrics. Four measurements of water quality (dissolved oxygen, conductivity, salinity and temperature) were measured at a single location within each reach. Biotic variables were characteristics of the fish assemblage sampled within a reach and were chosen to examine whether biotic interactions influence the presence or absence of fishes in prairie streams of Montana; these variables have not been used in prior modelling studies in other Great Plains streams to date. Biotic variables were calculated using Structured Query Language (SQL) in Microsoft Access (2003).

Catchment-scale characteristics were defined as the attributes of the catchment upstream of the sampled reach. Twenty-eight variables (Table I) were quantified using various geographic information system (GIS) data layers in ArcGIS (version 9; www.arcgis.com). Variables were selected based on other studies on catchment-scale characteristics and the occurrence and abundance of fish species (Jackson & Harvey, 1989; Angermeier & Winston, 1998; Oakes *et al.*, 2005; Smith & Kraft 2005) or other hypotheses regarding which variables may be important in explaining the presence or absence of fishes in eastern Montana.

TABLE I. Family, scientific name, common name, status [N, native to eastern Montana; I, introduced to eastern Montana according to Brown (1971) and Holton & Johnson (2003)] and occurrence (*i.e.* the number of presences) of fishes collected in Great Plains prairie streams of Montana from 1999 to 2004

Family	Scientific name	Common name	Status	Occurrence
Hiodontidae	*Hiodon alosoides*	Goldeye	N	4
Cyprinidae	*Couesius plumbeus*	Lake chub	N	7
	Cyprinus carpio	Common carp	I	48
	Hybognathus argyritis	Western silvery minnow	N	7
	Hybognathus hankinsoni	Brassy minnow	N	35
	Hybognathus placitus	Plains minnow	N	35
	Macrhybopsis gelida	Sturgeon chub	N	1
	Margariscus margarita	Pearl dace	N	2
	Notropis atherinoides	Emerald shiner	N	3
	Notrophis hudsonius	Spottail shiner	I	2
	Notropis stramineus	Sand shiner	N	33
	Phoxinus eos	Northern redbelly dace	N	9
	Phoxinus neogaeus × P. eos	Northern redbelly dace × finescale dace	N	4
	Pimephales promelas	Fathead minnow	N	92
	Platygobio gracilis	Flathead chub	N	20
	Rhinichthys cataractae	Longnose dace	N	42
	Semotilus atromaculatus	Creek chub	N	12
Catostomidae	*Carpoides carpio*	River carpsucker	N	48
	Catostomus catostomus	Longnose sucker	N	9
	Catostomus commersonii	White sucker	N	80
	Catostomus platyrhynchus	Mountain sucker	N	6
	Ictiobus cyprinellus	Bigmouth buffalo	N	2
	Moxtostoma macrolepidotum	Shorthead redhorse	N	20
Ictaluridae	*Ameiurus melas*	Black bullhead	I	43
	Ictalurus punctatus	Channel catfish	N	18
	Noturus flavus	Stonecat	N	10
Salmonidae	*Prosopium williamsoni*	Mountain whitefish	N	1
Esocidae	*Esox lucius*	Pike	I	20
Cyprinodontidae	*Fundulus kansae*	Northern plains killifish	I	13
Gasterosteidae	*Culaea inconstans*	Brook stickleback	N	22
Centrarchidae	*Lepomis cyanellus*	Green sunfish	I	28
	Lepomis gibbosus	Pumpkinseed	I	2
	Micropterus dolomieu	Smallmouth bass	I	1
	Pomoxis annularis	White crappie	I	1
Percidae	*Etheostoma exile*	Iowa darter	N	16
	Perca flavescens	Yellow perch	I	8
	Sander canadense	Sauger	N	2
	Sander vitreus	Walleye	I	4

ANALYSES

The presence and absence of fishes that occurred at ≥ 10 sites were related to reach and catchment-scale characteristics using tree classifiers in R 2.0.1 [TREE package; Ihaka & Gentleman (1996)]. Rare fishes were eliminated from the analysis because of the unreliability of models based on <10 sites (Breiman *et al.*, 1984). For each species, a hierarchy of models was developed: (1) reach-scale models, (2) catchment-scale models and (3) models that used both reach and catchment-scale characteristics (*i.e.* combined-scale models).

Tree classifiers can be used to build species-habitat models and evaluate their ability to explain the presence or absence of species (Breiman *et al.*, 1984). These models use variables to reduce the amount of null deviance within a model. Null deviance is a measure of variability in the occurrence of the species and is calculated as: $D = -2n[p_i \ln(p_i) + (1 - p_i)\ln(1 - p_i)]$, where D is the null deviance of the model, n the sample size under consideration and p_i the proportion of sites occupied by the species. A recursive partitioning algorithm is used to minimize the deviance in the model and create completely or nearly homogeneous categories of species presence or absence. The result is a dichotomous key that is relatively easy to interpret (Breiman *et al.*, 1984).

Tree classifiers can be developed until groups (*i.e.* sites where the species is present and sites where the species is absent) are homogeneous or until a minimum n (in this case, $n = 5$ sites) has been reached. The tree models may over-fit the data and must be cross-validated to find the most parsimonious tree size to fit the population rather than the sample at hand (Breiman *et al.*, 1984). Thus, trees were pruned to a smaller size with fewer nodes. An automated ten-fold cross-validated procedure was used to determine the minimum number of nodes that reduced a significant amount of the null deviance while conserving cost complexity within the tree. As the minimum number of terminal nodes in any functional tree is two, any tree in which only one terminal node was recommended was regarded as being no better than chance alone and was not considered significant (Breiman *et al.*, 1984).

Three metrics [per cent deviance reduced, misclassification error rate (MER) and improvement in MER] were calculated to evaluate successful models for their explanatory abilities. The per cent deviance reduced by a variable within a model was used to summarize how well each explained the occurrence of a species; this was simply calculated as the ratio between the deviance explained by the variable and the null deviance for that model. MER was defined as the percentage of sites where the model incorrectly identified the presence or absence of a species and was calculated using a cross-validation procedure (Ihaka & Gentleman, 1996). Low MER values potentially indicate high explanatory ability of individual species-habitat models. Per cent improvement in MER is the ratio between the MER reduced and the null error rate expressed as a percentage. The null error rate was calculated as the ratio between the number of occurrences of a species and the total number of sites under consideration. Large improvements in MER indicate potentially high explanatory ability as the inclusion of variables help to describe the presence or absence of a species better than chance alone.

Residual mean deviance (D^2) and average D^2 for each scale were used to determine which scale modelled the occurrence of individual species and prairie fishes overall. Calculation of this metric is similar to that of a generalized linear model (Breiman *et al.*, 1984); the model type with the lowest D^2 value by species and the average among all species was determined to be the scale that best explained the species' occurrences. No formal statistical tests could be used to compare the D^2 values between scales because variables in the combined-scale models were not independent of the variables used in reach and catchment-scale models. Rather, the C.I. around each scale average was examined to determine which scale best explained the presence or absence of prairie fishes overall.

RESULTS

FISH COLLECTIONS

Thirty-nine fish species, including 27 fishes native to eastern Montana and 12 fishes not native to the region, were sampled from the 120 sites (Table I). Species

occurrence (*i.e.* the number of presences) varied from one to 92 (Table I). The two most common native species were fathead minnow *Pimephales promelas* Rafinesque 1820 followed by white sucker *Catostomus commersonii* Lacépède 1803. The most common non-native species were common carp *Cyprinus carpio* L. 1758 followed by black bullhead *Amieurus melas* (Rafinesque 1820). Mountain whitefish *Prosopium williamsoni* (Girard 1856) and sturgeon chub *Macrhybopsis gelida* (Girard 1856) were the rarest native species. Non-native species collected at only a single site were rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), smallmouth bass *Micropterus dolomieu* Lacépède 1802 and white crappie *Pomoxis annularis* Rafinesque 1818.

MODEL RESULTS BY SCALE

Reach-scale models were developed for 19 species from the presence data for 105 sites (15 sites had missing physicochemical data). The reduced number of sites used in the analysis resulted in an omission of stonecat *Noturus flavus* Rafinesque 1818 from the analysis as this species was found at <10 of these sites. Four of the 19 (21%) models were significant, and all four included only one variable (Table II). Null deviance was reduced by an average of $30 \pm 13\%$ ($\pm 95\%$ C.I.) among all models. The MER averaged $14 \pm 10\%$ among the four models, which was an average improvement of $34 \pm 30\%$ from null error rates.

Catchment-scale models were developed for 20 species from 106 sites (14 sites had missing catchment-scale data). Four models (20%) were significant and included only one variable each. The average null deviance reduced among these models was $29 \pm 9\%$ (Table II). The MER of the four models averaged $15 \pm 7\%$; improvements in MER averaged $28 \pm 29\%$.

Combined-scale models used data from 101 sites to evaluate occurrence of 19 species. Omission of sites with missing reach and catchment-scale information removed *N. flavus* from the analysis ($n < 10$). Six models (37%) were significant, and each of the models included one variable in the final pruned model (Table II). Of the six different variables used in successful models, four were catchment-scale and two were reach-scale variables. The average null deviance reduced among all of the models was $32 \pm 5\%$. The MER averaged $12 \pm 6\%$ among the six models, which was an average improvement of $37 \pm 22\%$ from null error rates.

SCALE COMPARISONS

The occurrences of eight species (40%) were modelled at one or more scales. Three species were modelled at only one scale; five species had significant models for at least two scales (Table III). The average D^2 was lowest among the combined-scale models, followed by the reach and catchment-scale models (Table III). The 95% C.I. broadly overlapped, indicating no significant differences in unexplained deviance among the three scales. Occurrences of two of the five species that were modelled at multiple scales were better modelled using a combination of reach and catchment-scale variables. One species [shorthead redhorse *Moxostoma macrolepidotum* (LeSueur 1817)] was best modelled using only reach-scale variables. The remaining two species were equally well modelled using only catchment-scale variables or both reach and catchment-scale variables (Table III).

TABLE II. Models that successfully explained the occurrence of Montana Great Plains stream fishes at each scale (n, number of sites where the fish was present in the database for each scale). Per cent reductions in deviance refer to the proportion of null deviance reduced by the variable. Misclassification error rate (MER) is the ratio between the number of incorrect classifications of presence or absence for the given model and the total number of sites in the data set. Per cent improvement in classification describes whether or not the model improved the classification of presences and absences for that species compared to the null error rate

Scale	Species	n	Null deviance	Variable	% Reduction in deviance	MER (%)	% Improvement in classification
Reach	*Carpoides carpio*	12	74·63	Per cent of reach area composed of algae and aquatic macrophyte areal cover <1·59%	35	8	33
	Etheostoma exile	17	86·12	Bank height <0·63 m	20	14	0
	Moxostoma macrolepidotum	20	102·30	Native species richness ≥8	47	5	75
	Couesius plumbeus	42	141·30	Per cent of assemblage composed of introduced piscivores <0·63%	22	29	29
Catchment	*Semotilus atromaculatus*	12	74·87	Longitude >−105·87	36	11	0
	M. macrolepidotum	17	93·34	Catchment area >3131 km²	36	8	51
	Lepomis cyanellus	28	122·40	Drainage basin: Little Missouri River and Yellowstone River	29	25	6
Combined	*Rhinichthyes cataractae*	36	135·80	Mean catchment elevation <1242 m	17	15	56
	S. atromaculatus	11	67·35	Longitude >−105·87	33	11	0
	Carpoides carpio	12	71·25	Per cent of reach area composed of algae and aquatic macrophyte areal cover <1·59%	36	7	42
	Culea inconstans	15	81·82	Per cent of catchment area covered by fallow >14·32%	23	6	60
	M. macrolepidotum	17	88·06	Native species richness ≥8	38	8	53
	L. cyanellus	27	111·40	Drainage basin: Little Missouri River and Yellowstone River	25	28	7
	R. cataractae	33	120·10	Mean catchment elevation <1242 m	35	15	62

TABLE III. Comparisons of residual mean deviance (D^2) by species and scale for Montana Great Plains stream fishes. Values in bold indicate the models with the lowest D^2 for that scale or species. Numbers in parentheses are 95% C.I. of mean D^2

	Scale		
Species	Reach	Catchment	Combined
Carpoides carpio	0·47		**0·46**
Culea inconstans			0·38
Couesius plumbeus	1·07		
Etheostoma exile	0·67		
Lepomis cyanellus		0·84	**0·36**
Moxostoma macrolepidotum	**0·21**	0·56	0·56
Rhinichthyes cataractae		**0·79**	**0·79**
Semotilus atromaculatus		**0·45**	**0·45**
Mean	0·61 (±0·35)	0·66 (±0·18)	**0·50 (±0·13)**

DISCUSSION

Catchment variables have been shown to explain and predict the presence or absence of fishes more accurately than reach-scale variables in many ecoregions (Jackson & Harvey, 1989; Mandrak, 1995; Gido *et al.*, 2006; Steen *et al.*, 2008), and such variables are often less expensive to use and analyse with GIS compared to on-the-ground biotic or physicochemical reach-scale habitat measurements (Wall *et al.*, 2004; Gido *et al.*, 2006; Steen *et al.*, 2008). This study did not, however, support the idea that catchment-scale variables were superior to reach-scale variables in explaining prairie fish occurrences. No large differences between reach and catchment-scale models were found when comparing average D^2, the mean sum of per cent deviance reduced, MER and the per cent improvement in MER. Kautza & Sullivan (2012) reported that reach-scale variables were more important in explaining fish assemblages in Idaho streams compared to Ohio streams, indicating that relative influences of habitat characteristics at each scale may vary depending on geographic region. Not surprisingly, using both reach and catchment-scale variables in combination produced the most significant models, and similar results have been demonstrated in other studies (Gido *et al.*, 2006; Steen *et al.*, 2008). But the metrics used to evaluate all three model types in the study described here were not significantly different for combined *v*. reach or catchment-scale only models. In total, it appears that measurements of habitat at both scales are necessary for explaining the presence or absence of fishes in eastern Montana streams.

The scale comparisons of this study may indicate the influence of an individual species' autecology on the results of a model. Ruiz & Peterson (2007) hypothesized that the occurrences of habitat specialists may be more accurately modelled using local (reach) features, whereas generalists that can occupy a wider variety of habitats could be modelled accurately using larger-scale habitat data. This hypothesis is supported to an extent in this study of Montana prairie streams. For example, Iowa darter *Etheostoma exile* (Girard 1859), which are intolerant benthic invertivores (Goldstein & Simon, 1999) were only successfully modelled using reach-scale variables. In contrast, creek chub *Semotilus atromaculatus* (Mitchill 1818),

which are tolerant invertivore-carnivores with no specific feeding habitat (Goldstein & Simon, 1999; Bramblett *et al.*, 2005), were successfully modelled at the catchment scale. Closer inspection of other models at all scales, however, may reveal other ecological relationships such as predator–prey interactions [*e.g.* lake chub *Couesius plumbeus* (Agassiz 1850) reach-scale model] or invasion success (*e.g.* the green sunfish *Lepomis cyanellus* Rafinesque 1819 catchment-scale model). The selection of variables at any scale must be carefully chosen prior to modelling and the results of the model were thoroughly examined to ensure that the model will provide useful information for management and conservation.

Apart from the observed patterns in scale comparisons, an important finding in this study was the paucity of significant models at any scale. Among all of the species and scales examined, only 20-37% of the models were significant at each scale. Similar studies have produced greater numbers of models, but may have only used MER or similar metrics to evaluate each model (Olden & Jackson, 2002; Wall *et al.*, 2004; Oakes *et al.*, 2005). Mullen *et al.* (2011) found that general predictions about prairie fish structure and function were possible in five intermittent, adventitious North-western Great Plains streams. For example, species richness increased in the lower sections of a stream as the levels of fine substrata decreased (Mullen *et al.*, 2011). Several reasons may explain why only few significant models were found in this study. First, the rigour by which the models in this study were evaluated may have contributed to the scarcity of significant models. This study was the first in fish ecology that required cross-validated statistical significance before evaluating models further using additional metrics. Models that do not require significant amounts of null deviance to be reduced are no better than chance alone at explaining or predicting species' occurrences (Breiman *et al.*, 1984). Furthermore, the ability to accurately explain or predict the presence or absence of a species is related to the prevalence of that species. For example, the rarest and most common species are typically identified as being absent or present at most sample sites owing to simple random chance. Conversely, species that occur at an intermediate number of sites are more difficult to model (Olden *et al.*, 2002). Therefore, examining MER alone to evaluate models is not appropriate when determining the explanatory and predictive effectiveness of a model.

Other factors may also have contributed to the scarcity of significant models in this study. Sampling each site only once may have played a role. Species-habitat models assume that the presence of a given species indicates that a particular site provides the suitable habitat needed to support that species throughout its life and that absence signifies unsuitable habitat (Breiman *et al.*, 1984; Jongman *et al.*, 1995; Ruiz & Peterson, 2007). Such assumptions may be commonly violated in prairie streams, particularly when only visiting a stream once. For example, during a drought, fishes may be occupying a site because it is a temporary refuge (Magoulick & Kobza, 2003). Conversely, fishes may be absent from a site because of localized faunal extirpations (Matthews, 1998) and eliminated connectivity due to little or no stream flow (Labbe & Fausch, 2000; Matthews & Marsh-Matthews, 2003) during drought. The northern Great Plains were subjected to drought conditions during the sampling period of this study as indicated in the Canadian Drought Watch (www.agr.gc.ca/drought) and U.S. Drought Monitor (http://droughtmonitor.unl.edu) archives, and some areas received record low precipitation (Sauchyn *et al.*, 2003). Additionally, although some of the physicochemical explanatory variables used in this study fluctuate temporally

because of seasonal changes and unpredictable flooding and drying (Matthews, 1988; Zale *et al*., 1989; Ostrand & Wilde, 2002, 2004; Dodds *et al*., 2004; Falke *et al*., 2012), these changes may not be accompanied by concomitant changes in the fish assemblage (Bramblett & Fausch, 1991) unless lethal thresholds are reached (Smale & Rabeni, 1995; Ostrand & Wilde, 2004). Sampling the same site during multiple periods under varying environmental conditions would have provided additional information on stability and persistence of fish assemblages as it relates to variability in physical and chemical conditions. For example, Mullen *et al*. (2011) found that four samples spread across seasons are sometimes needed to detect all of the fishes that occur at a particular site in prairie streams. Inclusion of temporal variability in fish assemblages and habitat conditions or detection probability in species-habitat models has been suggested by other authors to improve accuracy (Wiley *et al*., 1997; Hayer *et al*., 2008; Steen *et al*., 2008; Falke *et al*., 2012) and may have improved the number of significant reach and catchment-scale models in this study. Matthews (1990) in a study of fish communities in riffle habitats of the Roanoke River, Virginia, U.S.A., and Mullen *et al*. (2011) in a study of Montana prairie streams, however, have both found that spatial variation in fish assemblages was greater than temporal variation. Furthermore, Shearer & Berry (2003) found long-term persistence of most native prairie fishes between dry and wet periods due to the tolerance of these species to variable physicochemical conditions, and Matthews & Marsh-Matthews (2003) found that the influences of drought on fish assemblages in prairie streams of Oklahoma, U.S.A., may be short lived as recolonizations of fishes may be rapid during improved conditions. Thus, the adaptability of stream fishes to stochastic conditions aid in their persistence at a given site over time (Ross *et al*., 1985).

The prevalence of tolerant fishes in prairie streams (Matthews, 1987; Bramblett & Fausch, 1991; Goldstein & Simon, 1999; Bramblett *et al*., 2005) may also have contributed to the small number of significant models. Many similar previous modelling studies have focused on fish assemblages in more mesic regions (Maret *et al*., 1997; Angermeier & Winston, 1998; Rashleigh, 2004; Oakes *et al*., 2005; Smith & Kraft, 2005) that probably have fewer and shorter severe disturbance episodes (*e.g*. flooding and drying), more available refugia and less-tolerant species than prairie streams (Matthews, 1988). The frequency and duration of disturbances have favoured the prevalence of tolerant taxa in prairie streams (Matthews, 1988). Occurrences of generalist species are more difficult to model because they are tolerant to a wide variety of environmental conditions. For example, Steen *et al*. (2008) found that ubiquitous, tolerant stream fishes were modelled with low accuracy because models were not able to distinguish streams in which the species were present or absent. Similar patterns were found in this study. Seven of the eight fishes that were successfully modelled at any scale are classified as either intolerant or moderately tolerant (Goldstein & Simon, 1999; Bramblett *et al*., 2005); the one tolerant fish that was successfully modelled is an introduced species that occurs only in a relatively confined area (Brown, 1971).

Finally, the modelling technique used in this study (*i.e*. tree classifiers) may have contributed to the scarcity of significant models. Previous studies have shown that non-parametric techniques often provide more accurate models than parametric techniques because of the lack of normality in the presence–absence data (Olden & Jackson, 2002). Among different non-parametric modelling tools, tree classifiers

have been shown to produce models with relatively high levels of accuracy compared to other statistical techniques such as logistic regression, ordination techniques and neural networks (Oakes *et al*., 2005). The best statistical techniques may, however, vary by species, whereby certain species are modelled more accurately with one technique compared to others (Oakes *et al*., 2005; Ruiz & Peterson, 2007). This study did not compare the explanatory power of different modelling techniques, but such an exercise may provide additional significant models of prairie-fish occurrences in the future.

The paucity of significant models obtained suggests that there is still much to be learned about what influences the occurrence of fish species in prairie streams. Yet, some information that could be used to guide future research was gleaned from this study. The fact that catchment-scale models did not explain prairie-fish occurrences with significantly greater accuracy than reach-scale characteristics measured in the field demonstrates the need to continue measuring habitat at smaller scales to further understand prairie-fish distributions. Furthermore, future sampling should include multiple sampling efforts to examine potential temporal habitat influences on species-habitat models. Finally, other methods to model tolerant arid-region species should be examined to determine whether other techniques may effectively model and explain the distributions of such fishes. Incorporation of these suggestions in the future may help provide more accurate models that will allow for better understanding of the ecology of prairie-fish species.

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APPENDIX

APPENDIX I. Habitat characteristics measured at the reach (physical, chemical and biotic) and catchment scale for each sample site for the purpose of modelling the occurrence of Montana Great Plains stream fishes. Ranges and mean ± s.d. of each variable are provided. Physical and chemical characteristics of the habitat were measured following the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Programme protocol (Kaufman & Robison, 1998). Catchment characteristics were quantified using various geographic information system (GIS) data layers in ArcGIS (Version 9)

Type	Variable	Range	Mean ± s.d.
Physical	Agricultural disturbance within riparian area index	0·0–2·3	1·3 ± 0·5
	Anthropogenic disturbance within riparian area (all types) index	0·0–2·8	1·5 ± 0·5
	Channel sinuosity	0·6–2·9	1·3 ± 0·4
	Maximum velocity index	0·0–5·0	1·4 ± 0·5
	Mean bankfull height (m)	0·1–1·3	0·6 ± 0·3

APPENDIX I. Continued

Type	Variable	Range	Mean ± S.D.
	Mean bankfull width (m)	2·4–70·0	11·1 ± 9·1
	Mean bank undercut distance (m)	0·0–0·2	0·0 ± 0·1
	Mean % embeddedness of channel substratum	22·6–100·0	84·7 ± 18·0
	Mean incision height (m)	0·5–4·3	1·6 ± 0·7
	Mean $\log_{10}$ (diameter of substratum)	−2·1 to 2·3	−0·4 ± 1·3
	Mean ratio between wetted width and thalweg depth	5·1–173·0	28·9 ± 26·7
	Mean thalweg depth (cm)	2–142·3	39·3 ± 24·3
	Mean velocity index	0·0–2·5	0·5 ± 0·7
	Mean wetted width (m)	0·4–19·6	5·6 ± 4·0
	% Algae and aquatic macrophyte areal cover within reach	0·0–96·4	22·8 ± 21·7
	% Brush and small woody debris areal cover within reach	0·0–21·4	1·6 ± 3·5
	% Dry channel within reach	0·0–81·0	10·8 ± 22·5
	% Falls, cascades, rapids or riffles within reach	0·0–43·0	6·5 ± 9·7
	% Glides and pools within reach	57·0–100·0	93·5 ± 9·7
	% Large woody debris areal cover within reach	0·0–12·7	1·0 ± 1·9
	% Overhanging vegetation areal cover within reach	0·0–48·2	7·1 ± 8·6
	% Pools within reach	0·0–100·0	58·5 ± 31·0
	% Riparian herbaceous and woody vegetation ground cover	13·6–91·6	55·1 ± 17·3
	% Substratum larger than sand or gravel (diameter >2 mm)	0·0–80·6	26·2 ± 24·6
	% Smaller than sand or gravel (diameter <2 mm)	19·0–100·0	73·6 ± 24·6
	S.D. of ratio between wetted width and thalweg depth	0·1–95·7	6·8 ± 11·6
	S.D. of thalweg depth	3·6–55·4	20·2 ± 11·3
	S.D. of velocity index	0·0–1·2	0·3 ± 0·4
	S.D. of wetted width	0·4–10·0	2·4 ± 1·7
	Water surface gradient (%)	0·0–1·6	0·8 ± 0·4
Chemical	pH	6·0–10·3	8·6 ± 0·8
	Specific conductivity (10^2 μS cm^{-1})	3·0–109·7	2·5 ± 2·1
	Temperature (°C)	7·1–27·2	19·6 ± 4·5
	Turbidity (NTU)	1·1–5704·0	127·3 ± 569·8
Biotic	Native species richness	0·0–14·0	4·8 ± 2·7
	% Black bullhead *Amieurus melas*	0·0–88·9	7·9 ± 19·3
	% Common carp *Cyprinus carpio*	0·0–74·5	4·7 ± 11·4
	% Green sunfish *Lepomis cyanellus*	0·0–58·9	4·2 ± 12·2
	% Introduced piscivores (not including pike)	0·0–87·5	7·5 ± 16·1
	% Pike *Esox lucius*	0·0–87·5	3·0 ± 11·4
	% Introduced non-piscivores	0·0–97·1	14·5 ± 25·7
	% Native piscivores	0·0–27·7	0·9 ± 3·8
	Presence of *E. lucius*	0·0 or 1·0	NA
	Shannon–Weiner diversity index (H')	0·1–2·1	1·1 ± 0·5
Catchment	Annual flood frequency index from STATSGO data	0·0–0·8	0·0 ± 0·1
	Density of irrigation ditches by length (km km^{-2})	0·0	0·0 ± 0·0
	Density of roads by length (km km^{-2})	0·0	0·0 ± 0·0
	Elevation of sampled site (10 m)	59·0–133·60	85·8 ± 16·6
	Latitude of sampled site (degrees)	45·0–48·8	NA
	Level III ecoregion (Omernik, 1987)	NA	NA
	Level IV ecoregion (Omernik, 1987)	NA	NA
	Longitude of sampled site (°)	−111·9 to 104·0	NA

APPENDIX I. Continued

Type	Variable	Range	Mean ± s.d.
	Major drainage basin (Little Missouri, Missouri and Yellowstone)	NA	NA
	Mean elevation of catchment (m)	682·3–1958·0	1034·0 ± 235·1
	Mean soil erodibility factor from STATSGO	−937·2 to 0·6	−26·3 ± 126·0
	Mean soil permeability (cm h^{-1})	0·1–7·9	1·2 ± 1·0
	Mean soil salinity (μS cm^{-1})	0·1–5·6	2·5 ± 0·8
	Mean water table depth (cm)	0·1–6·0	5·6 ± 1·2
	Maximum precipitation within catchment (10^5 m^3)	1·1–139299·0	10290·7 ± 18923·7
	Maximum soil salinity (μS cm^{-1})	0·1–9·4	1·7 ± 1·2
	Minimum water table depth (cm)	0·1–6·0	5·6 ± 1·2
	Number of dams within catchment	0·0–122·0	15·1 ± 23·3
	Number of groundwater wells within catchment	0·0–7068·0	255·3 ± 862·0
	% Land cover (defined by National Land Cover Database)	NA	NA
	Number of dams between sampled site and large river	0·0–3·0	0·2 ± 0·5
	Ratio between distance to nearest major river and Strahler (1957) stream order	0·0–69818·8	3656·1 ± 8165·8
	Relative gradient (%)	0·0–1·8	0·2 ± 0·2
	Strahler (1957) stream order	2·0–6·0	NA
	Total length of irrigation ditches (10^3 km)	0·0–1234·6	40·3 ± 150·2
	Total length of roads (10^3 km)	6·8–11202·6	739·4 ± 1489·4
	Catchment area (10^6 km^2)	37·7–13929·9	1146·0 ± 1975·7

NA, not applicable. STATSGO, state soil geographic database, U.S. Geological Survey.