Fish assemblages, habitat conditions, and grazing effects in rolling prairie and badlands streams of the Northern Great Plains

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Fish sampling was conducted over a two-year period (May to August, 2004 and 2005) in seven streams traversing the Little Missouri River National Grassland and Theodore Roosevelt National Park, western North Dakota. Fish communities of the two stream types in the region (rolling prairie and badlands) differed significantly despite their close geographic proximity, overlapping by only 18% in species composition and having only 8 of the 21 total fish species in common. As summer progressed, rolling prairie streams showed an increase in total fish density while total fish density in badland streams decreased. Badland and rolling prairie stream fish communities responded differently to the physical habitat variables of pool surface area, volume, mean depth, maximum depth, and width-to-depth ratio. Fish in badland streams appeared to be more susceptible to rapid physical habitat changes associated with late summer dewatering, while the more stable flows of rolling prairie streams prevented significant isolation of individuals in pools. Livestock grazing produced no significant detectable impacts to aquatic habitat availability. Streams within the region have always been subjected to contrasting natural periods of flood and drought, along with legacy effects of intensive domestic livestock grazing for more than a century. Conditions that impact fish assemblage structure, abundance, distribution, and survival are strongly influenced by changing physical habitat conditions such that the fish communities persist opportunistically within environmental instability. Naturally harsh, highly variable conditions and a lack of adequate experimental domestic livestock exclosures complicate proper evaluation of effects of land use practices. Establishment of some long-term, extensive exclosures over a period of years or decades would facilitate the evaluation of the roles of abiotic factors, biotic factors, and land use practices in shaping fish communities.

Key words: streams, ecology, North Dakota, badlands, grazing

INTRODUCTION

In the northern Great Plains of the United States, small streams, both permanent and intermittent, supply water for plants, fishes, wildlife, domestic livestock, and human activities in a typically semi-arid to arid environment (Meador et al. 1990). Fish assemblage structure in such streams can be strongly influenced by abiotic, physical habitat conditions (Schlosser 1982, 1985), biotic factors and interactions among taxa (e.g., predation and competition; Gorman and Karr 1978; Gorman 1986; Capone and Kushlan 1991), seasonal immigration and emigration events (Taylor and Warren 2001; Falke et al. 2012), and a high level of stochasticity (Grossman et al. 1982). Although ecological preferences and physiological specializations of individual fish species can be used to propose which specific habitats a particular fish assemblage will prefer (Jackson et al. 2001), fish assemblage structure and movement patterns can vary on a fine scale among and within watersheds (Wilkinson and Edds 2001). Several studies on northern plains and western streams have found that habitat quality for fishes is also directly and indirectly influenced by domestic livestock grazing (Platts 1979, 1991; Meehan 1991; McDowell and Magilligan

1997; Belsky et al. 1999). The effects have been apparent in depletion of riparian vegetation (Gunderson 1968; Platts 1979; Armour et al. 1994; Hoover et al. 2001), physical changes such as sedimentation, channel widening and loss of channel depth, less stable water temperatures (Armour et al. 1994; Rinne 1999), altered organic matter inputs and geomorphic and hydrologic functioning (Van Haveren and Jackson 1986), and changes in aquatic macroinvertebrate communities (MacFarlane 1983) and fish assemblage structure. Effects of livestock on fish assemblages can be exacerbated in arid landscapes with intermittent streams, where residual pools can provide important habitat for fish in dry periods (Scarnecchia 2002). Such pools have also been shown to lose depth and residual volume under conditions of excessive grazing (McDowell and Magilligan 1997). Effective management of the streams and their riparian zones is thus important for the sustainability of fishes and other aquatic resources, as well as for a water source for sustainable livestock use on the landscape.

One method that has been used to assess the impacts of grazing on stream and riparian assemblages is the use of exclosures (Platts and Wagstaff 1984; Hoover et al. 2001; Bayley and Li 2008), which typically consist of a small fenced experimental area from which livestock is excluded. Although exclosures may provide a somewhat artificial exclusion of grazing animals, they may also mimic more typical conditions in which grazing is more sporadic than would occur under conditions with confined, continually grazing livestock.

In the western North Dakota region, streams typically dissect either badland or rolling prairie topography (Gonzalez 2007). Badland streams are found in the Little Missouri Badlands within the historic river floodplain. Rolling prairie streams are typically located farther from the historic floodplain of the Little Missouri River than are the badland streams, in the Missouri Slope Upland, which is characterized by rolling to hilly plains and gentle slopes (Bluemle 1991). Intermittency

is less common than in badland streams. Rolling prairie streams tend to be in more stable, less incised channels with more extensive grasses in riparian zones than the badlands streams. Because of the distinct habitat differences between the two stream types, their fish communities, species composition, and responses to grazing might also be expected to differ. Because of the higher prevalence of intermittency in badlands streams, the fish assemblage responses might also be expected to differ in response to late summer drought conditions.

We tested four inter-related hypotheses in this study: first, that fish assemblage composition in small streams of western North Dakota would be distinctly different between the two common stream types in the region (badland and rolling prairie), a result of adaptive responses to different habitat conditions; second, that the fish communities in the two stream types differ in their response to late summer drought conditions; third, that for both stream types, fish abundance, density, and diversity would be influenced by specific abiotic habitat features such as depth, residual pool volume, pool surface area, and width-to-depth ratio, and fourth, that domestic livestock grazing would influence all of these habitat variables and the response of the fish communities to grazing practices would differ by stream type.

STUDY AREA

Area Profile
Much of western North Dakota includes rolling prairies and badlands covered by sedimentary rocks such as sandstone, shale, and lignite that were deposited by water, wind, and glaciers during the last 620 million years (Bluemle 1980, 1991). The Little Missouri Badlands were carved between 600 and 700 thousand years B.P. when glaciers diverted the path of the Little Missouri River (Bluemle 1991). This diversion caused the river to occupy a shorter, steeper path, leading to the erosional landscape of the badlands today (Godfread 1994). At the end of the last ice age between 12,500 and

10,000 years ago, rolling prairies replaced the forests that covered much of southwestern North Dakota as the climate became drier and more temperate. Today, much of the region lies about 760 m above sea level and less than 50 cm of precipitation typically falls annually, with higher elevations receiving greater amounts. In the past 150 years, the landscape of open, uninterrupted expanses of grasslands grazed by bison *Bison bison* and other native animals have been developed into farms, ranches, railroads, and towns (Dakota Prairie Grasslands 2002).

The Little Missouri Badlands have eroded at an irregular rate primarily as a result of hill slope processes such as slope wash, as opposed to river and stream channel processes. Scant vegetative cover and drought, common in these areas, increases landscape instability and leads to accelerated erosion of barren clay slopes (Bluemle 1991).

Badlands streams are generally characterized by a poorly vegetated riparian zone, few or no aquatic macrophytes or algae, wide, shallow channels, a mixture of sediments ranging from silt to cobble, and highly variable hydrologic responses with relatively high peak discharges per unit area and relatively low base flows per unit area (Gonzalez 2007). Intermittency of streamflows is common during late summer.

Rolling prairie streams contain more riparian vegetation than badland streams (mostly grasses and woody shrubs, in-stream macrophytes, and concentrations of often dense algae), tend to have more entrenched channels, and typically contain predominately fine sediments such as sand and silt. Since they are located in low runoff-generating areas, rolling prairie streams have lower stream energy, lower sediment loads, and less dynamic channel responses than badland streams (Gonzalez 2007). Domestic livestock grazing practices vary widely in western North Dakota. The 445,000 Ha Little Missouri National Grasslands (LMNG) is managed by the United States Forest Service (USFS) for multiple uses (Dakota Prairie Grasslands 2002). Streams in the Grasslands, both rolling prairie and badlands types, provide forage and water for wildlife and livestock, and recreation. Sheep and cattle grazing are the dominant agricultural activities. In contrast, the contiguous Theodore Roosevelt National Park (TRNP), encompassing 28,500 ha in two disjunct units (North Unit, 9,740 ha; South Unit 18,680 ha), is managed to preserve the natural and cultural resources within the park and provide public recreational opportunities (Harmon 1986). Domestic livestock grazing is prohibited. Both TNRP units are almost entirely surrounded by the LMNG and consist primarily of badland topography similar to the LMNG.

Study Sites: The study streams, all located in western North Dakota, were selected based on several criteria: stream type, our ability to effectively sample (high water conductivities precluded the use of electrofishing), accessibility through public land, and absence or presence of domestic livestock grazing. However, only one non-grazed, rolling prairie stream reach could be identified. In 2004 (Year 1), preliminary sampling was conducted on six reaches in two streams. In 2005 (Year 2), the study design was expanded to include an additional reach in five new streams, or seven streams in all (Table 1).

The two streams sampled in both Year 1 and Year 2 were selected because they contained grazing exclosures, each approximately 800 m in length. Ash Coulee and Whitetail Creek Creeks flow west into the Little Missouri River, with portions of each stream located on USFS land. The exclosure on Ash Coulee Creek encompasses 25 ha of an 8,700 ha watershed; the exclosure on Whitetail Creek encompasses 14 ha of a 9,900 ha watershed. Each exclosure is thus less than one percent of the watershed areas. Ash Coulee Creek at the study sites flows through an arid, badland topography. The stream is subject to extremely low flows during late summer and intermittency during drought conditions. Sampling occurred in three 800-m reaches, one reach containing the exclosure, a second reach downstream from the exclosure,

Table 1. Habitat (Stream - Reach) and fish sampling timeline for Year 1 (2004) and Year 2 (2005).

Year	Stream – Reach	Early		Late	
		Date	Number of pools	Date	Number of pools
2004	Ash Coulee - downstream	21-Jun	6	20-Jul	6
	Ash Coulee - exclosure	23-Jun	5	21-Jul	5
	Ash Coulee – upstream	24-Jun	7	21-Jul	6
	Whitetail - downstream	2-Jul	3	28-Jul	3
	Whitetail – exclosure	30-Jun	4	29-Jul	4
	Whitetail - upstream	1-Jul	3	30-Jul	2
2005					
	Ash Coulee - exclosure	6-Jun	6	14-Jul	6
	Ash Coulee - upstream	16-Jun	6	14-Jul	6
	Knutson	23-Jun	6	1-Aug	6
	Paddock	17-Jun	6	1-Aug	6
	Philbrick	1-Jun	6	15-Jul	5
	Sand	4-Jul	6	28-Jul	6
	Squaw	22-Jun	6	27-Jul	6
	Whitetail - downstream	31-May	3	12-Jul	3
	Whitetail - exclosure	30-May	3	12-Jul	3
	Whitetail - upstream	30-May	3	13-Jul	3

and a third reach upstream of the exclosure. Reaches were not contiguous to reduce the possibility of autocorrelation.

Whitetail Creek, within the study area, flows through a rolling prairie topography. Unlike Ash Coulee Creek, Whitetail Creek has a very well vegetated riparian zone consisting of grasses, forbs, and woody vegetation. Several types of in-stream obstacles such as woody debris, aquatic vegetation, and beaver dams potentially help to retain water during drought conditions. Therefore, Whitetail Creek is less prone to intermittency than Ash Coulee Creek, even though punctuations in the continuity of flow may occur during late summer.

In Year 2, an additional five streams were sampled. These included three badland streams within the boundaries of TRNP (Knutson Creek and Paddock Creek in the Park's South Unit and Squaw Creek in the North Unit) draining land grazed by native wildlife but not by domestic livestock. The other two of the five streams, Philbrick Creek and Sand Creek, were rolling prairie streams that traversed LMNG property and were accessible to livestock. All streams were in the Little Missouri River drainage,

except for Philbrick Creek, which empties into the Cannonball River, a Missouri River tributary. Coordinates and photographs for all streams and sections are provided in Stephens (2008).

METHODS

Habitat quality and fish assemblage structure were assessed in both years in exclosed and grazed areas (Table 1) during two different sample periods; first within the period May 30-Jul 4 during higher flow conditions, and within the period July 12-Aug 1 during lower flow conditions (the two periods are hereafter referred to as early and late; Table 1).

Habitat assessment was conducted using elements of Basin-wide Visual Estimation Techniques (BVET) (Hankin and Reeves 1988; Dolloff et al. 1993) in order to rapidly assess the critical habitat aspects of in-stream habitat quality and availability. The sampling crew walked the stream reaches and measured the distance between individual habitat units that were to be sampled for fish. Due to the intermittent nature of these streams, only habitat units identified as pools were selected for fish

sampling. Systematic sampling of every fifth pool was conducted wherever possible, typically occurring every 75 to 125 meters. However, if a pool was selected that appeared highly likely to become dry later in the year, the next closest unit was selected instead to avoid sampling pools that would become completely dewatered. In Ash Coulee Creek, five to seven pools were selected per reach. In Whitetail Creek, either three or four pools were selected per reach. In Whitetail Creek, some pools contained numerous in-stream obstacles (mostly brush and branches) that made seining impossible. Electrofishing was also infeasible in these streams because of high conductivity. Therefore, the sampled pools in Whitetail Creek were unavoidably limited to those that could be effectively sampled.

Within each pool, seven abiotic habitat characteristics were measured: wetted stream width, average depth, maximum depth, pool length, conductivity, turbidity, and temperature. The proportion of riparian zone around each pool covered by vegetation was also assessed between July 19 and August 1 with line intercept methodology. A 25-m transect was laid out on each side of individual habitat units, centered at the middle of the pool. Transects were placed within 0 – 2 m of the bankfull channel boundary, and presence or absence of vegetation was recorded at 1-m intervals on each side of the stream. These data were used to calculate the proportion of riparian zone covered by vegetation.

Fish sampling immediately followed pool selection and habitat sampling for both sample periods (Table 1). Fish sampling consisted of two seine hauls of equal effort per pool. Bag seines measured 3.05, 4.57, or 9.14 m in length and between 1.22 and 1.83 m tall depending on the size of the habitat unit, and all were constructed of 4.76-mm mesh. The bag measured 1.22 x 1.22 m on the smaller seine and 1.83 x 1.83 m on the larger seine. Block nets were placed at the upper and lower extremes of the defined habitat unit to prevent immigration or emigration during seining. Fish sampled

were identified using the best available keys (Ryckman 1981; Page and Burr 1991; Table 2) in the field when possible and measured to the nearest mm; most fish were released after both seine hauls were complete for a particular pool. Although most fish were easily identifiable in the field, some fish were unfamiliar, particularly rare, or consisted of closely related species that could not be distinguished by external taxonomic characteristics. Examples of those fish were preserved and later identified after dissection. Only fish ≥ 40 mm total length (TL) were tallied; most fish less than 40 mm passed through the seine mesh and were captured only if they became entangled in vegetation or debris.

ANALYSIS

In Year 1, three reaches of Ash Coulee Creek, a badland stream, were compared to three reaches of Whitetail Creek, a rolling prairie stream, to assess differences in fish assemblage structure. In Year 2, the four badland streams (Ash Coulee, Knutson, Paddock, and Squaw Creeks; six total reaches) were compared with the three rolling prairie streams (Philbrick, Sand, and Whitetail; five total reaches). Fish assemblage structure was examined by calculating the relative abundance of individual species collected in a given stream reach during both early and late sampling periods. Relative abundance was expressed as the proportion of all fish collected in a stream reach consisting of a particular species. These proportions were used in an absolute correlation cluster analysis to determine the differences in fish assemblage structure between badland and rolling prairie stream types. The cluster analyses group streams based on similarities in fish assemblage structure. The two most similar streams are grouped first, then the next most similar is added to create a new cluster, and so on (Johnson 1998). The last two groups clustered represent the lowest observed level of similarity.

In addition to assessing if the two stream types contained significantly different fish communities, the stream types were compared

Table 2. List of all species collected and the abbreviations used in subsequent tables.

Species Common Name	Scientific Name	Abbreviation
Black bullhead	*Ictalurus melas*	*I_melas*
Brassy minnow	*Hybognathus hankinsoni*	*Hy_hankinsoni*
Brook stickleback	*Culaea inconstans*	*C_inconstans*
Common carp	*Cyprinus carpio*	*Cy_carpio*
Creek chub	*Semotilus atromaculatus*	*S_atromaculatus*
Fathead minnow	*Pimephales promelas*	*Pi_promelas*
Flathead chub	*Platygobio gracilis*	*Pl_gracilis*
Green sunfish	*Lepomis cyanellus*	*L_cyanellus*
Iowa darter	*Etheostoma exile*	*Et_exile*
Johnny darter	*Etheostoma nigrum*	*Et_nigrum*
Lake chub	*Couesius plumbeus*	*C_plumbeus*
Longnose dace	*Rhinichthys cataractae*	*R_cataractae*
Northern pike	*Esox lucius*	*Es_lucius*
Northern redbelly dace	*Phoxinus eos*	*Ph_eos*
Plains minnow	*Hybognathus placitus*	*Hy_placitus*
River carpsucker	*Carpiodes carpio*	*C_carpio*
Sand shiner	*Notropis stramineus*	*N_stramineus*
Stonecat	*Noturus flavus*	*No_flavus*
Western silvery minnow	*Hybognathus argyritis*	*Hy_argyritis*
White sucker	*Catostomus commersoni*	*Ca_commersoni*
Yellow perch	*Perca flavescens*	*P_flavescens*
Unknown minnow		*UN_cyprinidae*

as to their changes in fish densities from early to late summer periods. Response of the fish assemblage to late summer drought conditions was assessed by first calculating the total density of all species (fish/m²) present in each habitat unit of the respective stream types. The mean change in total density between early and late sample periods per stream reach was expressed as a positive or negative proportion, and then used in a one-way analysis of variance (Evans 2003) to determine if total fish densities in rolling prairie and badland streams responded differently to decreases in aquatic habitat availability as summer progressed.

To test the hypothesis that fish communities were significantly related to habitat characteristics, correlation and regression analyses were used to examine the interactions between fish metrics and abiotic, physical habitat conditions. Only the second sampling event from each year was used in order to eliminate the influence of the short-term spawning movements performed by many of the species collected in the study. The fish metrics of interest were total fish density, total number of individuals, total number of

species, and Simpson's diversity index (SDI = $1 - \Sigma (n (n\text{-}1) / N (N\text{-}1))$, where n is the total number of organisms of a particular species and N is the total number of organisms of all species; DeJong 1975). The physical habitat metrics were pool surface area, volume, mean depth, maximum depth, and width-to-depth ratio. It was hypothesized that fish assemblage structure might respond differently to late summer drought conditions in badlands and rolling prairie streams, so the two stream types were analyzed independently.

To assess if active livestock grazing influenced available aquatic habitat, physical habitat characteristics (width-to-depth ratio, change in pool volume between early and late summer, change in mean and maximum depth between early and late summer, and pool surface area) were measured in both early and late periods from 11 reaches of seven streams. Measurements were analyzed using a two-way Analysis of Variance to identify any significant differences between characteristics in reaches grazed by domestic livestock and reaches not grazed by domestic livestock (hereafter referred
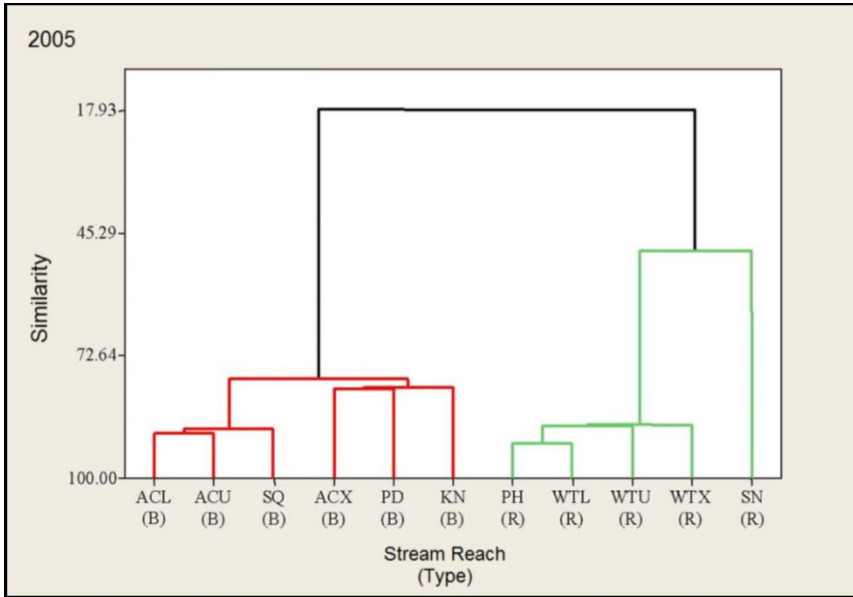
Figure 1. Absolute correlation single linkage cluster analysis showing similarity based on the proportion of the fish assemblage comprised of a particular species for 11 stream reaches in Year 2 (2005). Stream abbreviations: ACL – Ash Coulee downstream; ACU – Ash Coulee upstream; SQ – Squaw; ACX – Ash Coulee exclosure; PD – Paddock; KN – Knutson; PH – Philbrick; WTL – Whitetail downstream; WTU – Whitetail upstream; WTX – Whitetail exclosure; SN – Sand.

to as grazed and non-grazed respectively) of both badland and rolling prairie stream types. Observational units were individual pools, and these values were used to obtain a mean for each stream reach used in the analyses. Additionally, for the Year 2 data, a two-way Analysis of Variance was used to identify any significant differences in the amount of non-vegetated (bare) ground between grazed and non-grazed stream reach riparian zones for both stream types. For all tests, $P < 0.05$ was used to determine significance.

RESULTS

Fish Assemblage Structure – Badland vs. Rolling Prairie: Distinct differences in fish assemblage structure were found between rolling prairie and badland stream types. In Year 1, fish communities of Ash Coulee and Whitetail Creeks only overlapped by 18 percent; Ash Coulee Creek was dominated by plains minnows, flathead chubs, and fathead minnows whereas Whitetail Creek was dominated by

fathead minnows and brook sticklebacks. Northern redbelly dace were also present in some pools (Table 3). In Year 2, when sampling involved four badland streams with six total reaches and three rolling prairie streams with five total reaches, fish assemblage structure again exhibited distinct differences between stream types. All badland streams combined contained 17 identified species, and rolling prairie streams contained 12 species, with eight species collected in both stream types. Single-linkage cluster analysis again indicated only an 18 percent overlap in fish assemblage structure between the two stream types. All rolling prairie and badland reaches were more distinct from reaches of the other stream type than from any reaches of the same stream type (Fig. 1). For the badland type streams (three reaches each of Ash Coulee, Knutson, Paddock, and Squaw Creeks), plains minnows, flathead chubs, and longnose dace were the dominant species (Table 3). In contrast, brook sticklebacks and fathead minnows constituted much of the fish assemblage of the rolling prairie streams,

Table 3. Species, number, length, and density of all individuals collected during both sampling events in the two years, 2004 and 2005.

Year 1 (2004)

				Period		
		Early (Jun 21 - 24)			Late 2 (Jul 20 - 21)	
Species	N	Length Range (Mean) mm	N/m² range	N	Length Range (Mean) mm	N/m² range
Ash Coulee Creek Downstream						
C_carpio	1	60 - 60 (60)	0.02 – 0.02	*	*	*
Cu_inconstans	1	50 - 50 (50)	0.02 - 0.02	*	*	*
Hy_placitus	832	42 - 109 (73.3)	0.71 - 5.82	101	58 - 114 (78.8)	1.11 - 3.01
L_melas	1	106 - 106 (106)	0.01 - 0.01	*	*	*
N_stramineus	*	*	*	1	48 - 48 (48)	o.03 – 0.03
Pi_promelas	75	41 - 66 (48.6)	0.11 – 0.51	18	42 - 57 (50.4)	0.06 - 0.44
Pl_gracilis	92	50 - 149 (56.8)	0.07 - 0.65	6	71 - 130 (91)	0.05 - .014
R_cataractae	7	55 - 68 (63.9)	0.04 – 0.05	*	*	*
UN_cyprinidae	*	*	*	1	45 - 45 (45)	0.03 - 0.03
Ash Coulee Creek Exclosure						
Hy_placitus	80	50 - 109 (74.1)	0.02 - 2.74	3	78 - 87 (83.3)	0.16 – 0.16
Pi_promelas	158	40 - 94 (46.7)	0.27 - 1.19	*	*	*
Pl_gracilis	95	50 - 132 (75.6)	0.04 - 3.35	*	*	*
R_cataractae	7	45 - 59 (54)	0.04 – 0.14	*	*	*
S_atromaculatus	2	106 - 108 (107)	0.07 - 0.07	*	*	*
Ash Coulee Creek Upstream						
Hy_placitus	813	49 - 106 (73.9)	0.2 – 0.41	294	51 - 109 (79.3)	0.11 - 2.33
Pi_promelas	86	40 - 71 (49.4)	0.03 - 0.55	77	42 - 70 (50.5)	0.38 – 0.58
Pl_gracilis	183	47 - 137 (81.8)	0.07 - 1.24	298	43 - 137 (80.5)	0.04 - 3.37
N_stramineus	45	40 - 66 (52.6)	0.09 – 0.42	63	40 - 68 (50.2)	0.04 – 0.36
R_cataractae	47	43 - 68 (53.9)	0.2 - 0.41	91	41 - 75 (55.1)	0.11 - 1.48
S_atromaculatus	2	105 - 106 (105.5)	0.11 – 0.11	16	40 - 119 (74.1)	0.06 – 0.16
UN_cyprinidae	2	57 - 64 (60.5)	0.06 - 0.06	1	57 - 57 (57)	0.04 - 0.04

Year 1 (2004)

				Period		
		Early (Jun 30 – Jul 2)			Late (Jul 28 - 30)	
Species	N	Length Range (Mean) mm	N/m² range	N	Length Range (Mean) mm	N/m² range
Whitetail Creek Downstream						
C_plumbeus	1	94 - 94 (94)	0.01 – 0.01	*	*	*
Ca_commersoni	*	*	*	3	50 - 60 (53.3)	0.03 – 0.03
Cu_inconstans	34	41 - 58 (48.8)	0.01 - 1.15	27	40 - 64 (48.2)	0.2 - 1.52
Pi_promelas	1	65 - 65 (65)	0.05 – 0.05	2	40 - 67 (53.5)	0.02 – 0.1
Whitetail Creek Exclosure						
C_plumbeus	3	69 - 121 (91)	0.02 – 0.02	*	*	*
Ca_commersoni	9	62 - 308 (182.7)	0.07 – 0.07	24	40 - 310 (105.5)	0.07 - 0.48
Cu_inconstans	105	40 - 57 (47.2)	0.17 – 1.48	142	40 - 56 (47.8)	0.69 - 1.76
Ph_eos	18	40 - 61 (50.1)	0.09 – 0.12	13	48 - 62 (54.8)	0.09 – 0.09
Pi_promelas	32	40 - 70 (56.5)	0.04 – 0.22	49	47 - 75 (64.8)	0.35 - 0.35
S_atromaculatus	2	110 - 234 (172)	0.01 – 0.01	2	135 - 236 (185.5)	0.01 – 0.01
Whitetail Creek Upstream						
C_plumbeus	2	50 - 56 (53)	0.09 - 0.09	*	*	*
Ca_commersoni	1	243 - 243 (243)	0.02 – 0.02	1	262 - 262 (262)	0.02 - 0.02
Cu_inconstans	119	40 - 63 (49.6)	1.27 - 1.53	76	43 - 62 (50.2)	0.96 - 1.53
Pi_promelas	217	41 - 68 (52.3)	1.81 - 2.73	122	41 - 62 (54.8)	0.71 - 4.01

including three reaches of Whitetail Creek and the single reach on Philbrick Creek (Table 3). The fish assemblage structure of Sand Creek differed in that there was only a 45 percent overlap between its fish assemblage and the other four rolling prairie stream reaches. In addition to fathead minnows, Sand Creek had higher numbers of green sunfish and creek chubs than the other two rolling prairie streams (Table 3).

Response to Late-Summer Drought Conditions – Badland vs. Rolling Prairie: Badland and rolling prairie streams showed different trends

Table 3 Con't.

Year 2 (2005)

| | | Early (May 30 – Jul 4) | | | Late (Jul 12 – Aug 1) | |
| | | Length Range | | | Length Range | |
Species	N	(Mean) mm	N/m² range	N	(Mean) mm	N/m² range
Ash Coulee Creek Downstream						
Hy_placitus	473	40 - 103 (69.5)	0.51 - 1.61	194	43 - 103 (71.8)	0.17 - 1.26
L_cyanellus	*	*	*	1	52 - 52 (52)	0.02 - 0.02
N_stramineus	*	*	*	1	54 - 54 (54)	0.03 - 0.03
No_flavus	*	*	*	1	63 - 63 (63)	0.02 - 0.02
Pi_promelas	10	40 - 63 (46.8)	0.01 - 0.09	18	40 - 60 (46.5)	0.02 - 0.12
Pl_gracilis	202	42 - 155 (74.4)	0.17 - 1.80	28	53 - 123 (87.5)	0.04 - 0.22
R_cataractae	41	44 - 77 (55.8)	0.03 - 0.26	27	46 - 63 (54.5)	0.12 - 0.21
S_atromaculatus	28	45 - 195 (57.5)	0.03 - 0.61	25	46 - 71 (60.5)	0.03 - 0.21
UN_cyprinidae	2	48 - 66 (55)	0.03 - 0.03	*	*	*
Ash Coulee Creek Exclosure						
Hy_placitus	245	42 - 107 (76.4)	0.04 - 1.51	4	71 - 104 (86.0)	0.06 - 0.15
N_stramineus	14	40 - 60 (53.4)	0.08 - 0.18	6	40 - 58 (49.0)	0.06 - 0.13
Pi_promelas	25	40 - 59 (46)	0.05 - 0.18	16	40 - 60 (46.3)	0.04 - 0.15
Pl_gracilis	55	48 - 120 (84)	0.9 - 0.41	12	56 - 128 (90.0)	0.04 - 0.35
R_cataractae	28	44 - 81 (54.6)	0.05 - 0.23	11	50 - 63 (57.9)	0.06 - 0.35
S_atromaculatus	32	43 - 53 (47)	0.09 - 0.41	11	64 - 77 (64.2)	0.04 - 0.31
UN_cyprinidae	2	60 - 68 (64)	0.04 - 0.06	*	*	*
Ash Coulee Creek Upstream						
Ca_commersoni	*	*	*	1	102 - 102 (102)	0.04 - 0.04
Hy_placitus	195	43 - 122 (78)	0.7 – 1.45	196	52 - 104 (76.2)	0.25 - 1.89
N_stramineus	25	43 - 62 (52.9)	0.03 - 0.12	29	40 - 76 (48.8)	0.06 - 0.28
Pi_promelas	67	40 - 71 (47.8)	0.08 - 0.64	54	40 - 87 (45.3)	0.11 - 1.17
Pl_gracilis	46	65 - 142 (94.5)	0.07 - 0.39	50	72 - 114 (91.8)	0.19 - 0.3
R_cataractae	46	43 - 82 (57.5)	0.03 - 0.35	107	47 - 82 (56.2)	0.06 - 1.09
S_atromaculatus	71	41 - 136 (55.4)	0.17 - 0.31	44	49 - 137 (61.2)	0.09 - 0.28
UN_cyprinidae	2	76 - 86 (81)	0.06 - 0.06	1	81 - 81 (81.0)	0.12 - 0.12
Knutson Creek						
C_carpio	14	49 - 119 (87.4)	0.05 - 0.22	*	*	*
Ca_commersoni	14	62 - 174 (106.7)	0.03 - 0.2	12	78 - 214 (132.8)	0.07 - 0.19
Cu_inconstans	2	42 - 43 (42.5)	0.06 - 0.06	4	42 - 47 (44.0)	0.11 - 0.11
Cy_carpio	2	98 - 136 (117)	0.03 - 0.03	16	42 - 73 (58.0)	0.22 - 0.22
Et_nigrum	*	*	*	2	49 - 50 (49.5)	0.05 - 0.05
Hy_argyritus	60	65 - 116 (94.3)	0.09 - 1.73	*	*	*
Hy_hankinsoni	56	41 - 73 (53.6)	0.06 - 0.47	66	44 - 82 (61.6)	0.1 - 1.04
Hy_placitus	426	40 - 115 (61.6)	0.46 - 4.59	23	40 - 108 (74.4)	0.03 - 0.57
I_melas	4	47 - 154 (107.5)	0.02 - 0.06	1	109 - 109 (109)	0.03 - 0.03
L_cyanellus	10	36 - 39 (37.4)	0.04 - 0.15	2	57 - 58 (57.5)	0.06 - 0.06
N_stramineus	10	46 - 54 (50.2)	0.05 - 0.1	1	42 - 42 (42)	0.03 - 0.03
No_flavus	2	65 - 66 (65.5)	0.23 - 0.23	*	*	*
P_flavescens	1	67 - 67 (67)	0.07 - 0.07	1	103 - 103 (103)	0.05 - 0.05
Pi_promelas	17	41 - 70 (54.4)	0.05 - 0.31	12	41 - 52 (45.8)	0.03 - 0.19
Pl_gracilis	2	86 - 92 (89)	0.23 - 0.23	*	*	*
R_cataractae	20	50 - 75 (57.7)	0.03 - 0.35	1	52 - 52 (52)	0.11 - 0.11
S_atromaculatus	54	41 - 158 (76.3)	0.15 - 0.38	35	56 - 169 (88.8)	0.1 - 0.4
UN_cyprinidae	2	56 - 68 (62)	0.04 - 0.04	4	43 - 75 (62.5)	0.11 - 0.11

in change in total fish density between early and late sample periods. In both Year 1 and Year 2, a significant difference was found (ANOVA, $P<0.001$) in the change in total density between badland and rolling prairie stream types. In late summer drought conditions, rolling prairie streams showed a mean increase in overall fish density compared to the early sample period whereas badland streams showed a decrease (Fig. 2). For example, in Year 2, several pools in badland streams contained no fish during late summer sampling, most notably Paddock Creek, which contained no fish in any pools sampled. Conversely, some rolling prairie pools in Whitetail Creek contained fish communities approaching a 900 percent increase in total fish density (Fig. 3).

Table 3 Con't.

Year 2 (2005)

		Period				
		Early (May 30 – Jul 4)			Late (Jul 12 – Aug 1)	
		Length Range			Length Range	
Species	N	(Mean) mm	N/m² range	N	(Mean) mm	N/m² range
Paddock Creek						
Hy_placitus	207	46 - 111 (79.5)	0.6 - 4.46	*	*	*
Pi_promelas	9	56 - 76 (65.4)	0.03 - 0.2	*	*	*
Philbrick Creek						
Cu_inconstans	247	40 - 70 (47)	0.12 - 2.11	368	40 – 76 (54.7)	0.15 - 4.92
Et_exile	4	47 - 51 (48.5)	0.01 - 0.07	2	50 – 52 (51.0)	0.02 - 0.04
Hy_hankinsoni	5	72 - 87 (78.6)	0.06 - 0.06	*	*	*
L_cyanellus	*	*	*	1	119 - 119 (119)	0.04 - 0.04
Pi_promelas	110	40 - 88 (63.2)	0.02 - 0.7	57	41 – 85 (60.6)	0.12 - 0.67
Sand Creek						
Ca_commersoni	16	88 - 263 (160.8)	0.02 - 0.11	49	40 - 236 (113.6)	0.13 - 0.36
Es_lucius	*	*	*	1	283 - 283 (283)	0.01 - 0.01
Et_nigrum	2	47 - 52 (49.5)	0.02 - 0.03	7	52 – 57 (53.6)	0.03 - 0.13
Hy_hankinsoni	*	*	*	50	59 – 95 (75.3)	0.09 - 0.85
I_melas	3	130 - 159 (150.3)	0.02 - 0.06	23	78 - 173 (123.7)	0.06 - 0.16
L_cyanellus	54	40 - 128 (77.9)	0.02 - 0.64	70	47 - 130 (72.7)	0.11 - 0.49
Ph_eos	30	41 - 73 (51.4)	0.01 - 0.34	38	44 – 74 (52.5)	0.05 - 1.02
Pi_promelas	105	40 - 74 (54.5)	0.27 - 0.78	213	40 – 82 (55.6)	0.19 – 2.24
S_atromaculatus	23	60 - 179 (100.5)	0.05 - 0.13	117	40 - 191 (75.1)	0.04 - 10.3
Squaw Creek						
C_carpio	2	87 - 94 (90.4)	0.03 - 0.07	*	*	*
Ca_commersoni	*	*	*	3	60 - 104 (75)	0.04 – 0.16
Cu_inconstans	1	53 - 53 (53)	0.02 - 0.02	*	*	*
Cy_carpio	*	*	*	1	52 - 52 (52)	0.02 – 0.02
Hy_argyritus	41	41 - 107 (78.2)	0.08 - 0.56	2	65 - 85 (75)	0.05 – 0.05
Hy_placitus	130	40 - 103 (67.1)	0.14 - 2.67	39	47 – 91 (70.5)	0.05 – 0.05
Pi_promelas	3	40 - 49 (45.3)	0.02 - 0.05	22	40 – 64 (46.4)	0.17 – 0.34
Pl_gracilis	17	48 - 108 (68.2)	0.21 - 0.55	*	*	*
Whitetail Creek Downstream						
C_plumbeus	*	*	*	4	82 - 106 (94.0)	0.25 – 0.25
Ca_commersoni	4	53 - 122 (94.5)	0.05 - 0.07	8	40 - 155 (111.8)	0.11 - 0.19
Cu_inconstans	57	40 - 64 (47.6)	0.12 - 3.19	159	40 – 61 (44.6)	0.76 – 5.89
Hy_hankinsoni	*	*	*	3	65 – 70 (67.0)	0.19 – 0.19
Ph_eos	*	*	*	10	46 – 59 (52.5)	0.02 – 0.56
Pi_promelas	59	40 - 73 (53.7)	0.12 - 3.58	31	40 - 58 (46.4)	0.06 – 0.58
S_atromaculatus	8	47 - 87 (60)	0.52 - 0.52	11	40 - 151 (82.2)	0.04 - 0.56
Whitetail Creek Exclosure						
C_plumbeus	6	48 - 113 (87.5)	0.04 - 0.04	3	96 – 97 (96.3)	0.02 – 0.02
Ca_commersoni	94	40 - 294 (116.6)	0.2 - 0.61	21	40 - 253 (142)	0.10 - 0.23
Cu_inconstans	23	42 - 55 (47.9)	0.09 - 0.3	279	40 – 58 (43.0)	0.61 – 1.71
Hy_hankinsoni	30	41 - 92 (62.9)	0.16 - 0.26	1	78 - 78 (78)	0.06 – 0.06
Ph_eos	38	40 - 68 (48.9)	0.28 - 0.28	5	42 – 51 (46.4)	0.01 – 0.4
Pi_promelas	153	40 - 80 (52.2)	0.06 - 1.09	102	40 - 56 (46.5)	0.06 – 0.63
S_atromaculatus	78	40 - 261 (90.7)	0.12 - 0.53	13	64 - 179 (103.5)	0.06 – 0.07
Whitetail Creek Upstream						
Ca_commersoni	24	50 - 72 (57.3)	0.04 - 0.83	12	89 - 149 (113.5)	0.1 - 0.37
Cu_inconstans	24	40 - 66 (50.7)	0.04 - 0.36	114	40 – 59 (47.1)	10.1 – 1.55
Ph_eos	1	63 - 63 (63)	0.04 - 0.04	*	*	*
Pi_promelas	35	41 - 82 (58.1)	0.09 - 0.57	79	41 – 68 (55.1)	0.22 – 2.11
S_atromaculatus	1	53 - 53 (53)	0.04 - 0.04	*	*	*

Physical habitat variables and fish abundance by stream type: The fish communities responded to physical habitat variables differently in badlands streams than in rolling prairie streams. For Ash Coulee Creek (badland type) in Year 1, total fish density was significantly positively correlated with only mean and maximum depth. Total number of fish was significantly and positively correlated with surface area, volume, and maximum depth. Total number of
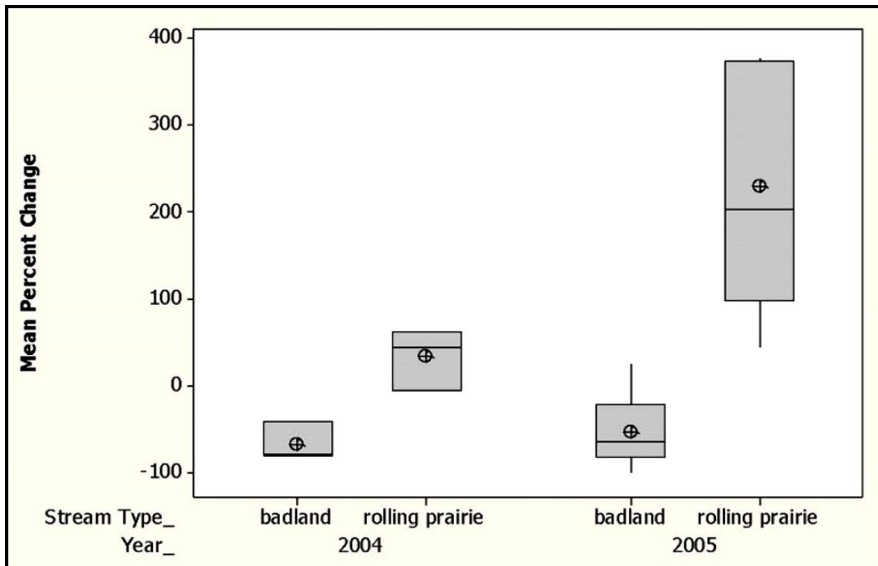
Figure 2. Boxplot for mean change in total fish density by stream type between early and late samples during Year 1 (2004) and Year 2 (2005).

species was correlated with volume, mean depth, and maximum depth; and diversity was not significantly correlated with any of the physical habitat variables. For Whitetail Creek (rolling prairie type) in Year 1, the only significant correlations found were positive between the total number of fish and pool volume, surface area, and width-to-depth ratio.

In Year 2, total fish density in pools of badland streams was positively and significantly correlated with pool volume, mean depth and maximum depth. Total number of fish was similarly related to surface area, volume, mean depth, and maximum depth. The total number of species was significantly positively correlated to volume, mean depth, and maximum depth. The rolling prairie streams in Year 2 showed significantly positive correlations between total number of fish and surface area, pool volume, mean depth, and maximum depth. All other relationships were not significant. A comprehensive list of models evaluated can be found in Stephens (2008).

Grazing, Stream Type, and Aquatic Habitat Availability: Of seven habitat variables assessed, only one (vegetative cover) differed between

grazed and non-grazed stream reaches, and none of the observed habitat variables differed between badland and rolling prairie streams.

Width-to-depth ratio: No significant differences were found in either year or either sample period (early and late) in width-to-depth ratios between grazed and non-grazed stream reaches or between badland and rolling prairie stream types (ANOVA; $P>0.08$).

Changes in pool volume: No significant differences were found in either year in change in mean pool volume between early and late periods between grazed and non-grazed reaches (ANOVA; F=2.60 and 0.02; P=0.248 and 0.883) or between badland or rolling prairie stream types (ANOVA; F=7.22 and 0.70; P=0.115 and 0.431).

Changes in mean and maximum depth: No significant differences were found in either year in changes in mean and maximum depth from early to late periods between grazed and non-grazed stream reaches (mean depth ANOVA; F=0.25 and 0.78; P=0.667 and 0.407) (maximum depth ANOVA; F=0.33 and
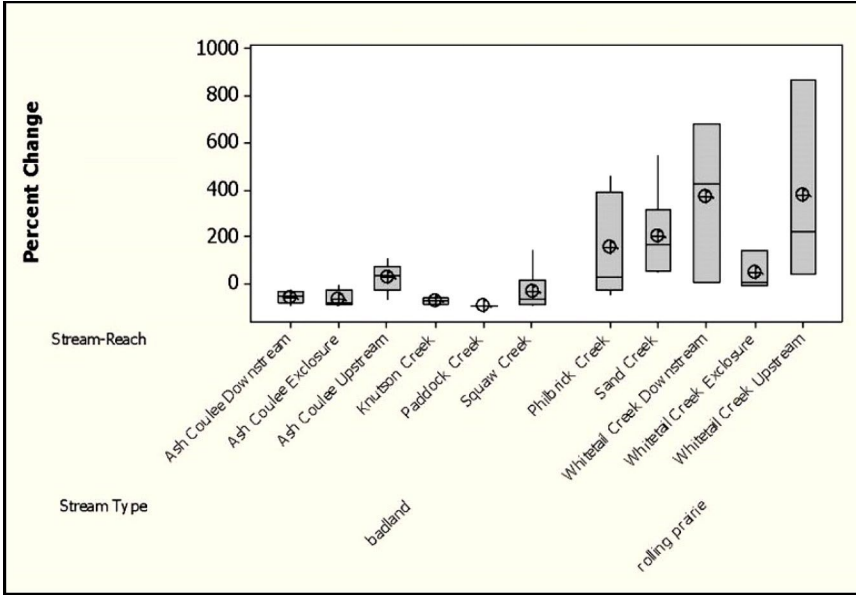
Figure 3. Boxplot for mean change in total fish density by stream reach between early and late samples during Year 2 (2005).

0.98; *P*=0.622 and 0.354) or between badland and rolling prairie stream types (mean depth ANOVA; F=2.07 and 1.82; *P*=0.287 and 0.220) (maximum depth ANOVA; F=1.87 and 1.75; *P*=0.305 and 0.228).

Changes in pool surface area: No significant differences in changes in pool surface area between early and late periods were found in either year between grazed and non-grazed stream reaches (ANOVA; F=1.06 and 0.86; *P*=0.411 and 0.385) or between badland and rolling prairie stream types (ANOVA; F=1.13 and 0.09; *P*=0.398 and 0.769).

Vegetative cover: No significant differences in percent bare ground were detected between grazed and non-grazed stream reaches in Year 2 (ANOVA; F=2.03; *P*=0.197). Significant differences were found, however, in the proportion of riparian area with no vegetative cover between badland and rolling prairie stream types. For both grazed and non-grazed stream reaches combined, the riparian zone in badland stream reaches had significantly higher proportions of bare ground than in rolling

prairie stream reaches (ANOVA; F=8.81; *P*=0.021). The exclosure reach on Ash Coulee Creek had the highest portion of the riparian zone containing bare ground (60%), while Philbrick Creek had the lowest (2%; Fig. 4).

DISCUSSION

Fish Assemblage Structure and Stream Type
The distinct differences observed in fish assemblage structure between badland and rolling prairie streams were associated with distinct differences in the numerically dominant species and their habitat preferences. For example, the plains minnow, the dominant species found in most badland reaches, is known to prefer turbid, shallow, sand filled channels with some current (Tomelleri and Eberle 1990; Pflieger 1997; Taylor and Warren Jr. 2001). Tomelleri and Eberle (1990) noted that plains minnows require strong currents during some portions of their life cycle. Typical badland streams are subject to sudden, drastic spring run-off events that would favor this portion of the fishes' life cycle more so than the more slowly meandering rolling prairie streams.
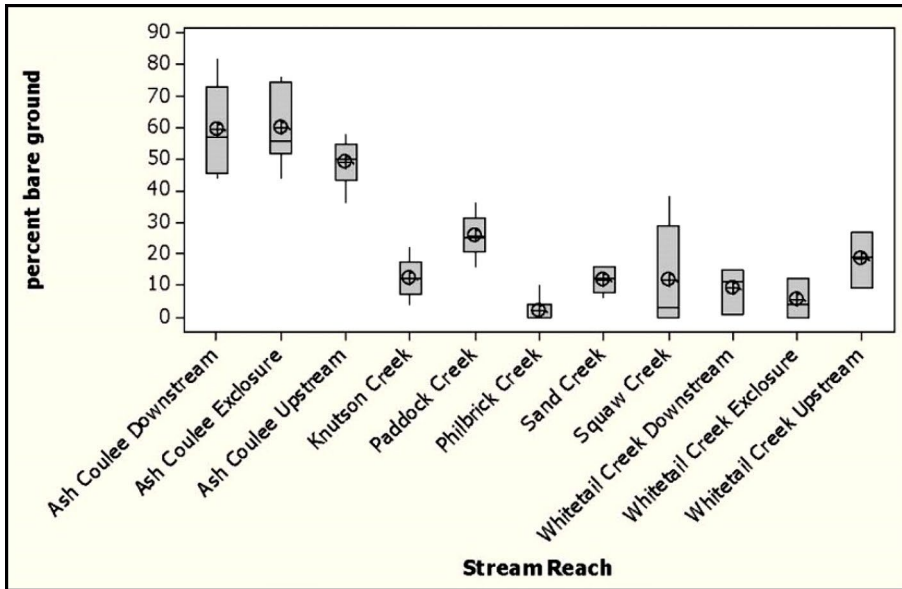
Figure 4. Boxplot of mean percent bare ground in the riparian zone by stream reach for Year 2 (2005).

The flathead chub, a second dominant species in the badland streams but rarely found in prairie streams, has also been reported to prefer turbid flowing waters (Scott and Crossman 1973) with moderate to strong currents and naturally fluctuating hydrographs, and often is the predominant species in streams with very high turbidity, such as those found in the Little Missouri River drainage (Olund and Cross 1961). While they tend to be common in larger lotic systems, Olund and Cross (1961) noted that there is a small-stream subspecies of flathead chub. Although these fish appear to be opportunistic feeders with their success dependent on an individual's ability to adapt to changing environmental conditions, they are equipped with abundant taste buds on the snout, barbels, lips, and pectoral fins which allow them to detect food non-visually (Davis and Miller 1967), making them well adapted to fluctuating flows in badland streams.

A third species, the longnose dace, is the most intolerant of poor water quality (Bramblett et al. 2005) of all the commonly collected species in the badland streams. Generally, the longnose dace prefers clean, swift, permanent streams with gravel or boulder substrates (Scott and

Crossman 1973; Tomelleri and Eberle 1990). Mullen and Burton (1995) noted that they are a highly adapted riffle species, suggesting that pool refugia were seasonally sought out of necessity rather than preference.

Although no riffles were sampled in this study due to the ephemeral nature of shallow, flowing water in these streams, the abundance of species that prefer swifter currents suggests that the badland streams provide adequate or even preferred aquatic habitat for these fish during at least some portion of the year. Persisting in the still-water pools over summer may thus be only a necessary response during seasonally harsh conditions. However, the two most common species in badland streams, plains minnows and flathead chubs, have distinct physiological adaptations such as well-developed chemosensory structures and reduced optic lobes that allow them to succeed in high turbidity habitats (Davis and Miller 1967). Such fishes inhabiting fluctuating environments have evolved tolerance to potentially stressful factors. They also have evolved the ability to occupy streams subject to great changes in habitat and water quality by changing locations to optimize their local environment (Matthews and Hill 1980).

In contrast to the badland streams, the dominant species of the rolling prairie streams sampled are reported to have very different habitat preferences. For example, brook stickleback, a common species in Whitetail and Philbrick Creeks, prefer cold, clear to slightly turbid still waters with moderate to dense aquatic vegetation (Scott and Crossman 1973, Becker 1983, Tomelleri and Eberle 1990). Schlosser (1995) found that brook sticklebacks in a Minnesota headwater exhibited primarily downstream movement during periods of high stream discharge, producing a downstream sink effect and suggesting poor resilience in stream pools with frequently fluctuating hydrographs.

Fathead minnows, another common species in Whitetail and Philbrick Creeks as well as in Sand Creek, can be found in a wide range of habitats due to their high tolerance for extreme temperatures, turbidities, and low dissolved oxygen, but tend to prefer pools with silty, stillwater habitats in both permanent and intermittent streams (Scott and Crossman 1973; Tomelleri and Eberle 1990; Pflieger 1997). They tend to be generally intolerant of competition with other species, but often coexist with creek chub, black bullhead, and green sunfish (Pflieger 1997). Starrett (1950) found large numbers of fathead minnows in Boone County, Iowa, only in streams with emergent vegetation and few other minnows, with brook stickleback as the only other abundant fish.

Northern redbelly dace were also much more common in rolling prairie streams than in badland streams. This species prefers quiet waters laden with woody debris (Stasiak 2006), detritus or silt and is often associated with beaver, *Castor canadensis,* ponds (Scott and Crossman 1973; Becker 1983; Tomelleri and Eberle 1990). In one study in Colorado, all northern redbelly dace collected were from cool, clear, standing water habitats off main channels, usually containing cool springs, macrophytes (Morey and Berry 2004), and lacking large piscivorous fishes (Bestgen 1989). These habitat

preferences account for their designation as a sensitive species and their overall scarcity in the LMNG (Scarnecchia 2002) and the Plains region in general (Stasiak 2006).

The preference for slower or slack water habitats exhibited by many of the common rolling prairie species is consistent with the idea that rolling prairie streams may not be subject to high velocity flow events as much as the badland streams. The consistently differing fish communities observed in badland and rolling prairie stream types throughout the summer support the idea that fundamental differences in overall (year-round) habitat, rather than geographic location, are important in determining which species are present in a given stream by the onset of late summer drought. Lyons (1989) found that the physical habitat types available in Wisconsin streams influenced fish assemblage structure far more than geographic proximity. Grossman et al. (1998) likewise noted that environmental variability was most likely a strong mechanism for determining assemblage structure in a North Carolina drainage subject to drought conditions. Conversely, Meador and Matthews (1992) found that although spatial and temporal elements both influence fish assemblage structure, spatial differences among sites accounted for the majority of variation. While the results of this study are limited to only a few streams in the LMNG and TRNP, further investigations of other badland and rolling prairie streams in the region could help to explain how strongly local fish assemblage structures are tied to these distinct stream types.

Response to Late Summer Flows by Stream Type
In this study, badland and rolling prairie streams also responded differently to changing stream conditions between early and late summer; total fish density decreased for badland streams but increased for rolling prairie streams. The observed differences in density response between the two stream types were most likely associated with

their significantly different fish assemblage structures. Fish communities in badland streams contained species such as plains minnows and flathead chubs that have been typically associated with larger rivers and significant current at high water periods of the year; they are also associated with more turbid streams prone to dewatering in summer (Olund and Cross 1961; Pflieger 1997). The result would be lower total fish densities in intermittent pools during late summer. In contrast, rolling prairie streams contained species such as brook sticklebacks and fathead minnows that prefer habitats with slower currents and more stable conditions (Becker 1983; Pflieger 1997), and may represent a more permanent resident fish assemblage, as opposed to a fish assemblage that varies seasonally with drastic habitat changes. Taylor et al. (1993) found that species within assemblage groups often exhibited similar responses to a changing environment in Great Plains streams.

Results from this study thus suggest that badland stream fishes were more susceptible than rolling prairie stream fishes to physical habitat variable changes associated with dewatering. Water levels affect the availability of lotic habitat and refugia for fish during vulnerable periods (Power et al. 1988). Individuals found in pools during late summer may have been stranded remnants of spawning migrations that occurred during the higher flows of spring or early summer. Consequently, fish communities in badland streams would be expected to show stronger correlative relationships to habitat availability. The effects of stream channel drying on fish assemblages can vary drastically depending on the extent of drying (Gasith and Resh 1999) and the characteristics of fish species present in the stream (Capone and Kushlan 1991). If drying is slower, as often is the case in rolling prairie streams, fish are less apt to become isolated in pools that lack the available habitat to support a given fish assemblage. Overall abundance can remain high or even increase as fish gradually move into isolated

pools that maintain water. These conditions in rolling prairie streams would produce non-significant differences in total fish density, number of species, and diversity across a range of available habitat levels. However, if drying occurs more rapidly, as in many badland streams, abundance can decrease as a result of fish being suddenly stranded in pools that either become completely dry or lack suitable habitat conditions for long-term survival.

Fish Densities, Number of Species, Diversity, and Habitat Characteristics
Both the total density of fish and the number of species were hypothesized to be strongly related to pool volume and pool depth; overall results supported this hypothesis. In these streams, habitat quality may be particularly related to pool depth. Magoulick and Kobza (2003) noted that useable refuge habitats are often deeper, more complex, and more permanent than surrounding habitats. Ross et al. (1985) found that harsh drought conditions did not have a lasting effect on fish assemblages and this consistency may be related to a much larger geographic scale. Most fish species in these typically harsh stream systems are at least in part capable of tolerating or withstanding drought and the associated range of conditions (Larimore et al. 1959; Marsh-Matthews and Matthews 2000). Gorman and Karr (1978) found that depth was a primary factor in determining fish diversity parameters, but species composition may produce varying responses to habitat variables across a gradient of different stream reaches. Connell and Sousa (1983) proposed that fish assemblage stability may occur either through resistance, the ability of a system to withstand disturbance, or adjustment, the ability of a system to recover rapidly following disturbance. It appears that the stronger correlative responses of stream fish communities to reductions in aquatic habitat and other habitat changes in badland streams as opposed to rolling prairie streams in this study indicate that badland stream fish assemblages tend toward stability through adjustment, or recovery from disturbance. They also tend to

be closer to larger river habitats (i.e., the Little Missouri River) than rolling prairie streams, facilitating their recolonization after dewatering. Rolling prairie stream fish communities, in contrast, tend toward stability through resistance by withstanding disturbances associated with dewatering and loss of aquatic habitat.

Grazed versus Non-grazed
The absence of significant differences in measured habitat variables (pool surface area, volume, mean depth, maximum depth, and width-to-depth ratio) between grazed and non-grazed stream reaches in this study differs from the results of other studies. For example, in an overview of western U. S. exclosure studies, McDowell and Magilligan (1997) found that water retention properties of streams tend to respond positively to grazing exclusion. Trimble and Mendel (1995) concluded that livestock grazing in riparian areas reduces the ability of the stream banks to resist erosion. Knapp and Matthews (1996) found that in two consecutive years, large differences occurred between physical stream characteristics of grazed and non-grazed areas in the Golden Trout Wilderness of California, noting that exclusion of livestock appeared to promote riparian and stream channel recovery.

In contrast, some studies have shown results similar to this study. For example, Nagle and Clifton (2003) found that some grazed stream reaches in Oregon showed increased mean depth and decreased width-to-depth ratios, although some of these differences were not statistically significant. Furthermore, George et al. (2002) detected no significant streambank erosion as a result of livestock grazing in three stream reaches of the Sierra Nevada foothills of California.

The lack of differences in habitat variables between grazed and non-grazed streams in this study can result from several factors. First, even without livestock grazing, high levels of erosion, sedimentation, and turbidity occur naturally in many Great Plains streams

(Fausch and Bramblett 1991). The high background levels are a result of geology, aridity, highly variable and unpredictable rainfall and stream discharge. In response to high natural levels of erosion, sedimentation, and turbidity, especially in badlands streams, native fish species have adapted to rigorous conditions by evolving distinct sensory and reproductive characteristics, such as small eyes and optic lobes and specialized non-visual sense organs (Cross and Moss 1987). Highly variable environmental conditions occurring today in the region may mask most differences between the two land use practices. Streams have been subject to naturally altering forces such as glaciations (and their residual effects), floods, and droughts since the time they were formed (Platts 1979), and especially so in the Great Plains region, where Dodds et al. (2004) noted that channel intermittency or complete desiccation during late summer and early fall is a common seasonal occurrence. Under these highly variable environmental conditions, the current and recent levels of grazing may not have been intense enough to produce detectable differences in habitat characteristics between grazed and non-grazed sites. The naturally harsh conditions typical of prairie and badland streams thus make it difficult to differentiate the effects of modern land use practices on fish from the natural historical conditions. In a review of several studies addressing the influences of livestock grazing on stream and riparian habitat, Belsky et al. (1999) found that some studies reported no significant differences in stream reach conditions between grazed and non-grazed sites. They attributed the absence of significant differences in those studies to study design problems or stochastic variation such as unpredictable flooding (Clary et al. 1996) rather than to grazing having no impact on stream conditions.

Second, the native fish fauna of the Great Plains evolved under naturally grazed conditions by bison and other herbivorous wildlife populations historically grazed in the region. Grazing is a natural and necessary component of the ecosystem in these areas. Roaming bison

herds would heavily graze a riparian area as they encountered it, but then quickly move on, thus providing an opportunity for the land to recover (Environment Canada 2001). Stream habitats were thus historically impacted by factors somewhat similar to modern livestock grazing, although the impacts were typically more sporadic.

Third, in situations where fish communities provide few recreational, and thus immediate economic, benefits, there are few incentives for protection compared to the short-term, immediate economic benefits of continued livestock grazing. Seldom have studies been conducted for sufficiently long periods with sufficiently intensive sampling for the relationships between grazing and fish communities to be clarified. Detecting any differences between grazed and non-grazed stream reach habitat features in this study may be difficult because of the inadequacies of the exclosures and TRNP to represent truly "ungrazed" land. Bayley and Li (2008) proposed that short exclosures (< 450m) are too small and infrequent to be effective in improving the quality of northeastern Oregon salmonid habitat at the population or basin-wide scales. The exclosure sites in this study outside of TRNP were small, containing only 800 m of stream channel each and encompassing less than one percent of the total watershed area, and in some cases were of recent origin (within 5 years on Ash Coulee Creek; 35 years on Whitetail Creek). Similarly, grazing by native herbivores in the exclosures and in TRNP may significantly impact the results in this study. Bison, wild horses, *Equus caballus*, elk, *Cerrus elaphus*, pronghorn, *Antilocapra americana*, mule deer, *Odocoileus hemionus*, white-tailed deer, *Odocoileus virginianus*, mountain sheep, *Ovis canadensis californiana*, and longhorn cattle, *Bos taurus* (as a historic demonstration) all have access to the stream reaches within TRNP (National Park Service 2007), which often contain some of the best riparian feeding opportunities (Armour et al. 1994). Although even tiny exclosures can show

fairly rapid responses in grass cover and some other terrestrial responses (Chew 1982), in erodible lands such as the LMNG, an exclosure adequate to result in measurable improvements may need to not only be in place for more than a few years, but also cover either a significant percentage of the watershed, or if not, a high percentage of the entire riparian corridor.

Fourth, many of the most pronounced effects of livestock grazing on streams in the region, such as headcutting, stream widening, loss of pool habitat, and more pronounced intermittency, may be so-called legacy effects (Borman 2005; Throop and Archer 2007) that occurred long before the streams and impacts were studied and recorded. Fleischner (1994) noted that most exclosure sites in western North America had been grazed, often heavily, prior to eliminating livestock grazing, and also that the initial grazing event is normally the most disruptive. In the LMNG, there is little information on how the streams and riparian systems functioned historically (USDA Forest Service 2002), and many of the streams probably had different physical characteristics than today. The intermittency now observed in many streams in the LMNG may thus be a legacy effect that cannot be verified today. Although a complete cessation of grazing may not necessarily result in return to a pre-grazing condition (Hughes 1983; Brown and McDonald 1995), continued intensive livestock grazing could hinder any return in the direction of original, more favorable conditions.

Synthesis

The lack of consistent responses of badland and rolling prairie stream fish communities in this study to either abiotic or biotic factors suggests that these systems are not responding to a single influential variable. Fish assemblages are rarely structured by a single factor (Marsh-Matthews and Matthews 2000), and several hypotheses have been forwarded as to why single factors or sets of factors may not produce detectable influences on fish communities. Huston (1979) argued that because stream

ecosystems are abiotically controlled, physical disturbances typically maintain populations at sufficiently low densities that biotic interactions are unimportant. Grossman et al. (1998) proposed that abiotic (hydrologic) variation in a North Carolina stream over 10 years overrode biotic interactions, suggesting that abiotic factors were dominant in shaping fish communities. The relative importance of biotic and abiotic factors undoubtedly varies, however, according to factors such as fish assemblage density and environmental variations (Power et al. 1988). Many abiotic influences have been shown to shape fish communities by driving or exacerbating the effects of biotic interactions. For example, Matthews and Marsh-Matthews (2003) postulate that drought causes a decrease in pool area and volume, which increases the density of fish, therefore increasing biotic interactions. Ostrand and Wilde (2002) found that in an intermittent Texas prairie stream, the relative importance of abiotic and biotic factors varied longitudinally. According to Taylor et al. (1993), headwater reaches of Great Plains streams were highly variable and primarily controlled by abiotic factors and disturbances, whereas downstream reaches were often less extreme, containing a greater number of coexisting species and driven by biotic factors (competition and predation; Lohr and Fausch 1997). When abiotic influences are highly variable and unpredictable, subtle relationships among and between abiotic and biotic variables may be obscured.

In this study, the streams of the LMNG and TRNP are strongly influenced by changing physical conditions and fish communities persist within great environmental instability. In harsh, dynamic conditions, environmental selective forces may be so cluttered by noise from widely varying disturbances across streams, space, and time that local patterns of response and adaptation may not be apparent (Poff 1992). In these systems, longer term, more intensive monitoring of abiotic components (e.g., duration and extent of stream flooding and drying), and biotic factors (e.g.,

spatial and temporal recruitment and mortality) than conducted here may be necessary to adequately understand which abiotic and abiotic factors and relationships allow these fish communities to persist.

Similarly, results from this study suggest that the effects of land use practices on the LMNG and TRNP in determining aquatic habitat availability and quality (and resultant stream intermittency) are often masked by naturally occurring stochastic events, such as floods, drought, and grazing by native herbivores. The dynamic aquatic systems of this region are subject to such naturally drastic conditions that the impacts of the current level of livestock grazing are most likely masked by centuries of environmental instability and prior undocumented land use practices and habitat changes. The resultant intermittency now observed in many streams may be a residual effect that can distort perceived effects of current effects of livestock on fish assemblage structure. A good way to test this hypothesis would be to establish some long-term large exclosures and evaluate effects of grazing and riparian changes, including beaver colonization Pollock et al. 2007; 2012), over a period of years or decades (Scarnecchia et al. 2014). Many complex direct and indirect relationships between fish communities and livestock grazing could then be quantified at several trophic levels (Rinne 1999) and key variables can be isolated more easily (Trimble and Mendel 1995).

In addition to factors reported in this paper, other factor such as the presence of piscivorous predators and competitive species interactions can have substantial influences on fish assemblage structure in these small streams (Schlosser 1987; 1988). Stream blockages can also have an impact on community structure by impeding fish movements and preventing recolonization following dessication (Perkin et al. 2015). With the large number of potential biotic and abiotic factors potentially affecting fish assemblage structure, a much more

comprehensive study with more replication will be necessary to fully understand the complex relationships among factors ultimately affecting fish assemblage structure and grazing effects in these streams.

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